HISTORICAL BACKGROUND OF THE FLORA OF THE PACIFIC NORTHWEST

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ABSTRACT

The modern flora of the Pacific Northwest is characterized by associations which show affinities to floras now occupying widely separated areas (Eurasia, South and Central America) and to floras shown by paleobotanical evidence to have occupied all these areas, but particularly the American West. Distinct distribution patterns, both in time and space, manifest themselves. These patterns are and have been influenced by topographic and climatic changes from the Cretaceous to the present. Three principal sources of associations are evident: evolution *in situ*; northern regions as shown in the Arcto-Tertiary Geoflora; western Mexico and the southwestern United States as shown in the Madro-Tertiary Geoflora.

FOREWORD

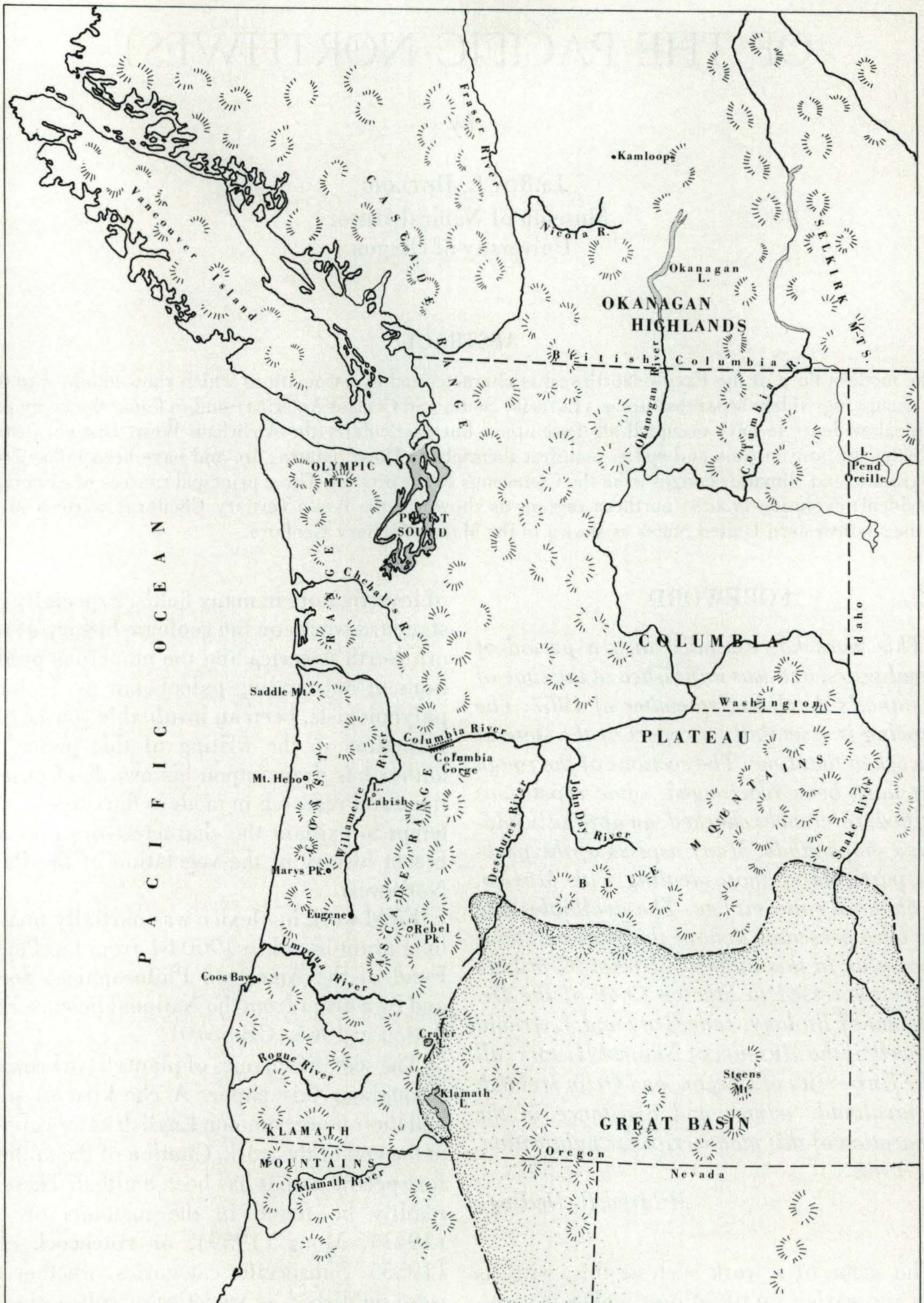
(This work has extended over a period of several years, and was unfinished at the time of the author's death in September of 1967. The following is essentially a report of the state of the work at that time. The sections of the rough draft have been rearranged, some repetitions clarified, references checked, an appendix added and maps made. Many aspects of the problem, particularly those dealing with Mexico, are obviously incomplete. The available data have been presented in hope that they will have some value in this unfinished form. Gratitude is here expressed to Stanton Cook of the Department of Biology, Jane Gray and J. Arnold Shotwell of the Museum of Natural History, all of the University of Oregon, and Orlin Ireland, for invaluable advice and assistance in the preparation of this manuscript for publication. July 1968

Mildred R. Detling)

The scope of a work such as this, with its wide and varied ramifications, makes it necessary to rely heavily upon the published work of investigators in many fields. Especially have standard works on the geologic history of western North America and the numerous publications of outstanding paleobotanists, including palynologists, been an invaluable source of information in the writing of this paper. The author has drawn upon his own field observations and research in modern floristics in an attempt to explain the characteristics and more recent history of the vegetation of the Pacific Northwest.

Field work in Mexico was partially financed by a grant-in-aid in 1960-61 from the Penrose Fund of the American Philosophical Society and by a grant from the National Science Foundation in 1965 (GB-3670).

The scientific names of plants have been used throughout this paper. A checklist of plants and their more common English names appears at the end of the work. Citation of the authority for specific names has been omitted. These can readily be found in the manuals of Peck (1941), Munz (1959), or Hitchcock *et al.* (1955). Subspecific categories, whether they were published as varieties or subspecies, are all referred to as simple trinomials.


Fraser River
Kamloops
Vancouver Island
CASCADE RANGE
Nicola R.
Okanagan L.
OKANAGAN HIGHLANDS
SELKIRK MTS.
British Columbia
Okanagan River
Columbia R.
L. Pend Oreille
OLYMPIC MTS.
PUGET SOUND
PACIFIC OCEAN
Chehalis R.
COAST RANGE
COLUMBIA
Washington
PLATEAU
Idaho
Saddle Mt.
Columbia River
Columbia Gorge
Mt. Hebo
L. Labish
Willamette River
Deschutes River
John Day River
BLUE MOUNTAINS
Snake River
Marys Pk.
Eugene
Rebel Pk.
Umpqua River
Coos Bay
Crater L.
Rogue River
Klamath L.
Steens Mt.
GREAT BASIN
KLAMATH MOUNTAINS
Oregon
Nevada
Klamath River

INTRODUCTION

The region commonly designated as the Pacific Northwest is a natural one floristically, in spite of the great diversity of its habitats and the attendant diversity of life forms, vegetation types, and local plant communities. This is largely because throughout their geologic history the various sectors of the region have in general undergone the same major climatic shifts and been subjected to the same floral invasions and evolutionary influences. And although its flora has received significant contributions in relatively recent times from adjacent major floras, the resulting composite communities have become stabilized in ecological niches of varying extent.

As delimited for this study the region extends from the 42nd to the 52nd parallel of latitude north, and from the Pacific Ocean to the 116th meridian west. Thus it comprises the whole of the states of Oregon and Washington, a narrow strip of western Idaho extending to the base of the Bitterroot and Salmon River Mountains, and that part of southern British Columbia lying between the Selkirk Range and the Pacific Ocean, including Vancouver Island. It includes the northern fringe of the Klamath Mountains located in Oregon, the Klamath basin, and the northernmost part of the Great Basin but excludes the mountain massif of central Idaho (Fig. 1).

(Material on vegetation areas in northern and central Mexico was apparently intended by the author to provide background on the Madro-Tertiary elements in the Northwest flora. Such information as written in rough form by the author has been incorporated.)

GEOLOGIC HISTORY

The oldest land masses in western North America are members of a series of massive granitic batholiths forming the Nevadan orogenic belt which includes (1) the Coast Mountains and Cascades of British Columbia, (2) the Okanagan Highlands, (3) the Idaho batholith of central Idaho, (4) the Blue Mountains, (5) the Klamath Mountains, (6) the Sierra Nevada and (7) the mountains of southern California and Baja California (King 1959, Clark and Stearn 1960). The first five of these form an arc, open to the west, of volcanic masses which were intruded from middle Jurassic to middle Cretaceous times along what was then the western margin of the North American continent (Fig. 2). None of them has ever been completely submerged in the sea since the Cretaceous. Mesozoic land plants have left remains in Jurassic rocks of southwest Oregon (Chaney 1956).

During early Cenozoic times the great gulf bounded by the orogenic arc was largely filled in by sedimentation and some uplifting. Fossil leaf deposits assigned to the Oligocene have been found as far west as the Willamette valley (Sanborn 1935, Lakhanpal 1958), giving evidence of a terrestrial habitat there by that time.

The central and southern portions of the Cascade Range were formed by uplift and vulcanism beginning in the Eocene and continuing through the Tertiary. This range formed directly across the recess of the orogenic arc. Volcanic activity beginning in the Pliocene, but apparently taking place largely in the Pleistocene, formed the high ridges and volcanic cones from Glacier Peak and Mount Baker in Washington to Mount Lassen in California. Meanwhile, during the last half of the Cenozoic, the Oregon and Washington sectors of the Coast Range, including the Olympic Mountains, were formed by the upfolding of the sediments of the early Cenozoic coastal plain.

During the Miocene and long before the Cascade Range had reached its final elevation, there occurred the great outpouring of the basalts that form the Columbia Plateau. It is believed that the center of the flows may have been in southeastern Washington and northeastern Oregon. The molten mass did not issue from volcanoes but rather from fissures, and eventually formed beds thousands of feet in thickness.

Figure 1. *The Pacific Northwest.*

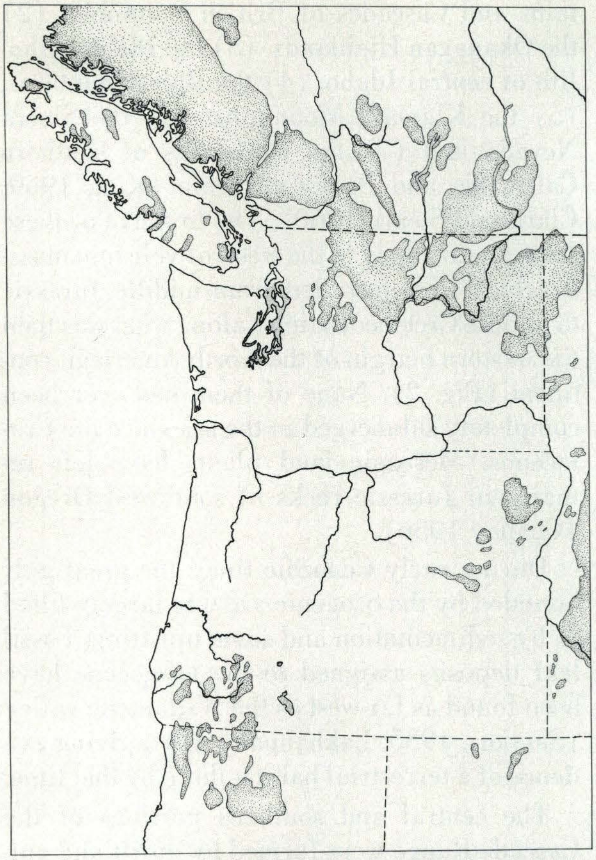


Figure 2. *The Nevadan orogenic arc, formed by batholiths composed of igneous rock in Jurassic and Cretaceous times (after McKee,* et al., *1956, and Smith and Stevenson, 1956).*

Such in brief were the geologic events that produced the modern physiography of the Pacific Northwest whose major features have determined the climates of the region and marked the pathways of its plant migrations.

PHYSIOGRAPHIC FEATURES

The modern physiography of this region is dominated by a series of mountain ranges with intervening systems of river basins, in general running north and south, and an extensive plateau region (Fig. 1). The westernmost mountains, the Coast Range, parallel the coast throughout the whole of the region. It joins the Klamath Mountains in southwestern Oregon, includes the Olympic Mountains of northwest Washington, and continues north of the Strait of Juan de Fuca as the Vancouver Island Mountains. It is separated from the ocean by a narrow strip of flat land which tapers to nothing in the south where it borders the Klamath Mountains and in the north along the western edge of Vancouver Island.

Farther inland a higher range extends northward from the eastern edge of the Klamath Mountains; at the northern end of Puget Sound it swings northwestward along the coast of the British Columbia mainland. In British Columbia it is usually called the Coast Range, although frequently known as the Cascade Range. To minimize confusion, in this paper the entire range shall be referred to as the Cascades.

Between these ranges lies a series of river basins and troughs. North of the Klamath Mountains and draining into the sea are the Rogue and Umpqua River basins. The Willamette and Puget troughs are separated by the gash cut through the mountains by the Columbia River. The northward extension of the Puget trough is partly covered by the marine waters of Puget Sound and the Georgia, Johnstone and Queen Charlotte Straits.

East of the Cascade Range is a broad expanse of tableland. The portion occupying south central and southeastern Oregon constitutes the northernmost extension of the Great Basin of Nevada and Utah. The northern Oregon and eastern Washington part form the Columbia Plateau. This tableland is bounded on the east by the foothills of the Bitterroots in northern Idaho, the Blue Mountains in Oregon and Washington, and by way of the Snake River Plains of southern Idaho, by the Rocky Mountains. Topographically the Columbia Plateau merges at the north through the north-south oriented valleys of the Okanagan Highlands with the plateau of south central British Columbia, dissected by the upper drainage basins of the Fraser, Okanogan and Columbia Rivers.

The importance of the north-south trend of our major physiographic features from the standpoint of vegetation migrations and evolution cannot be overestimated. The effect of the mountain ranges in intercepting moisture from the prevailing westerly winds is to produce climatic belts with extreme differences in precipitation and temperatures. At the same time the mountain and basin axes provide nearly unbroken pathways for the north-south movements of plants. So far as topography is concerned the flora of the Mexican Meseta Central (Fig. 6) has had free access across southern and western Arizona, Nevada, eastern Oregon and Washington, and well into the plateau country of British Columbia. Also plant species moving northward from the Great Valley of California, once they have negotiated the warm valleys and canyons of the Klamath Mountains, have had only a few low transverse ranges to impede their progress up the series of basins ending in the lowlands of Vancouver Island and adjacent mainland British Columbia. On the other hand, the two major mountain axes of the Pacific Northwest reach well into the subarctic regions of northern Canada and Alaska. South of the 52nd parallel the only places where the boreal life zones of the Cascades have been broken are where the Fraser, Columbia and Klamath Rivers have cut their gorges. In like manner the boreal zones of the Blue Mountains are nearly continuous with those of the Rockies, separated only in the vicinity of the Snake River canyon.

CLIMATE

The mild oceanic climate west of the Cascades is created by latitude and proximity to the sea. Winter temperatures are highest and summer temperatures in general lowest along the narrow coastal lowland strip. In the series of basins lying east of the Coast Range and Vancouver Island Mountains temperatures are still moderate but the extremes are greater. East of the Cascades the climate is continental in nature, with extreme winter minima and summer maxima. The Cascade axis and Blue Mountains, because of their elevation, experience very low temperatures during the winter and have moderately low summer maxima. Within any north-south belt both winter and summer temperatures tend to be higher in the south and lower in the north.

A series of rain shadows occurs in the path of the prevailing westerly winds. Most of the precipitation throughout the Pacific Northwest occurs during the winter months, from November to April. West of the Cascades summer rainfall is negligible. East of the range the ratio of summer to winter precipitation is appreciably higher. This is particularly true of the interior plateau of British Columbia. Farther south, especially in the mountains, the ratio is increased by frequent local thunderstorms.

Various combinations of winter and summer temperatures along with varying precipitation patterns have given rise to 19 distinct climatic areas in the Pacific Northwest, which correspond quite closely to the major vegetation areas of the region. The writer (Detling 1948a, b) has devised a vegetation map (Fig. 3) for Ore-

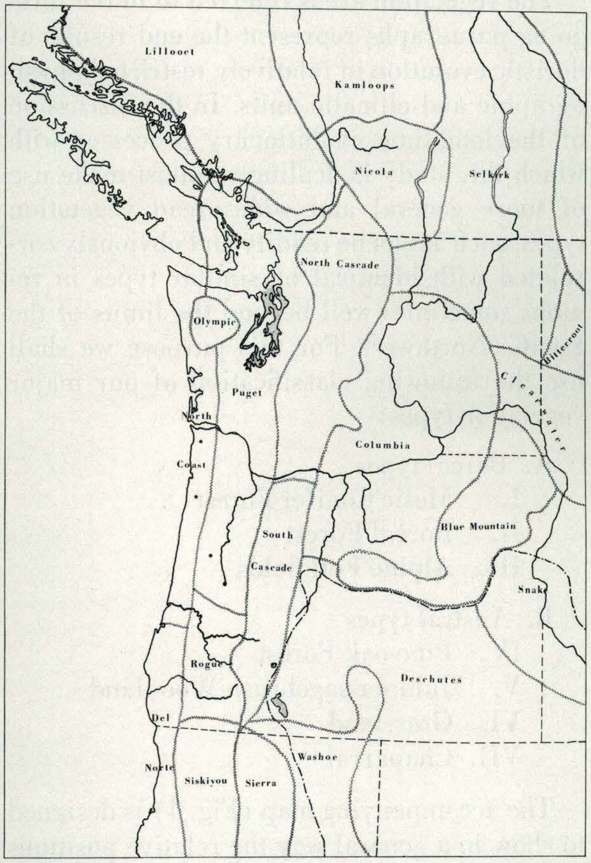


Figure 3. *Vegetation areas of the Pacific Northwest.*

gon and Washington based upon these temperature and rainfall data along with length of growing season. Since these areas have both climatic and floristic bases, it is apropros to introduce them here in order to present in detail some of the climatic differences which apparently have been most instrumental in establishing a distinct vegetation type in each area. For purposes of this study the vegetation map has been extended to include southern British Columbia. One change in area name has been made.

The Rogue and Umpqua basins, although physiographically distinct, are here treated as a single vegetation area, as they were in the original paper. This will simplify later references to the floristic characteristics of the area.

MAJOR VEGETATION TYPES

The vegetation areas referred to in the foregoing paragraphs represent the end results of floristic evolution in relatively restricted physiographic and climatic units. In the discussion of the long-time evolutionary processes with which this study is dealing we must make use of more general and widespread vegetation types, such as can be readily and obviously correlated with identical or similar types in regions sometimes well beyond the limits of the Pacific Northwest. For this purpose we shall use the following classification of our major vegetation types:

A. Boreal types
- I. Mesic Conifer Forest
- II. Boreal Forest
- III. Alpine Fell-fields

B. Austral types
- IV. Pine-oak Forest
- V. Juniper-sagebrush Woodland
- VI. Grassland
- VII. Chaparral

The accompanying map (Fig. 4) is designed to show in a general way the relative positions and extent of these types, except the Alpine Fell-fields. In our region these latter tend to occur in small areas above timber line.

This classification has been found particularly useful in this study because (a) the units are easily recognizable, (b) they are relatively homogeneous throughout, (c) they have similar distribution changes, (d) most of them are already recognized under some name by plant ecologists, (e) the names selected are self-explanatory, (f) as will be more evident later, the component species and genera of each type have apparently originated in the same geographic regions of the world and have followed the same migration routes throughout their history. For each type there is a list of characteristic species, tabulated to show its apparent relationships to floras beyond the Pacific Northwest. The species selected are all at least moderately abundant in their type, and insofar as possible are widespread within it. The lists are sufficiently extensive and carefully selected to furnish valid *basic communities* for the following discussion.

MESIC CONIFER FOREST

Of the vegetation types in the Pacific Northwest the most basic from all points of view is the Mesic Conifer Forest. It is the most widespread, and generally speaking the most nearly continuous throughout its range. In the northwest this forest, largely coincident with the Douglas fir forest, roughly forms an arc open to the south (Fig. 4) (Heusser 1960). One arm of the arc extends from western British Columbia southward west of the Cascade Range. An eastern arm follows the Rocky Mountains southward from eastern British Columbia. The central curve of the arc connects these two arms across the valleys and low ranges of central British Columbia. Along the coast the type extends from near sea level to an elevation of 4000 feet or more. In the Rocky Mountains both its lower and upper limits are higher. In the northern part of its range it forms a relatively narrow belt altitudinally. Excluded from the mesic forest are a narrow strip along the Oregon, Washington, and Vancouver Island coast occupied by Boreal Forest, and the lower

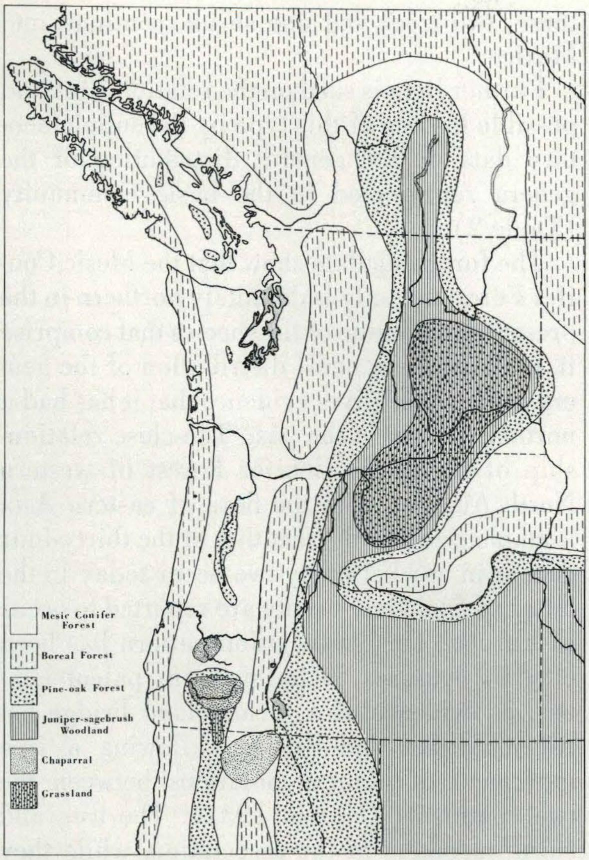


Figure 4. *Vegetation types of the Pacific Northwest.*

elevations of the Rogue River basin occupied by Pine-oak Forest or Chaparral. It occurs at middle elevations in the Blue Mountains and the Okanagan Highlands. The arc thus formed partially encircles an area, to be discussed later, occupied by a fringe of Pine-oak Forest and by extensive areas of Grassland and Great Basin Juniper-sagebrush Woodland.

The dominant species in this type is most commonly *Pseudotsuga menziesii.* This is especially true west of the Cascade axis. East of the mountains *Pseudotsuga* is usually present in greater or lesser abundance, but dominance may be shared by or lost to other species, such as *Tsuga heterophylla, Abies concolor* or *A. grandis.* Local variations in the environment, such as streamside conditions, account for variations in the associations within the framework of the major type.

The species most commonly associated with *Pseudotsuga* west of the Cascades and comprising a significant part of the lower stratum of the forest are *Acer circinatum, Gaultheria shallon, Mahonia nervosa, Corylus cornuta californica* and *Polystichum munitum.* Where the type occurs in eastern British Columbia and northern Idaho the subdominant association varies somewhat from the foregoing—*Acer circinatum* is replaced by *A. glabrum, Mahonia nervosa* by *M. repens, Gaultheria shallon* and *Polystichum munitum* are absent, while *Populus tremuloides* and *Betula papyrifera occidentalis* are added to the community. The altitudinal narrowing of the mesic forest belt in central British Columbia emphasizes the infiltration in that area of species which normally are characteristic of adjacent zones, particularly of the Boreal Forest above it, accounting for the abundance not only of the species of *Betula, Acer* and *Populus* already mentioned but also of *Arctostaphylos uva-ursi, Vaccinium ovalifolium, Cornus canadensis* and *Pachystima myrsinites.* However, a large number of other species characteristic of the forest west of the Cascades do persist east of the range, so that the general aspect of the forest is not essentially altered.

The Mesic Conifer Forest has a relatively wide tolerance of climatic extremes. In general it occupies an area of abundant rainfall or snow accumulation, with mild or at least not excessively cold winters, and cool to moderately warm summers. It is best developed and most distinctive in the oceanic climate west of the Cascades of Oregon and Washington. In the Douglas fir forests of this region annual precipitation ranges from 25 to 140 inches. In the continental climate of the interior the range of precipitation is approximately from 25 to 40 inches annually. The 25 inches which constitutes the lower limit for this type is apparently critical on both sides of the Cascades; below this figure the Douglas fir forest is replaced by a woodland of yellow pine and oak. East of the Cascades the mesic forest is probably controlled at its upper limits, both altitudinally and latitudinally, by temperature rather than precipitation. This seems to be true also along the coast where the type is bordered by a modified Boreal Forest, and where temperatures, especially those of the summer months, are moderately cool.

Temperature conditions within the range of the Mesic Conifer Forest vary considerably. Near the southern Oregon coast January means are about 45°F., but at middle elevations east of the Cascade crest they may be as low as 25°F. July means range from 60° along the coast to about 65° at some places in eastern Oregon.

The basic community of the Mesic Conifer Forest is comprised of the thirty-nine species listed in Table 1. The significance of the distributional units used will become evident with further discussion.

In this and following basic communities all taxonomic units considered subspecific have been included under the species listed. The subspecific breakdown of these species will be discussed later in this work where such information is pertinent.

The distributional data summarized in Table 1 show some features that become of interest when we look for the origins of the Mesic Conifer Forest.

The type as presently constituted is centered in the temperate part of western North America. None of the arboreal species and only two shrubs occur farther north than the Alaskan Panhandle or northern British Columbia. No trees and three shrub species reach central or eastern North America. The herbaceous species are in general more widespread toward the north and east. Of twenty-one species nine are either circumpolar or of northern Alaskan and Canadian distribution. Seven of these reach eastern North America. Four others occurring in the eastern part of the continent, while not now reported from the far north, probably did flourish there at one time. In the other direction, while all thirty-nine species representing the basic association of the type extend into California or northern Baja California, only three, two trees and one shrub, continue into Mexico.

Further light is shed on the relationships and possible history of this type by the supplementary data on the general distribution of the genera represented in the basic community (Table 2).

The foregoing data show that the Mesic Conifer Forest not only is definitely northern in the present distribution of the species that comprise it, but also the general distribution of the genera represented gives evidence that it has had a northern origin in the past. The close relationship of the Mesic Conifer Forest of western North America with the flora of eastern Asia is emphasized by the fact that of the thirty-four genera in our list thirty-two occur today in the latter region. Only twenty are reported to occur in Europe. This distribution pattern has been cited by botanists, including many paleobotanists, as evidence of a former land bridge between Alaska and Siberia, allowing a free movement of plant populations between the two continents (Hultén 1937). The tree and shrub members of the association, while they were undoubtedly originally continuous with populations in other parts of the world, particularly with those of eastern Asia, have been isolated for so long a period by extreme frigid conditions to the north that they have followed an independent evolutionary course. This seems to be true to a lesser extent of the herbaceous members of this type, since at least seven out of the twenty-one herbaceous species are still common to both continents.

Possible additions to Mesic Conifer Forest basic community:

Achlys triphylla
Aconitum spp.
Actaea spicata arguta
Allotropa virgata
Anemone deltoidea
Aplopanax horridum
Aquilegia formosa
Aruncus sylvester acuminatus
Asarum caudatum

Boykinia major
Cimicifuga elata
Circaea pacifica
Coptis laciniata
Corydalis scouleri
Cynoglossum grande
Dicentra formosa
Epilobium angustifolium
Fragaria bracteata
Galium aparine
Galium boreale
Galium trifidum
Galium triflorum
Geum macrophyllum
Heuchera micrantha pacifica
Hydrophyllum tenuipes
Lathyrus polyphyllus
Lonicera ciliosa
Lysichitum americanum
Menziesia ferruginea
Mertensia platyphylla subcordata
Mitella caulescens
Monotropa uniflora
Nemophila parviflora
Physocarpus capitatus
Pleuricospora fimbriolata
Populus trichocarpa
Prunus emarginata
Pyrolaceae genera and species
Rhamnus purshiana
Rosa gymnocarpa
Rosa pisocarpa
Rubus spectabilis
Sambucus glauca
Satureja douglasii
Stachys spp.
Symphoricarpos albus
Synthyris reniformis
Tellima grandiflora
Thalictrum hexandra
Tiarella unifoliata
Tolmiea menziesii
Trautvetteria grandis
Trientalis latifolia
Urtica holosericea
Urtica lyallii
Vicia americana

BOREAL FOREST

In this paper the term Boreal Forest is applied to all Pacific Northwest forest communities at altitudes above the Mesic Conifer Forest, or at lower altitudes when occurring under conditions of cooler summer temperatures where this is apparently the factor giving rise to such a community (Fig. 4). In the northernmost part of its range it is composed of the forests extending from the northern limit of trees in Alaska and the Yukon to the Douglas fir forests of the mesic conifer belt in central or southern British Columbia, reaching sea level in southern Alaska and northwest British Columbia. It extends southward in its typical form along the Cascade Range and the Sierra Nevada, and down the Rocky Mountains as far as Arizona and New Mexico, including the Blue Mountains of Oregon, occupying a belt progressively higher in elevation as it goes southward. A narrow strip of Boreal Forest extends from the main body in British Columbia south along the coast as far as northern California. This strip, rarely more than ten miles wide south of Vancouver Island, has been infiltrated by many species from the adjacent Mesic Conifer Forest, but contains enough characteristic species to maintain its distinctiveness and show its close relationship to the rest of the type as it occurs at middle or higher altitudes in the Cascade Range.

The most reliable indicators of the Boreal Forest are *Pinus contorta* in its two subspecies, *Picea engelmannii* or *P. sitchensis, Tsuga mertensiana,* and one or more species of *Abies, e.g., A. lasiocarpa, A. procera* or *A. amabilis.* In central and eastern British Columbia *Betula papyrifera* is a common indicator. Forming the shrub stratum under these dominants are most commonly found species of *Vaccinium* and *Ledum*, and *Acer glabrum douglasii,* while the most characteristic herbaceous species are *Polygonum bistortoides, Pedicularis* spp., *Anemone occidentalis, Rubus lasiococcus, R. pedatus* and *Xerophyllum tenax.*

Official climatic data from stations located in the Boreal Forest zone are scarce, except for

TABLE 1. DISTRIBUTION OF THE BASIC COMMUNITY OF THE MESIC CONIFER FOREST OUTSIDE OF THE PACIFIC NORTHWEST

	Arctic & subarctic N.A.	Northern Rocky Mts.	Cent. & NE. N.A.	Cent. & S. Rocky Mts.	Great Basin	N. & Cent. Calif.	SW. U.S. & Mexico
Abies concolor				X	X	X	X
Abies grandis		X				X	
Acer circinatum						X	
Acer macrophyllum						X	
Adenocaulon bicolor		X	X	X		X	
Alnus oregona						X	
Calypso bulbosa	X	X	X	X		X	
Chimaphila umbellata	X	X	X	X		X	
Clintonia uniflora		X				X	
Corallorhiza striata		X	X	X		X	
Cornus nuttallii		X				X	
Cornus stolonifera	X	X	X	X		X	
Corylus cornuta		X	X	X		X	
Disporum oreganum		X				X	
Gaultheria shallon						X	
Goodyera oblongifolia		X	X	X		X	
Hieracium albiflorum		X		X		X	
Holodiscus discolor		X		X		X	
Hypopitys latisquama	X	X	X	X		X	
Linnaea borealis	X	X	X	X		X	
Listera convallarioides		X	X	X		X	
Listera cordata	X	X	X	X		X	
Mahonia nervosa		X				X	
Montia sibirica	X	X		X		X	
Osmaronia cerasiformis						X	
Osmorhiza chilensis	X	X	X	X		X	
Oxalis oregana						X	
Polystichum munitum		X		X		X	
Pseudotsuga menziesii		X		X		X	X
Rhododendron macrophyllum						X	
Rubus parviflorus		X	X	X		X	X
Smilacina racemosa		X	X	X		X	
Smilacina stellata	X	X	X	X		X	
Spiranthes romanzoffianum	X	X	X	X		X	
Thuja plicata		X				X	
Trillium ovatum		X		X		X	
Tsuga heterophylla		X				X	
Vaccinium parvifolium		X				X	
Viola glabella		X		X		X	

TABLE 2. DISTRIBUTION OF THE GENERA REPRESENTED IN THE BASIC COMMUNITY OF THE MESIC CONIFER FOREST

	Eurasia	Arctic & subarctic N.A.	E. temperate N.A.	W. temperate N.A.	New World tropics	Temperate S.A.
Abies	X	X	X	X		
Acer	X		X	X		
Adenocaulon	X			X		X
Alnus	X	X	X	X		X
Calypso	X		X	X		
Chimaphila	X		X	X		
Clintonia	X		X	X		
Corallorhiza	X		X	X		
Cornus	X		X	X		X
Corylus	X	X	X	X		
Disporum	X		X	X		
Gaultheria	X		X	X		X
Goodyera	X		X	X		
Hieracium	X		X	X		X
Holodiscus				X	X	
Hypopitys	X		X	X		
Linnaea	X	X	X	X		
Listera	X	X	X	X		
Mahonia	X			X		
Montia	X		X	X		
Osmaronia				X		
Osmorhiza	X		X	X		X
Oxalis	X		X	X	X	X
Polystichum	X	X	X	X		X
Pseudotsuga	X			X		
Rhododendron	X		X	X		
Rubus	X		X	X		X
Smilacina	X		X	X		
Spiranthes	X		X	X	X	
Thuja	X		X	X		
Trillium	X		X	X		
Tsuga	X		X	X		X
Vaccinium	X	X	X	X		X
Viola	X		X	X		

the coastal strip. The following account of its climatic features is based upon the official records of the few stations available, and from extrapolations made from these. These sources probably give a reasonably accurate picture of the climatic environment of the type.

In central British Columbia and the adjacent Rocky Mountains the middle and higher elevations, at which the Boreal Forest occurs, receive approximately from 25 to 40 inches of precipitation annually. Much of this falls as snow. In general, precipitation in this region is evenly distributed throughout the year. Southward from British Columbia in the mountains of northern Idaho and the Blue Mountains of Oregon and Washington the annual preciptation remains about the same, but as was pointed out earlier, a smaller percentage of it falls during the warm season. Throughout the length of the Cascades and the coast strip, annual precipitation in the Boreal Forest is much higher than it is farther inland, ranging from nearly 60 inches in the south (Crater Lake) to 100 inches or more in many places in British Columbia and on the coast.

The Boreal Forest is tolerant of much lower winter temperatures than is the Mesic Conifer Forest, and requires significantly lower summer maxima. In the mountain ranges throughout the Northwest and in the interior plateau of British Columbia the mean January temperature in the type probably varies from about 10° to 26°F. Along the littoral belt this mean varies from 38° to 46°F. Insofar as we can determine, the July mean temperatures vary much less than do those in January. The July mean in the mountains and interior probably ranges from 52° to 58°F., while along the coast it runs from 57° to 61°F.

The following list of thirty-seven species (Table 3) is representative of the Boreal Forest, and will serve as a basic association like that of the Mesic Conifer Forest. The list has been selected to include the dominant or otherwise common species that characterize the type in as many of its areas as possible, *i.e.*, the littoral belt, the Cascades, and the Blue and Rocky Mountains.

The distribution of these species as tabulated shows the following pertinent features:

Only three species are reported from as far south as Mexico; on the other hand thirty-one are either circumboreal or at least occur in Alaska and northern Canada; all but two occur in the area comprised of southeastern British Columbia and northern Idaho. These two are largely restricted to the littoral belt.

The foregoing data point to the fact that the Boreal Forest is distinctly northern in its distribution and in all probability was northern in its origin, as was the Mesic Conifer Forest. Further evidence in support of this theory is supplied by the present distribution of the other species in the genera represented in the type (Table 4). Seven genera only are repeated from the mesic forest of Table 2; the remaining thirty-one are new.

A small but interesting group of species now closely associated with the coastal strip of Boreal Forest in Oregon appears to have a history relating them to the Madro-Tertiary Geoflora. The group is made up of *Arctostaphylos columbiana*, *Baccharis pilularis consanguineus*, *Garrya elliptica*, *Myrica californica*, *Rhododendron occidentale* and *Umbellularia californica*. They all follow the coast northward as far as Coos Bay, constituting an important part of the flora in this strip. *Baccharis*, *Garrya* and *Myrica* continue more or less sporadically along the Oregon coast, and *Arctostaphylos* as far as southern British Columbia. Only rarely are any of them found beyond the Klamath Mountains in the inland basins: *Rhododendron occidentale* in the Rogue valley at Myrtle Creek and on Nickel Mountain in the Umpqua basin, *Umbellularia* in the Umpqua basin, and *Arctosatphylos columbiana* occasionally in the Cascades of central western Oregon.

With the exception of *Rhododendron,* all the genera cited above are reported by Axelrod (1958) to occur among the fossils associated with the Madro-Tertiary Geoflora. Furthermore, as a group they occur today in central and southern California, sometimes as far inland as the Sierra Nevada, in formations rang-

	Eurasia	Boreal N.A.	Littoral	Cascades	California	SE. B.C. & N. Ida.	Blue & Cent. Rocky Mts.	Cent. & E. N.A.	Olympic Mts.	Other
Abies lasiocarpa		X		X		X	X		X	
Acer glabrum douglasii		X		X	X	X	X		X	
Alnus tenuifolia		X		X	X	X	X			
Anemone occidentalis				X	X	X	X		X	
Arctostaphylos uva-ursi	X	X	X	X	X	X	X	X	X	
Betula papyrifera		X		X		X		X		
Caltha leptosepala		X		X		X	X		X	
Cornus canadensis	X	X	X	X	X	X	X	X	X	
Empetrum nigrum	X	X	X		X			X		Mt. Rainier
Eriophorum chamissonis	X	X	X			X				
Eriophorum gracile	X	X		X	X	X	X	X		
Gaultheria ovatifolia				X	X	X	X		X	
Habenaria dilatata		X	X	X	X	X	X	X	X	
Heuchera glabra		X		X		X			X	
Juniperus communis	X	X		X	X	X	X	X	X	
Kalmia polifolia		X		X	X	X	X		X	
Ledum palustre	X	X	X			X		X		
Lonicera involucrata		X	X	X	X	X	X			Chihuahua
Luetkea pectinata		X		X		X	X		X	
Maianthemum dilatata	X	X	X	X	X	X				Col. Gorge, Saddle Mt.
Pachystima myrsinites				X	X	X	X		X	Coast Range
Pedicularis groenlandica		X		X	X	X	X	X	X	
Picea engelmannii		X		X		X	X			
Picea sitchensis			X							
Pinus contorta		X	X	X	X	X	X			
Polygonum bistortoides		X	X	X	X	X	X	X	X	Saddle Mt., Marys Pk.
Populus tremuloides		X		X	X	X	X	X	X	Chihuahua
Pyrola secunda	X	X		X	X	X	X	X	X	Mt. Orizaba, Tillamook
Rhododendron albiflorum				X		X	X		X	
Rubus pedatus		X		X		X			X	Saddle Mt., Tillamook
Shepherdia canadensis		X				X	X	X	X	
Trientalis arctica			X	X		X				
Tsuga mertensiana		X		X	X	X	X		X	
Vaccinium ovalifolium	X	X		X		X	X	X	X	
Vaccinium ovatum			X		X					
Vaccinium scoparium				X	X	X	X			
Veratrum viride		X		X		X		X	X	
Xerophyllum tenax			X	X	X	X	X		X	

TABLE 4. DISTRIBUTION OF THE GENERA REPRESENTED IN THE BASIC COMMUNITY OF THE BOREAL FOREST

	Western N.A.	Asia	N.A. General	N. Temp. Zone	Arctic & Subarctic	South America	Europe	Tropics
Abies		X	X	X	X		X	
Acer			X	X	X			
Alnus			X	X	X	X	X	
Anemone (Pulsatilla)				X	X			
Arctostaphylos			X					
Betula		X	X	X	X		X	
Caltha				X	X			
Cornus				X		X		
Empetrum	X	X		X	X	X	X	
Eriophorum				X	X			
Gaultheria		X	X	X		X		
Habenaria (*Limnorchis*)			X					
Heuchera			X					
Juniperus				X	X			
Kalmia			X					
Ledum				X	X			
Lonicera		X	X	X			X	X
Luetkea	X			X				
Maianthemum	X	X		X				
Pachystima			X					
Pedicularis		X		X		X	X	
Picea				X				
Pinus		X	X	X	X		X	
Polygonum		X	X	X	X	X	X	
Populus		X	X	X	X		X	
Pyrola		X	X	X	X		X	
Rhododendron		X		X			X	
Rubus			X	X		X		
Shepherdia			X					
Trientalis		X	X	X			X	
Tsuga		X	X	X	X			
Vaccinium		X	X	X		X	X	X
Veratrum			X	X				
Xerophyllum			X	X				

ing from chaparral and woodland to mixed conifer forests.

All the evidence points to these species, or at least their immediate ancestors, having migrated northward through California with the rest of the Madro-Tertiary Geoflora, reaching the Klamath Mountains and southwestern Oregon by early and middle Pliocene. There, in response to increasing cold and humidity, they became sufficiently adapted to this type of climate and edaphic conditions to invade the mild, wet coastal region of the Del Norte Area and the more northern coastal strip, where they have persisted until the present and mingled with the members of the Boreal Forest. The sporadic occurrences of *Baccharis pilularis* and *Garrya elliptica* northward suggest that this group at one time was common as far up the coast as western Washington, probably paralleling the advance of other Madro-Tertiary species through the western basins during the xerothermic maximum.

It was possibly in conjunction with the coastward and northward movement of these species, and this also perhaps at the xerothermic maximum, that *Quercus garryana* and *Rhus diversiloba,* dominant features of the interior oak woodlands, advanced up the coastal strip of the Del Norte Area (Fig. 3)—*Quercus* as far as Pistol River, *Rhus* as far as Cape Sebastian.

It is conceivable that an environment which at first glance appears to be moist and cool may in actual fact have an effect which is quite the reverse. A soil which is sandy and very well drained in an area where summer rainfall is negligible creates a xeric situation as far as plants growing in it are concerned. If, in addition, salinity of the environment is increased by sea water in the form of spray in the winter, the total effect is xeric (Heusser 1960). Summer temperatures, while tempered by proximity to the ocean, probably exert more than average influence if moisture is insufficient. The net result is a xerothermic condition. When this condition is extreme, as on the west coast of northern Mexico, cactus plants extend from the desert down into the upper margin of the beaches. In the Northwest *Arctostaphylos columbiana, Baccharis pilularis* and *Garrya elliptica* mix with those members of the Boreal Forest which tolerate this situation, and in the Del Norte Area *Quercus garryana* and *Rhus diversiloba* of the oak woodlands appear in the coastal strip.

ALPINE FELL-FIELDS

The Alpine Fell-fields comprise the treeless vegetation type that occupies the zone above the Boreal Forest, where the absence of trees and any but prostrate shrubs is the result of the extremely rigorous conditions resulting from low winter temperatures, short growing season, deep snow cover and high wind velocities.

In the southern Oregon Cascades, as at Crater Lake or on Mount McLoughlin, timber line, or the lower limit of fell-fields vegetation, is at an altitude of about 7500 feet. This line is lower in the north, and at the 52nd degree of latitude it varies from 4500 feet in the Canadian Cascades to 6500 or 7500 feet in the Selkirk Range (Kendrew and Kerr 1955). Still farther north it merges with the arctic tundra which continues on to sea level at the Arctic coast. In southern British Columbia, fell-fields occur in extensive areas in the Cascades and in the Selkirks. In Washington and Oregon the areas are smaller in size and more widely scattered southward through the Cascades the Blue Mountains, and in the Wallowas. They are not found in the Coast Range south of the Oympic Mountains.

Accurate climatic data are even more scarce for the fell-fields than for the Boreal Forest. Annual precipitation in most cases is about the same as in the Boreal Forest immediately below it, as is also its seasonal distribution. It is certain that January means are much lower than the 26°F. we have given as the upper limit in the Boreal Forest of the mountains, and that the July average is also lower, with night temperatures frequently falling below the freezing point throughout the summer.

The number of plant species above timber line is relatively small compared to those of other vegetation types. The fourteen species

TABLE 5. DISTRIBUTION OF THE BASIC COMMUNITY OF THE ALPINE FELL FIELDS

	Circumboreal	Alaska & N. Canada	Olympics	Cascades	Calif.	E. B. C. & N. Ida.	Rockies & Blue Mts.	Atlantic
Cardamine bellidifolia	X	X		X				X
Cassiope mertensiana		X		X	X	X		
Collomia debilis			X	X		X	X	
Hulsea algida						X	X	
Hulsea nana				X				
Lupinus arcticus		X		X				
Oxyria digyna	X	X	X	X	X		X	X
Phyllodoce empetriformis		X	X	X	X	X	X	
Phyllodoce glanduliflora		X		X		X	X	
Polemonium elegans				X			X	
Polemonium viscosum						X	X	
Polygonum phytolaccaefolium				X	X		X	
Saxifraga bronchialis	X	X		X		X	X	
Saxifraga tolmiei		X	X	X	X			

(Table 5) are closely restricted to these areas and together constitute a characteristic and well-defined community.

It is possible that the present geographical distribution of the species, as well as the general distribution of the genera represented (Table 6), indicates the northern origin of the alpine flora of the Pacific Northwest. It is interesting to note, however, that of the fourteen species representing it here, only three are circumboreal and only seven occur in northern Canada or Alaska. This is in contrast to the relatively large percentage of Boreal Forest species which extend far northward, and suggests that the alpine species either have been isolated for a longer time and have undergone rigorous selection, or that the species of *Collomia, Hulsea, Polemonium* and *Polygonum* arose in the western mountains.

PINE-OAK FOREST

The Pine-oak Forest has two major phases in the Pacific Northwest. A western phase occupies a considerable area at lower elevations in the Rogue River basin and occurs in scattered areas of variable extent in the succession of river basins reaching to the south end of Vancouver Island. The dominant species are commonly *Pinus pondersoa, P. jeffreyi,* one of several species of *Quercus,* and *Arbutus menziesii.* This mixed forest continues southward through California, across Arizona, and into the Sierra Madre Occidental of Mexico. In the Sierra Madre it typically occurs as a mixed community, although under extreme conditions of climate it may appear as pure stands of oak or pine. In the Pacific Northwest, while there is still considerable mixing of the dominants, there is a strong tendency for the oaks and the pines to segregate into altitudinal belts with the former concentrated at lower levels while the pines occupy a belt above them. *Arbutus menziesii* mixes freely with both.

The eastern phase of the type is the yellow pine forests east of the Cascade Mountains. It forms an arc within and roughly paralleling that of the Mesic Conifer Forest (Fig. 4), ex-

TABLE 6. DISTRIBUTION OF THE GENERA REPRESENTED IN THE BASIC COMMUNITY OF THE ALPINE FELL FIELDS

	Western N.A.	Asia	N.A. General	N. Temp. Zone	Arctic & Subarctic	South America	Europe	Tropics
Cardamine				X		X		
Cassiope		X	X		X		X	
Collomia	X					X		
Hulsea	X							
Lupinus			X			X	X	
Oxyria		X	X		X			
Phyllodoce		X	X		X		X	
Polemonium				X		X		
Polygonum				X	X			
Saxifraga				X				

tending from northeastern California through the Klamath basin and eastern Oregon, Washington and British Columbia as far as the latitude of Kamloops and Shuswap Lakes, and from there south and east into northern Idaho and through the Blue Mountains. The dominant species in the eastern phase is *Pinus ponderosa; Arbutus* is entirely absent and *Quercus* occurs only in a limited area in the vicinity of the Columbia Gorge. Further, a large percentage of the shrubby and herbaceous associates of the western phase is absent from the eastern. In spite of this there are reasons for treating the two phases as a single unit. They are not disjunct populations, being confluent in a broad area in northeastern California where the gradient of occurrence and dominance of the constituent species can be observed. A sufficiently significant number of species is common to both phases; besides *Pinus ponderosa* the most obvious are probably *Ceanothus velutinus* and *Arctostaphylos patula*. Finally the eastern and western forms of *Pinus ponderosa* are apparently identical throughout the Pacific Northwest, and although the eastern population does extend southward to Arizona east of the Sierra Nevada, it is distinct from though closely related to the more southern segregates that have sometimes been made of the species, *viz.*, *Pinus arizonica*, *P. latifolia* and *P. brachyptera*, thus minimizing the possibility that the eastern phase of the type is more closely related to a Great Basin or Rocky Mountain flora than to the Californian (Martinez 1948, Mirov 1967).

The Pine-oak Forest tolerates a more xeric climate than does the Mesic Conifer Forest. East of the Cascades it occurs where mean annual precipitation is from 15 to 25 inches. In the Rogue Area these figures are a little higher, from about 20 to 30 inches. January mean temperatures range from 25° to 30°F. east of the mountains and from 34° to 39°F. in the Rogue Area. There is less difference in the summer temperatures, the July means ranging from 61° to 71°F. and from 67° to 71°F. in the east and west respectively.

Because of the greater diversity of the subdominants on the two sides of the Cascade axis it is more difficult to select a basic association in the Pine-oak Forest than in the preceding types. The species list presented in Table 7 has been selected in such a way as to include (a) the major dominants and subdominants that occur commonly on both sides of the axis, (b)

TABLE 7. DISTRIBUTION OF THE BASIC COMMUNITY OF THE PINE-OAK FOREST

	Cent. Mex.-Ariz.-N.M.	B. Cal.-S. Cal.	Cal. w. of Sierra	Rogue—Puget—B.C.	Great Basin	Desch.-Col.—Okan. Areas	SE. B.C.—N. Ida.	Rockies—Blue Mts.	E. N.A.	
Arbutus menziesii		X	X	X						
Arctostaphylos patula	X		X	X	X					
Calochortus tolmiei			X	X						
Ceanothus integerrimus	X	X	X	X		X				Gorge migrant
Ceanothus prostratus			X	X	X	X				
Ceanothus velutinus			X	X	X	X	X	X		
Collomia grandiflora	X	X	X	X	X	X	X	X		
Erythronium hendersonii			X	X						Rogue only
Fritillaria lanceolata			X	X		X	X			
Gilia aggregata	X		X	X		X	X	X		
Horkelia fusca			X	X	X	X	X	X		
Kelloggia galioides	X	X	X	X		X		X		
Lupinus bicolor		X	X	X		X				Gorge migrant
Lupinus leucophyllus			X	X		X	X	X		
Lupinus micranthus		X	X	X		X				Gorge migrant
Mahonia repens	X				X	X	X	X		
Paeonia brownii			X	X	X	X				
Pinus jeffreyi		X								e. of Sierra
Pinus ponderosa	X	X	X	X		X	X	X		
Prunus virginiana	X	X	X	X		X	X	X		
Pterospora andromedea	X	X	X	X		X	X	X	X	farthest N.
Quercus chrysolepis	X	X	X	X						
Quercus garryana			X	X		X				Gorge migrant
Ranunculus occidentalis		X	X	X		X				
Rhus diversiloba		X	X	X						
Rhus radicans	X					X	X	X	X	
Smilax californica			X	X						Rogue only
Trillium rivale			X	X						Rogue only
Vitis californica			X	X						Rogue only
Whipplea modesta			X	X						
Zygadenus venenosus		X	X	X	X	X	X	X		

TABLE 8. DISTRIBUTION OF THE GENERA REPRESENTED IN THE BASIC COMMUNITY OF THE PINE-OAK FOREST

	N. Temp. Zone	Western U.S.	N.A. e. of Rockies	E. Asia	Tropics, gen.	S. America	Mex. & C. Am.	
Arbutus		X		X	X	X	X	
Arctostaphylos		X					X	
Calochortus		X					X	
Ceanothus		X	X				X	
Collomia			X			X	X	
Erythronium		X	X					
Fritillaria	X							
Gilia		X				X	X	
Horkelia		X						
Kelloggia		X						
Lupinus		X	X			X	X	
Mahonia		X		X			X	
Paeonia				X				All Asian exc. 1 sp.
Pinus	X							
Prunus	X				X			
Pterospora		X	X					
Quercus	X				X			
Ranunculus	X							Temp. to frigid
Rhus		X	X	X			X	
Smilax			X		X			
Trillium	X							
Vitis	X				X			
Whipplea		X						
Zygadenus	X							

important species entirely or largely restricted to one side or the other, but which at the same time have a fairly extensive range significant to the history of the whole type and (c) a certain number of Rogue and Siskiyou endemics which are strikingly characteristic of the pine and oak forests and woodlands of those areas and which indicate certain evolutionary tendencies there.

Several interesting distributional patterns are demonstrated by Table 7:

a) Eleven species occur in a south-centrally located region comprised of north central Mexico, Arizona and New Mexico (to be referred to here as the Interior Southwest).

b) Thirteen species extend northward on the west side only of the Sierra-Cascade axis. These include, however, four species which have obviously migrated through the Columbia Gorge and now occur in a restricted area near its upper or eastern end. Only two of these thirteen species are represented in the Interior Southwest region named above.

c) Two species extend northward on the east side only of the Sierra-Cascade axis. Both of these occur in the Interior Southwest.

d) Of fifteen species whose distribution extends north on both sides of the axis seven occur in the Interior Southwest.

e) All species occurring in the Rogue Area are found also in California west of the Sierra Nevada.

f) No species extends north of the Pacific Northwest region, *i.e.*, into northern Canada or Alaska.

g) Only two species range into eastern North America; both of these are connected with the western portion of their populations through Mexico, New Mexico or Arizona.

The foregoing brief analysis, along with consideration of the present distribution of the genera involved (Table 8), indicates that the Pine-oak Forest, in contrast with the preceding three types, is of southern origin. The center of diffusion of the species comprising the type was in all likelihood the region included in northwestern and central Mexico and Arizona (Fig. 6). This idea will be developed later. Whenever the original northern migrations may have occurred, the eastern and western phases of the type were at least eventually separated by the Sierra-Cascade axis, and significant divergent evolution has taken place on the two sides of the mountain ranges.

JUNIPER-SAGEBRUSH WOODLAND

The Juniper-sagebrush Woodland is the northward extension of the Great Basin pinyon-juniper woodland, from which association, at our latitude, the pinyon pines have dropped out. As indicated by the name the type is dominated by one of two species of *Juniperus* (*J. occidentalis* in the south and *J. scopulorum* in the north) and/or *Artemisia tridentata.*

It is most extensive in southeastern Oregon where it occupies the tableland that constitutes the northern end of the Great Basin, continuing southward into northeastern California and Nevada and eastward across southern Idaho. It is almost cut off by the Ochoco Mountains in central Oregon, but after passing through the gap of the Deschutes River between these mountains and the Cascades, the type continues northward as a more or less narrow strip inside the arc of the yellow pine forest, itself surrounding the grasslands of the Columbia Area of north central Oregon and southeast Washington (Fig. 4). In southeast British Columbia the Juniper-sagebrush Woodland extends northward to approximately the latitude of Kamloops. An interesting shift in the dominant species of this type takes place along its north-south axis. On the central plateau of northern Mexico the type is represented by a woodland of junipers and pinyon pines; sagebrush is absent. The latter species enters the community in Arizona, and the three are closely associated as far north as central or northern Nevada. Here the pinyon pines are eliminated and juniper and sagebrush dominate the type until the northern extremity of its range is reached. In southeastern British Columbia the junipers largely disappear and the sagebrush and its associates merge with the yellow pines, so that in this area it is frequently difficult or impossible to determine which type we are dealing with.

Climatically the Juniper-sagebrush Woodland is more xeric than the Pine-oak Woodland. Mean annual precipitation ranges from 7 to 13 (rarely up to 16) inches, most of which falls during the winter, although there are significantly heavy thunder storms during the summer months. Most of the plant species bloom during a short period in May and June, with only a few deep-rooted shrubs (*e.g. Artemisia* and *Chrysothamnus*) delaying their flowering season until late summer or early fall.

Winter temperatures in this community in the Pacific Northwest are moderately low, the January means ranging from 22° to 32°F., the lower averages tending to occur in central British Columbia, the northern extremity of the region, and the higher ones in the Deschutes Area (Fig. 3), the area in which we find probably the best development of this association in the Pacific Northwest. These temperatures are not greatly different from those in the Pine-oak Forest east of the Cascades, although January means average from five to seven degrees

TABLE 9. DISTRIBUTION OF THE BASIC COMMUNITY OF THE JUNIPER-SAGEBRUSH

	Mex.—Ariz.—N.M.	B. Cal.—S. Cal.	Cal. w. of Sierra	NE. Cal.—Sisk.	Rogue	Great Basin	Desch.-Col.-Okan. Areas	SE. B.C.—N. Ida.	Rockies	Great Plains	Other
Artemisia tridentata	X	X	X	X		X	X	X	X	X	
Astragalus lentiginosus	X	X	X	X		X	X	X			
Astragalus purshii				X		X	X	X	X	X	
Calochortus macrocarpus				X		X	X	X			
Calochortus nuttallii	X			X		X	X			X	
Cercocarpus ledifolius	X	X		X		X	X	X			
Chaenactis douglasii	X		X	X		X	X	X	X		
Chrysothamnus nauseosus	X	X		X		X	X	X		X	
Descurainia pinnata	X	X	X	X		X	X	X	X	X	SE. U.S.
Erigeron filifolius				X		X	X	X			
Eriogonum umbellatum	X	X	X	X		X	X		X		
Juniperus occidentalis		X		X		X	X				
Juniperus scopulorum	X						X	X	X		Replaces *J. o* northward
Leptodactylon pungens	X	X		X		X	X	X			
Lupinus argenteus	X		X	X		X	X			X	not n. of Ochocos, N. Cal. via NE. Cal.
Mentzelia albicaulis	X			X		X	X	X			
Mimulus nanus				X		X	X				
Penstemon speciosus		X		X		X	X				
Phacelia linearis				X	X	X	X	X			
Phlox hoodii				X		X	X		X	X	n. to Yukon & Alaska
Purshia tridentata	X			X		X	X	X			
Rhus glabra	X					X	X	X		X	E. N.A.
Ribes cereum	X	X		X		X	X	X		X	
Ribes viscosissimum	X					X	X	X			
Townsendia florifer						X	X				

TABLE 10. Distribution of the genera represented in the basic community of the Juniper-sagebrush

	N. Temp. Zone	Western U.S.	N.A. e. of Rockies	E. Asia	Tropics, gen.	S. America	Mex. & C. Am.	Boreal N.A.	
Artemisia	X					X			
Astragalus	X	X		X				X	
Calochortus		X					X		
Cercocarpus		X					X		
Chaenactis		X					X		
Chrysothamnus		X							1 sp. in Mex.
Descurainia	X					X			
Erigeron	X							X	
Eriogonum		X					X		
Juniperus (*Sabina*)	X								
Leptodactylon		X					X		
Lupinus	X					X		X	
Mentzelia		X				X	X		
Mimulus	X					X			esp. W. U.S.
Penstemon		X	X				X		esp. W. U.S.
Phacelia		X	X			X	X		esp. W. N.A.
Phlox		X		X			X		esp. W. N.A.
Purshia		X							
Rhus (sensu strictu)	X				X				
Ribes	X					X	X		esp. W. N.A.
Townsendia		X					X		

warmer in the Rogue Area Pine-oak Forest.

July mean temperatures range from 65° to 73°F. at stations in the juniper-sagebrush belt, running from two to four degrees higher than in the surrounding pine forests.

A group of twenty-five species can be readily selected which is clearly characteristic of the Juniper-sagebrush Woodland. This basic association is listed in Table 9 where the distribution of the various species is tabulated. Analysis of the tabulation shows that the community is compact and homogeneous, restricted in general to the intermontane region but with the same southward extension into the arid Southwest that was evident in the Pine-oak Forest. The following distributional details may be worth noting here:

a) Of the twenty-five species included in the basic association, all occur in the Great Basin and the Columbia Plateau and seventeen extend northward into southeastern British Columbia.

b) Twenty-one occupy the westward extension of the Great Basin in northeastern California. One of these, *Phacelia linearis*, crosses over into the Rogue Area while two, *Chaenactis douglasii* and *Lupinus argenteus*, occur in northern California west of the Sierra Nevada with no present-day connection with the type through southern California.

c) Sixteen species occur in the Interior Southwest area comprised of north central

Mexico, New Mexico and Arizona.

d) Only three species range to any appreciable distance from the Great Basin. One subspecies of *Descurainia pinnata* follows the southern coastal plain as far as North Carolina; *Rhus glabra* is common in central and eastern North America, while *Phlox hoodii* ranges northward along the western margin of the Great Plains to Yukon and central Alaska, the only one of our species to extend into boreal America.

The features of the present distribution of its constituent species, together with the general distribution of the genera involved (Table 10), indicate a southern origin for this community, with its center possibly on the Meseta Central of Mexico and in Arizona and western New Mexico (Fig. 6). Although in general the spread of this vegetation type and that of the Pine-oak Forest may have paralleled each other, the greater tolerance of the juniper woodland species for xeric conditions probably kept the two distinct in area and in time and stages at which they developed in any given area. It is noteworthy that of the genera represented in our selection of the basic flora of the Juniper-sagebrush Woodland, more than half are either restricted to western North America or are especially well developed there. It would seem that with the rigorous conditions under which this type has existed evolution has progressed rapidly at all levels.

CHAPARRAL FORMATION

As defined here chaparral is restricted in the Pacific Northwest to lower elevations in the Rogue Area, occurring extensively in the Rogue watershed, including that of its tributary, the Illinois River, and in relatively small areas in the Umpqua valley (Fig. 4). It is a formation dominated by shrubs with extensive root systems, usually growing in dense stands. The species are characterized by relatively small, thick, heavily cutinized leaves, usually but not always evergreen, borne on rigid twigs and branches. A recent paper by the author (Detling 1961) treats in detail the floristic constitution, climatic requirements, and probable postglacial history of this vegetation type in southwestern Oregon and northern California.

In our region the chaparral is usually dominated by *Ceanothus cuneatus*, although this species is sometimes largely replaced by *Arctostaphylos viscida* or *A. canescens*.

The chaparral species are more tolerant of drought conditions than are those of the Pine-oak Forest which usually occupies the slopes above them. Mean annual rainfall ranges from 12 to 20 inches, with less than 20 per cent occurring in the six driest months of the year. January mean temperatures are relatively high, running from 34° to 38°F. July means are from 69° to 73°F. These also are in general higher than those in the Pine-oak Forest, and more nearly approximate those occurring in the Juniper-sagebrush Woodland.

The species making up the Chaparral Formation are even more restricted in their range than are those of the juniper-sagebrush type. The basic community with its distribution is shown in Table 11. They all occur in the California Central Valley, Klamath Mountains and the Rogue Area, with about half of them extending southward to southern California or Baja California. Relatively few are found outside this general region. Of the four species listed for the Great Basin three occur in western Nevada only in that area. Only two go as far north as the Columbia River. The genera to which these species belong are mostly either restricted to western North America or are at least best developed there. The present-day chaparral may have developed from vegetation of a more southern origin (*cf.* Table 12), but many chaparral species probably developed in the areas in which they now occur. This view is supported by Stebbins (1952) who postulates that greater numbers of species in geologic time evolved in a dry habitat than in a mesic one because of a greater turnover in species, and that "environments limiting or deficient in one all important factor, moisture, have often promoted evolution."

TABLE 11. Distribution of the basic community of the Chaparral

	Mex.—Ariz.—N.M.	B. Cal.—S. Cal.	Cal. w. of Sierra	NE. Cal.—Sisk.	Rogue	Klamath Basin	Great Basin	Rockies	Great Plains	Puget	
Amelanchier pallida		X	X	X	X						
Arctostaphylos canescens			X	X	X						
Arctostaphylos viscida			X	X	X						
Asclepias cordifolia			X	X	X	X					
Ceanothus cuneatus		X	X	X	X		X				W. Nev. only
Cercocarpus betuloides		X	X	X	X						
Chlorogalum pomeridianum		X	X	X	X						
Eriodictyon californicum			X	X	X						
Fritillaria recurva			X	X	X		X				W. Nev. only
Garrya fremontii		X	X	X	X					X	
Lonicera interrupta	X	X	X	X	X						
Monardella villosa			X	X	X	X					
Quercus vaccinifolia			X	X	X						
Rhamnus californica	X	X	X	X	X		X				W. Nev. only
Rhamnus crocea	X	X	X	X	X						
Rhus trilobata	X	X	X	X	X		X		X		
Thysanocarpus radians			X	X	X						
Trichostema lanceolatum		X	X	X	X					X	

GRASSLAND FORMATION

Studies of post-Pleistocene pollen of the grasslands in eastern Washington show that the vegetation immediately following the Wisconsin period was similar to that found today (Hansen 1939). The grassland and desert zones increased in area for a time during the xerothermic interval following this time, and then the forest returned to approximately its present extent (Daubenmire 1942). Overgrazing and other man-induced factors may have accelerated the invasion of this type by secondary species often to the extent of eliminating the grasses that were originally dominant. Much of the plateau of southern Idaho (Craddock and Forsling 1939) and the Great Basin (Pickford 1932) that is now occupied by sagebrush was grassland before livestock grazed out the associated plants.

The most typical grassland left today is to be found in southeastern and south central Washington, particularly on the rolling hills of the Palouse and Snake River valleys (Fig. 4). There is evidence from relict areas that much of the Columbia Plateau north of the Ochoco Mountains in Oregon was once climax grassland. In British Columbia natural grasslands extend far north of our area on the floors and lower slopes of the interior valleys, where they are often interspersed with forest areas. In south central British Columbia much of the grassland has been seriously invaded by sagebrush and related vegetation (Tisdale 1947).

The Grassland Formation is dominated largely by bunchgrasses such as *Agropyron.* Streambank and frequently rimrock associations may contain shrub species, usually the same ones that occur in similar situations in the

TABLE 12. Distribution of the genera represented in the basic community of the Chaparral

	N. Temp. Zone	Western U.S.	Mex & C. Am.	N.A. e. of Rockies	E. Asia	Tropics, gen	S. America	Boreal N.A.
Amelanchier	X							
Arctostaphylos		X	X					
Asclepias		X	X	X			X	
Ceanothus		X	X	X				
Cercocarpus		X	X					
Chlorogalum		X						
Eriodictyon		X	X					
Fritillaria	X							
Garrya		X	X					
Lonicera	X					X		
Monardella		X	X					
Quercus	X					X		
Rhamnus	X					X	X	
Rhus		X	X	X	X			
Thysanocarpus		X	X					
Trichostema		X	X	X			Mostly Pac. Coast	

juniper-sagebrush type.

In general, the climatic requirements of grassland in the Pacific Northwest are not greatly different from those of the Juniper-sagebrush Woodland. Annual precipitation ranges from 7 to 18 inches, January mean temperatures from 29° to 33°F., and July mean temperatures from 65° to 76° F. What may be a significant factor in maintaining grassland rather than sagebrush and juniper is a fairly consistent tendency for relatively high amounts of rainfall to continue well through the late spring months (May and June) in the grassland areas.

Constituents of the Grassland

Agropyron inerme
Agropyron spicatum
Balsamorhiza sagittata
Clarkia pulchella
Clematis hirsutissima
Elymus glaucus
Festuca idahoensis
Festuca scabrella
Fritillaria pudica
Gaillardia aristata
Geranium viscosissimum
Helianthella uniflora
Iris missouriensis
Koeleria cristata
Lupinus sericeus
Mertensia longiflora
Poa secunda
Ranunculus glaberrimus
Sporobolus cryptandrus
Sporobolus columbianus
Stipa comata
Trillium petiolatum
Wyethia amplexicaulis

CRETACEOUS

The history of modern vegetation goes back largely to the Cretaceous. By this time the gymnosperms had undergone a long period of evoution. Many of their primitive lines were extinct, and of those remaining most were dwindling in importance. One of the last of their orders to evolve, the Coniferales, had originated at least by the beginning of the Mesozoic, and by late Cretaceous it was still the most important line of gymnosperms, and was widely distributed in both the Old and New Worlds.

By the end of the Cretaceous the flowering plants far surpassed the gymnosperms in numbers of families and genera and dominated the face of the earth. Their primitive representatives may have originated in the tropics and moved northward to undergo this great development (Axelrod 1952, 1959), or, as some botanists believe, they may have originated in the Holarctic regions (Just 1946). Most of the angiosperm families as we know them now, and many of our modern genera, are known from the Cretaceous of the Northern Hemisphere.

Whatever may have been the time and place of origin and early development of the angiosperms, by the end of the Cretaceous there was a well developed flora of modern aspect in Alaska, northern Canada, and Greenland, extending southward into eastern North America, the Rocky Mountain region and California. The constitution of this flora has been determined or otherwise called attention to by the work of Hollick (1930) in Alaska, Dorf (1942) in the central Rocky Mountains, Chaney (1946) and others. Let us recall that the only land masses in the Northwest not covered by the Cretaceous sea were the great batholiths forming the Nevadan orogenic arc (Fig. 2). Emergent land then existed in the mountain masses that have persisted as the Vancouver Island Mountains, the Canadian Cascades and the highlands forming the dissected plateau of southern interior British Columbia and north central Washington, the Selkirk and Bitteroot Ranges and the Blue and Klamath Mountains. During the long period of time encompassed by the Cretaceous the elevation of the land masses varied with stages in uplift and erosion, but they were never areas of low relief. These land masses were closely associated with those of Alaska, northern Canada and the Rocky Mountain axis, and from what we know of their Cretaceous floras and the evidence we have from the Vancouver Island Cretaceous (Chaney 1946) we can probably draw some very accurate conclusions regarding the flora of our region at the close of that period.

The vegetation of the uplands bordering the embayment of the northwestern Cretaceous sea apparently consisted of a forest cover made up largely of hardwood genera (Chaney 1946), Represented among them was a rather large number that still occur commonly in our flora. These genera are mostly associates of the cool-temperate forest, although some are found more regularly in other types. The more important members of the group include:

Abies
Acer
Alnus
Betula
Cornus
Corylus
Crataegus
Fraxinus
Gaultheria
Juglans
Larix
Lithocarpus
Mahonia
Malus
Myrica
Philadelphus
Picea
Pinus
Populus
Pseudotsuga
Quercus
Rhamnus
Salix
Sambucus
Sequoia
Smilax

Sorbus
Stipa
Torreya
Tsuga
Umbellularia
Viburnum
Vitis

These are genera which have persisted in western North America down to modern times and are referred to by paleobotanists as the West American Element of the early flora.

A second group of genera that was widespread in the Cretaceous forest occurs commonly today in the eastern part of North America but has been eliminated from the region west of the Rocky Mountains. This East American Element includes the following:

Aristolochia
Asimina
Carpinus
Carya
Cassia
Castanea
Celastrus
Comptonia
Cotinus
Diospyros
Fagus
Ilex
Lindera
Liquidambar
Liriodendron
Magnolia
Myrsine
Nelumbo
Nyssa
Ostrya
Piper
Sapindus
Sassafras
Taxodium
Tilia
Ulmus

Still a third group of genera, now restricted either to Asia or to tropical or subtropical regions of the New World, includes:

Ailanthus
Cercidiphyllum
Cinnamomum
Ficus
Ginkgo
Glyptostrobus
Grewia
Hedera
Keteleeria
Laurus
Metasequoia
Paulinia
Persea
Pistachia
Pterocarya
Sabal
Sterculia
Zelkova
Zizyphus

The present distribution of the genera represented in this whole Arcto-Cretaceous Geoflora indicates for that period a temperate to warm-temperate and humid climate, though not to the point of being subtropical, even in the subpolar region above the Arctic Circle. Abundant rainfall apparently was distributed fairly evenly throughout the year, as evidenced by the presence of genera which today are characteristic of climates that have abundant summer rainfall. Proximity to the sea doubtless minimized seasonal temperature variations.

Stebbins and Major (1965) and Axelrod (1959) postulate that the Madro-Tertiary Geoflora had it origins in an ancient xeric or semixeric floristic element which migrated from one continent to another. They point out that many relict species in California have close relatives in the other arid regions of the world —southwest Africa, the Mediterranean region and Chile. This great similarity suggests that they have evolved very little since they became separated.

Climatological evidence shows (Stebbins and Major 1965) that the Madro-Tertiary Geoflora could not have migrated from one continent to another in the Tertiary. The northern limits of the evidence is far south of any Tertiary climate capable of supporting such a flora.

Further, Stebbins and Major postulate the existence of pockets of xerophytic floras in late Cretaceous and Tertiary times when the climate of the American Southwest was tropical to warm-temperate. They cite similar formations in South America.

EOCENE

Certain major geologic and climatic changes occurred at about the close of the Cretaceous period that had a far-reaching effect upon the flora of the Northwest. The first of these was the elimination, through combined sedimentation and uplift, of the embayment of the sea bordered by the Nevadan orogenic arc. The result of this was to provide a relatively level lowland area extending from the Blue Mountains and Okanagan Highlands eventually almost to the present coast line of Washington and Oregon. The Cascade and Coast Ranges were formed much later, and in the absence of mountain barriers on the west, an oceanic influence prevailed in the climate of this entire plain.

A second significant change for which we have evidence from the Eocene was an increase in temperatures over those prevailing during the Cretaceous. This warming trend was general, at least throughout the Northern Hemisphere, so its effect on vegetation was not restricted to the Pacific Northwest (Chaney 1949, Axelrod 1958).

A few fossil floras have been uncovered in this region which have been referred to the Eocene, and which reveal the nature of the flora during the epoch. The best known of these are the Clarno (Knowlton 1902, Chaney 1946) in the John Day basin of eastern Oregon, and the Goshen (Chaney and Sanborn 1933) and Comstock (Sanborn 1935) floras of the Willamette valley in western Oregon. These floras indicate that the lowland plain was occupied by a broad-leafed forest whose genera came from two distinct sources. A relatively small number of genera had been represented in the temperate Cretaceous floras of Alaska and the central Rocky Mountains (Hollick 1930), and we may assume that these genera had been present in the mountains of British Columbia and in the Blue Mountains. This group was made up of species of *Aralia, Aristolochia, Celastrus, Cinnamomum, Diospyros, Ficus, Magnolia, Persea, Platanus, Quercus, Rhamnus, Smilax* and *Viburnum.* They are genera which are well represented today in warm temperate North America. We may suppose that as the Pacific shoreline advanced westward during upper Cretaceous and lower Eocene times this fragment of flora of boreal origin invaded the newly formed lowlands, and persisted there in spite of the warm climate, probably as newly evolved species adapted to the changed conditions.

The majority of the genera making up the lowland forest, however, were apparently new to this region and had no previous relation to the temperate boreal forest. Such were: *Anona, Aporosa, Astronium, Calyptranthes, Cordia, Cupania, Inga, Lucuma, Mallotus, Meliosma, Nectrandra, Ocotea, Sapium, Siparuna, Strychnos, Symplocos,* and *Tetracera.* These are genera which today are found largely in tropical or subtropical countries, many of them restricted to Central and South America. The fossil record shows that a closely related community was already in Central America in the Eocene, and persists there under subtropical conditions in such places as the central plateau of Costa Rica.

Chaney and Sanborn (1933), in discussing the Goshen flora, emphasize the point that the Eocene climate of the Pacific Northwest lowlands was probably not tropical but rather subtropical, similar to the present climate of upland Costa Rica. They postulate a mean annual temperature of about 68°F. and an annual rainfall of about 70 inches.

While the subtropical forest dominated the warm lowlands, the mountains that bordered them on the north, east and south—the Canadian Cascades, Blue and Klamath Mountains (Fig. 1)—undoubtedly served as refugia for the boreal flora of the region. Direct evidence of the constitution of this upland flora is scarce, although one layer of leaves in the Clarno formation in Oregon contains representatives of such typical temperate genera as *Metasequoia, Alnus, Lithocarpus* and *Ulmus*, mixed with the subtropical genera of the typical flora (Knowlton 1902). Chaney (1938) believes these represent the Eocene vegetation of the uplands of the Blue Mountain region. Later developments in the eastern Oregon and Washington flora seem to substantiate this view.

OLIGOCENE

Subtropical conditions persisted in the lowlands through the Eocene and into the early part of the Oligocene, but during the latter epoch there was initiated a return to a more temperate climate—a cooling and drying tendency that continued progressively through the remainder of the Tertiary Period, with only brief recessions.

Plant megafossils are not numerous in the Oligocene of the Pacific Northwest, but from those available, along with the evidence from such floras as the Weaverville in northern California (MacGinitie 1937), the Lower Cedarville in northwestern Nevada, and the Florissant in Colorado (MacGinitie 1953), and from the recent pollen studies by Gray (1964), we get what is probably an accurate general picture of the floristic changes that took place during the epoch.

With cooling temperatures the subtropical forest of the low plain was gradually replaced by a temperate forest very similar to that which dominated the upland region during the Cretaceous. Most of its species probably migrated down the slopes from the highlands bordering the plain, where temperatures had been cool enough for them to persist through the Eocene. Other species and genera may have come south with the changing climate from northern British Columbia and Alaska where the original temperate boreal forest still flourished.

It was still largely a broad-leafed deciduous forest. Many of its genera are familiar in more mesic situations in the Northwest today: *Acer, Alnus, Amelanchier, Betula, Corylus, Crataegus, Fraxinus, Mahonia, Malus, Philadelphus, Populus, Quercus, Ribes, Rosa, Salix, Sambucus, Viburnum* and *Vitis*. Others that were common at that time are now restricted to eastern North America: *Carpinus, Carya, Castanea, Fagus, Ilex, Liquidambar, Nyssa, Ostrya, Tilia* and *Ulmus*.

The conifers apparently were represented largely by members of the Taxodiaceae. Leaves of *Sequoia, Metasequoia* and *Taxodium* are common in the Oligocene sediments, and Gray (1964) reports that "... Oligocene strata at present are perhaps best characterized by the abundance of coniferous grains of presumed taxodiaceous affinities. . . ." *Thuja* and *Libocedrus* were probably present, especially in the uplands. Pollen of Cupressaceae is reported from both western and eastern Oregon and from Idaho, and both of these genera were present in the Miocene. While *Abies, Picea, Pinus, Pseudotsuga* and *Tsuga* were present and most widespread as shown by megafossils and pollen, they were not abundant, and the great coniferous forests made up largely of Pinaceae that today occupy so much of the Pacific Northwest at all elevations were still to develop.

MIOCENE

The Miocene and Pliocene floras of the Pacific Northwest are more abundant and better known than those of the preceding epochs. Our best known Miocene floras are the Eagle Creek (Chaney 1920), Molalla and Ashland in western Oregon, and the Mascall (Chaney 1925), Blue Mountains (Oliver 1934), Stinking Water (Chaney and Axelrod 1959), Sucker Creek (H. V. Smith 1938, 1939), Trout Creek (MacGinitie 1933), Lower Ellensburg, and Latah (Knowlton 1926) in eastern Oregon and Washington, and the Upper Cedarville (LaMotte 1936) in northwestern Nevada.

The tendency toward a cooler and drier climate that began in the Oligocene and continued through the Tertiary was a general one that was felt at least throughout the Northern

Hemisphere. A more local factor that eventually had a profound effect upon the climate, and thus upon the vegetation of the Pacific Northwest was the volcanic activity which was responsible for the building of the Cascade Range (Clark and Stearn 1960). During the lower and probably middle Miocene the mountains were low with only a moderate influence on the climate to the east. At that time *Metasequoia* was the dominant tree in the temperate forest of eastern Oregon and Washington. But by upper Miocene time, as revealed in the Mascall flora at the base of the Blue Mountains, while *Metasequoia* was still present it was greatly reduced in abundance. The Cascades were now intercepting some of the moisture from the Pacific Ocean, and seasonal temperature fluctuations and extremes were becoming more pronounced. Axelrod (1950), however, postulates still an average annual rainfall of 35 to 50 inches, distributed more or less evenly throughout the year, and moderate temperature ranges for the lowland areas of the Great Basin and Columbia Plateau, where the Arcto-Tertiary Geoflora was dominant.

The Pinaceae increased markedly during the Miocene. At the beginning of the Miocene members of the Taxodiaceae were predominant among the conifers, represented by *Sequoia*, *Metasequoia* and *Taxodium*. But by the end of the epoch several of our familiar genera among the Pinaceae, *e.g.*, *Abies*, *Picea* and *Pinus*, were often abundant, while *Pseudotsuga* and *Tsuga* are known to have been present, as well as *Thuja* and *Libocedrus* of the Cupressaceae.

Another Miocene feature which was probably the result of changing climatic conditions was the appearance of an increasing number of herbaceous types, including a few predominantly herbaceous families such as the Malvaceae, Onagraceae, Polemoniaceae, Umbelliferae, Gramineae, Cyperaceae and Compositae. Herbaceous types were much more highly developed at this time in California and the rest of the Pacific Southwest (Gray 1964), probably as a result of adverse climatic conditions for most trees and shrubs (in this case extreme drought), and it is to be expected that colder winters in the Northwest would be conducive as well to the herbaceous habit.

PLIOCENE

The culmination of the xeric trend was reached by middle Pliocene time. The Cascades and Coast Range had been elevated to approximately their present elevation and the modern pattern of ranges and intervening basins was well established. Rainfall east of the Cascades was reduced to the minimum reached at any time previous to the Pleistocene Ice Age. Axelrod (1950) postulates a middle Pliocene annual rainfall for the northern Great Basin and Columbia Plateau of about 15 to 17 inches, with somewhat less farther south. The continued presence of the East American Element in the forest, however, indicates that there was still considerable summer rainfall.

During the lower Pliocene the northern intermontane region in Oregon, with a rainfall of 25 to 30 inches, was dominated by a modified Arcto-Tertiary Geoflora which included *Abies*, *Acer*, *Amelanchier*, *Mahonia*, *Picea*, *Pinus*, *Populus*, *Pseudotsuga* and *Sorbus* (Axelrod 1944, Chaney 1944).

As early as the middle Eocene (Brown 1934) in the Southwest, where their evolution has been traced through abundant fossil records, there had been developing a series of vegetation types new to the Pacific slope. At that time they probably grew on some of the lowlands while the Arcto-Tertiary Geoflora was still dominant in the uplands. By Oligocene times differentiation of the generalized flora into specialized types adapted to varying degrees of aridity and temperature had reached the stage where Axelrod (1958) distinguishes: (a) a woodland savanna comprised of *Arbutus*, *Celtis*, *Dodonaea*, *Morus*, *Quercus* (live oak type), *Platanus*, *Rhus*, *Sapindus*, *Stipa* and *Vauquelinia*; (b) a chaparral type with *Ceanothus*, *Cercocarpus*, *Colubrina*, *Mahonia*, *Quercus* (scrub oak type) and *Rhus*; and (c) a thorn scrub of *Bursera*, *Caesalpinia*, *Colubrina*, *Euphorbia*, *Prosopis*, *Tephrosia*, *Thouinia* and *Zizyphus*.

For the most part they appeared in the Pacific Northwest in the Pliocene, and from the time of their first appearance they have played an important role in Pacific Northwest vegetational history. Middle Pliocene floras indicate that the climate throughout western United States at that time was semiarid, and milder and warmer than at present.

It was in response to these climatic changes that this new flora evolved in northern Mexico and southwestern United States from a warm-temperate flora that already existed there under humid conditions. The fact that the most closely related descendants of the original flora are found today in the Sierra Madre Occidental of northwestern Mexico or adjacent southwestern United States has resulted in the application to the whole flora of the name Madro-Tertiary Geoflora. The details of its evolution and migrations have been summarized by Axelrod (1958).

Axelrod lists almost 100 genera in which fossils have been described from the Madro-Tertiary Geoflora. The following selection lists some of the more important members of this group that are found today in northern Mexico and southwestern United States. The genera preceded by an asterisk extend northward today into the Pacific Northwest.

Acacia
Adenostoma
Agave
**Amelanchier*
**Arbutus*
**Arctostaphylos*
**Artemisia*
**Baccharis*
Bursera
Caesalpinia
Cassia
**Ceanothus*
**Celtis*
Cercis
**Cercocarpus*
**Chamaebatiaria*
Clethra
Condalia
Dendromecon
Dodonaea
**Ephedra*
**Euphorbia*
Eysenhardtia
Ficus
**Fraxinus*
Fremontia
**Garrya*
**Holodiscus*
**Juniperus*
Karwinskia
Leucaena
Lysiloma
**Mahonia*
Mimosa
**Myrica*
**Philadelphus*
Photinia
**Pinus*
Pithecolobium
Platanus
**Populus*
Prosopis
**Prunus*
**Purshia*
**Quercus* (live and scrub oaks)
Randia
**Rhamnus*
**Rhus*
**Ribes*
Sabal
Salvia
**Symphoricarpos*
**Umbellularia*

Central California was dominated by a live oak woodland during the middle Pliocene. Associated with *Quercus* were such genera as *Celtis, Lyonothamnus, Platanus, Populus, Robinia, Salix* and *Sapindus*. Some parts of the region were given over to chaparral, as evidenced by aggregations of *Arctostaphylos, Ceanothus, Cercocarpus, Dendromecon, Fremontia, Mahonia, Photinia, Quercus* (scrub oak) and *Rhus*. Bordering upland areas were forested with such genera as *Alnus, Arbutus, Cornus, Fraxinus, Populus* and *Prunus*. It is estimated that the central California middle Pliocene rainfall varied from 15 to 17 inches over the lowlands to 23 inches in the forested uplands (Axelrod 1948).

Southern California also was dominated by woodland, not greatly different from that farther north. Here, however, more arid conditions are indicated by desert-border communities including *Baccharis, Cercidium, Chilopsis, Condalia, Ephedra* and *Prunus* (*Emplectocladus*), and an arid subtropical scrub with *Dodonaea, Eysenhardtia* and *Ficus*. Rainfall must have been from 12 to 15 inches on the lowlands, distributed as summer showers and winter rains.

The northern Great Basin by middle Pliocene was apparently largely grassland (Axelrod 1948, 1958), with *Acer, Populus, Prunus* and *Salix* along the streams. The uplands were probably forested, a situation similar to that today in the Deschutes area with yellow pine and fir on the slopes of the Cascades.

The central Great Basin, with a rainfall of about 12 inches according to Axelrod (1948), had semiarid woodland over what is now desert, with *Juglans, Edwinia, Purshia, Rhus* and a live oak. Chaparral communities included *Arctostaphylos, Cercocarpus, Rhus, Ceanothus, Mahonia* and *Prunus* (*Emplectocladus*).

Only in the still more xeric southern intermontane areas did the flora include *Pinus* (the pinyon pines), *Robinia* and *Acacia*; these apparently never reached the Pacific Northwest.

The Madro-Tertiary Geoflora reached southwestern Oregon by early Pliocene, and undoubtedly reached its greatest development in this area by the middle of the epoch, just as it did in other areas throughout the west (Axelrod 1958). Its further development and spread in the Pacific Northwest was arrested after the middle Pliocene by the widespread climatic change that initiated a return to the moister and cooler conditions leading up to the glaciations of the Pleistocene. Whether it was ever entirely eliminated from the Rogue basin after it once arrived there is problematical. Yellow pine apparently was abundant in the upper Willamette valley at the beginning of the last glacial retreat, and if it persisted there through the cold maximum it is entirely possible that other xeric species of the Madro-Tertiary Geoflora persisted as far north as the Rogue basin.

However, the greatest importance for us of the Madro-Tertiary Geoflora at that stage lies in its continuing proximity to our region, to whose flora it made significant contributions in later times as climatic conditions allowed.

During late Pliocene times there began a trend toward cooler temperatures, which culminated in the ice ages of the Pleistocene. And while the Cascades still acted as a barrier to moisture from the Pacific Ocean, the lower temperatures and consequent lower evaporation rates may have resulted in a greater *effective* precipitation than that which obtained in the preceding middle Pliocene.

By late Pliocene a major secular change had occurred in the climate on both sides of the Cascades. The amount of summer rainfall proportionate to the annual total had dropped sharply (Chaney, Condit and Axelrod 1944). This resulted in the elimination from our flora of both the East American and East Asian Elements, species and genera which were dependent upon wet summers for their continued existence.

PLEISTOCENE

By the beginning of the Pleistocene and before the advance of the glaciers the modern pattern of vegetation in the Pacific Northwest must have been well established even to species, an association directly derived from the West American Element of the Arcto-Cretaceous and Arcto-Tertiary Geofloras. This forest covered the valleys and coastal strip and consisted of *Pseudotsuga, Tsuga, Larix, Thuja, Alnus, Acer macrophyllum, Cornus nuttallii* and *Populus,* with an understory of *Corylus, Acer circinatum, Mahonia nervosa, Philadelphus, Rhamnus purshiana, Sambucus glauca* and *Vaccinium parviflorum*.

A number of disjunct distributions among the Boreal Forest species, where their range is broken at or near the southern limit of the continental ice sheet, demonstrates the influence of the glaciers. Figure 5 shows the maximum extent of continental glaciation in our region (Flint 1945). This maximum occurred late in the series of ice advances, in most places during the last or Wisconsin stage, and its southern limit constitutes a critical line from the standpoint of the distribution of many northwest species.

Glaciologists have shown that during the ice age there was not just one advance of an ice sheet, but at least four, and that these advances presumably were separated by relatively warm periods. If this is so, we must assume that south of the glaciers the cold wet maxima alternated with periods during which the boreal flora took refuge in the non-glaciated areas in the high mountains, the far north and in the south. Evidence for these climatic fluctuations is found in the complicated vegetational pattern in the Pacific Northwest, demonstrated in modern times by peculiar species and subspecies distributions and by the presence of islands of boreal flora. Rand (1948) describes birds having continuous distributions which show biological discontinuity, and postulates temporary barriers in the form of glacial ice which permitted the fixing of genetic entities.

We may assume that the pattern of vegetational adjustment to conditions caused by either advancing or retreating glaciers would be much the same throughout the whole Pleistocene epoch since the temperatures of all the interglacial periods were about the same (Flint 1957). With increasing cold, mesic species would be eliminated from higher elevations of this region, and from lower elevations in the vicinity of the margin of the continental ice sheet. They would be replaced by more boreal types already occupying the highest mountain tops or the lower elevations to northward. Judging by present distributions, the climate adjacent to the ocean, at least as far south as northern California, was cool enough to permit the invasion of the coastal lowlands by this same boreal flora.

We have used relict islands of boreal vegetation to show past distribution patterns of boreal associations. Another type of vegetation which left its pattern in disjunct distributions was more xeric in its requirements and invaded the warmer and drier areas as they appeared in the wake of receding glaciers. These xeric vegetation types, the Pine-oak Forest, Juniper-sagebrush Woodland, Chaparral and Grassland, moved north from the Great Basin or developed approximately in the areas they now occupy (Axelrod 1950).

This evidence is particularly striking in the Pacific Northwest where there is great physiographic and climatic variation. Even here, however, the evidence of retreat and advance is not clear-cut. As a result of subsequent advances and retreats the locus of an island might or might not be repopulated with the same combination of species as before. We have no way of knowing which glacial advance or which interglacial maximum brought elements of the flora of a given present-day relict island into place. And it is probable that the present islands are not all of the same age. This increases the difficulty of determining the chronology of successive waves of floral migration, and seems to be particularly true of our boreal flora.

That part of the continental ice sheet which affected the Pacific Northwest was centered in the Canadian Rockies. At its maximum stage it extended southward well into Washington and northern Idaho (Fig. 5). East of the Cascade Range it reached its southern limit about where the Columbia River forms the southern boundary of Okanogan County in Washington. It extended beyond the present site of Spokane, and in Idaho extended south of Lake Pend d'Oreille. West of the Cascades a lobe of the same glacier covered the Puget Sound basin as far south as the valley of the Chehalis River. Apparently all of southern British Columbia was ice-covered during the maximum glacial advances.

Besides the lowlands and plateaus covered by the main ice sheet, extensive areas of some of the mountain ranges were covered by gla-

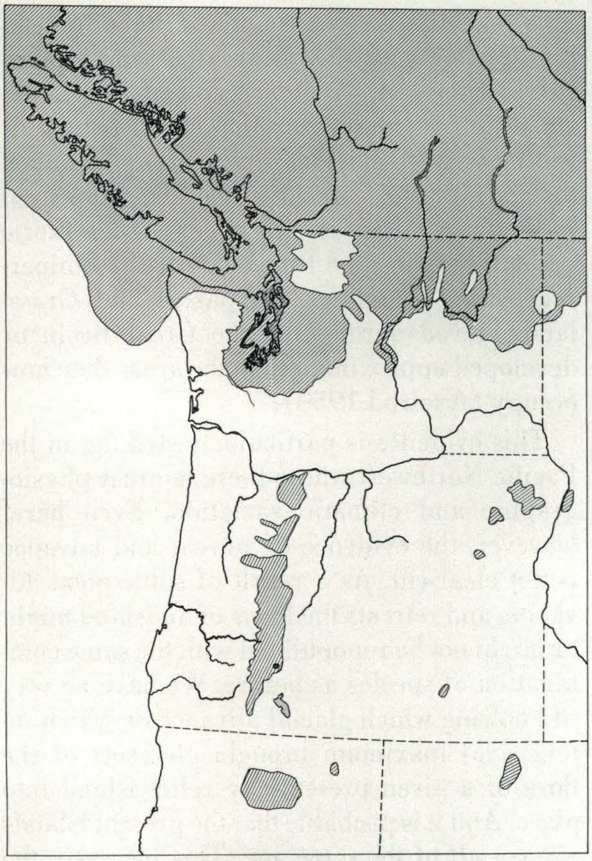


Figure 5. *Maximum continental glaciation in the Pacific Northwest during the Pleistocene epoch (after Flint 1945).*

ciers which originated at high elevations and moved downward in response to decreasing temperatures. Such glaciers were almost continuous in the Cascades as far south as the Klamath Gap. Widespread glaciation occurred in the Wallowas and the Olympic Mountains (Flint 1957).

Two relict islands are of major importance in our subsequent discussion of the former extent of the boreal flora. The most extensive in area of these islands is the Columbia River Gorge (Fig. 1). This local flora was discussed in some detail by the writer in a previous publication (Detling 1958). The gorge has been carved through the Cascade Range by the Columbia River, its cutting having kept pace with the gradual rise of the range since its beginning. In some place precipitous walls rise to a height of 2500 feet.

The boreal flora of the Columbia Gorge occurs at numerous places along the bottom of the canyon at elevations ranging from 50 to 1500 feet, mostly along the south wall in the almost constant shade of the steep bluffs. Many of the species thrive in the cool misty situations about the numerous waterfalls and in the narrow lateral canyons. The nearest related flora occurs above the 4000-foot level on the north facing slopes that rise toward Larch Mountain and Mount Hood, but the two populations are separated by at least 2500 vertical feet of Mesic Conifer Forest.

A second boreal island, less extensive in area but equally as significant in its implications, is on Saddle Mountain (Fig. 1). This flora also has been discussed in detail by the writer in a previous paper (Detling 1954). Located in the Coast Range of Clatsop County, Oregon, this peak rises to a height of 3250 feet. The sheer cliffs and interspersed hanging meadows near its summit harbor about forty species that are distinctly boreal in their distribution. Many of them occur again no nearer than the Olympic Mountains, the Columbia Gorge, or at other stations in the Cascade Mountains of Washington or Oregon.

The most ambitious project aimed at determining the succession of vegetation types in the Pacific Northwest since the last glacial retreat has been the study of fossil bog pollen carried on for the last thirty years by Henry P. Hansen. By 1947 Hansen had investigated some sixty-seven bogs in this region and has since added several more to the list. Most bogs suitable for study occur west of the Cascade Mountains, but a sufficiently significant number were found in eastern Washington and Oregon to furnish valuable clues to climatic shifts in that area as well. His work shows that most of our bogs were initiated at about the beginning of the last retreat of the continental ice.

Pollen profiles from the glaciated region show that *Pinus contorta* was in all cases the first arboreal invader of the newly uncovered ground. The species is well adapted to cool temperatures and disturbed edaphic conditions, and probably established itself close to the retreating glacier.

South of the ice sheet *P. contorta* was present in greater or lesser abundance at the time of glacial maximum. It was especially abundant west of the Cascades as at Lake Labish (Fig. 1) and Silverton bogs in the central Willamette valley, but in lesser degree was present east of the range as far south as the northern Great Basin, where it probably was limited to upland situations from which its pollen was carried to adjacent bogs.

Pollen of this species is usually most abundant at the lowest levels of the bog profiles, where it is dominant. It soon decreases upward and is gradually replaced west of the Cascades by *Pinus monticola, Picea sitchensis* and *Pseudotsuga menziesii,* the last two of which eventually become dominant in certain areas. East of the Cascades *Pinus contorta* was replaced by *P. monticola, Abies* spp., or over much of the area, finally by *Pinus ponderosa.*

Heusser (1960) interprets the pollen record in the Pacific Northwest in general as follows:

The maximum advance of the last Wisconsin glaciation, which occurred about 15,000 years ago, was followed by a cool moist period of about 10,000 years duration. This was the period of dominance of the more boreal forest species such as *Pinus contorta, P. monticola* and *Abies* spp. The period from 13,000 to 11,000 years ago was one of increasing warming and drying, represented in the vegetation by an expansion of the more mesic species, *viz., Pseudotsuga menziessi, Picea sitchensis* and *Tsuga heterophylla* west of the Cascades, and *Pinus ponderosa* to the east. The next postglacial period extended from 11,000 to 4000 years ago. During this time average temperatures were slightly higher and average precipitation less than at present. Vegetation was marked by the dominance of *Quercus garryana* in the valleys west of the Cascades, and a maximum of grasses, composites and chenopods in the mid-Columbia and Great Basin areas. *Picea sitchensis* apparently was dominant along the coast. The period from 4000 years ago to the present has been one of cooler and moister climate marked by an increase in *Pseudotsuga menziesii* and *Pinus ponderosa* at the expense of *Quercus garryana* and the grasses, composites and chenopods.

By utilizing the results of pollen research and what we know of present relict floras we can piece together with fair accuracy the general story of Pacific Northwest vegetation since the early Postglacial.

At the glacial maximum a boreal forest dominated by *Pinus contorta* and *P. monticola* extended along the ice front from the Washington coast to the Rocky Mountains of northern Idaho (Heusser 1960). It was probably similar to the present Boreal Forest occurring at elevations of 4000 to 6000 feet in the Cascade Range of Oregon and at lower elevations northward.

This forest extended southward along the coast as far as northwestern California (Hansen 1947), although at its southern limits it probably was infiltrated by austral genera and species. It occupied the western Washington and Oregon valleys as far as the Calapooya Mountains between the Willamette and Umpqua drainages. A relict flora in a bog 22 miles west of Eugene today contains *Ledum glandulosum columbianum,* the coastal counterpart of the montane *L. glandulosum glandulosum, Ranunculus reptans strigulosus, Hypericum anagalloides* and *Drosera rotundifolia,* all boreal species or subspecies. In the same bog Hansen found pollen of *Pinus contorta* and *P. monticola,* the former of which was present almost to recent times. An abundance of *Pinus ponderosa* pollen in the lower half of the profile confirms our belief that the southern end of the Willamette valley was near the margin of the Boreal Forest so far as the interior basins are concerned. *Picea sitchensis* was present at other points in the central Willamette valley during this time, at Onion Flats and Lake Labish (Hansen 1947). *Betula glandulosa* was collected at Lake Labish by Thomas Howell in 1893, and *Picea sitchensis* is now growing on the Nisqually River in the Cascades of western Washington.

The disjunct occurrence of a number of boreal species, mostly on mountain tops throughout the range, indicates that the Boreal Forest covered the Coast Range southward through most of Oregon. The following representative species occur as members of typical boreal associations at several points. The letters in parentheses following the species names indicate the localities (Fig. 1) (S=Saddle Mountain, Clatsop County; H=Mt. Hebo, Tillamook County; M=Marys Peak, Benton-Lincoln Counties; R=Roman Nose, Douglas County; T=high Coast Mountains, Tillamook County).

Abies procera (S-M)
Acer glabrum doublasii (S-M)
Cornus canadensis (H)
Cryptogramma acrostichoides (S-R)
Heuchera glabra (M)
Lomatium martindalei augustatum (M)
Lupinus lepidus lyallii (M-R)
Penstemon davidsonii menziesii (S-H)
Phleum alpinum (S-M)
Polystichum munitum imbricans (R)
Pyrola secunda (T)
Rubus lasiococcus (H)
Rubus pedatus (S-T)
Senecio triagularis (H-M)
Vaccinium membranaceum (M)
Vaccinium ovalifolium (H)

Climatic conditions in the Cascades were severe enough to push the boreal forest to valley level in the Columbia Gorge area. About fifteen per cent of the species listed by the writer (Detling 1958) as occurring in the Columbia Gorge are constituents of the boreal flora being considered here. Following are a few of the more striking representatives of the group. Species preceded by an asterisk occur also on Saddle Mountain.

**Acer glabrum douglasii*
**Alnus sinuata*
Antennaria racemosa
**Campanula rotundifolia*
Cornus canadensis
**Cryptogramma acrostichoides*
Dodecatheon dentatum
Habernaria unalaschensis
Haplopappus hallii
Lewisia columbiana
Lomatium martindalei martindalei
Mitella trifida
**Penstemon nemorosus*
Penstemon rupicola
**Phlox diffusa longistylis*
**Polypodium vulgare columbianum*
**Saxifraga bronchialis vespertina*
**Saxifraga caespitosa*
**Saxifraga rufidula*
Suksdorfia violacea
Vaccinium membranaceum

All of these species occur in other boreal situations more or less distant from the Columbia Gorge.

Two other members of the Columbia Gorge boreal flora, *Bolandra oregana* and *Sullivantia oregana*, otherwise endemic in the area, are of interest here because they have been collected also at Elk Rock, a sheer northeast-facing bluff on the Willamette River at Oswego, about twenty miles from the west portal of the gorge. They furnish additional evidence that the gorge boreal flora formerly extended out over the Willamette valley floor at least as far as Oswego.

To summarize for this early Postglacial time we may assume for southwestern Washington and the Willamette valley, as well as for the valleys and ridges of the Coast Range and for the Columbia Gorge, a forest dominated by *Pinus contorta* and *P. monticola*, and in some areas by *Abies procera* and *Picea sitchensis*, with an understory composed of *Acer glabrum douglasii*, *Vaccinium membranaceum*, *V. ovalifolium*, *V. scoparium*, *Rhododendron albiflorum* and *Cladothamnus pyrolaeflorus*. Forming the ground cover among the shrubs were the more or less woody trailing *Rubus nivalis*, *R. pedatus*, *R. lasiococcus* and *Cornus canadensis*, as well as *Pyrola secunda* and patches of *Xerophyllum tenax*. On steep slopes and rocky ledges grew several species of *Penstemon* (*davidsonii*, *fruticosus*, *rattanii*), *Lomatium martindalei*, *Saxifraga ferruginea* and other species of *Saxifraga*, *Montia parvifolia flagellaris*, *Valeriana sitchensis scouleri, Heuchera glabra*, and the fern species *Polystichum munitum imbricans* and *Cryptogramma acrostichoides*. Where conditions favored the persistence for any length of time of open meadows, these were dominated by *Carex* spp., *Koelaria cristata* and *Phleum alpinum;* but interspersed among the sedges and grasses were *Lupinus lepidus lyallii, Viola adunca, Erythronium grandiflorum, Senecio triangularis* and *Anemone lyallii*. Swampy places were occupied by various species of *Salix, Ledum glandulosum columbianum*, and such small herbaceous species as *Drosera rotundifolia, Hypericum anagallidoides, Trientalis arctica* and *Ranunculus reptans strigulosus*.

This is the assemblage of species which today occupies the slopes of the Cascade Range between the elevations of approximately 4500 and 5500 feet, and at lower elevations is essentially the forest of north central British Columbia.

The littoral belt of the Boreal Forest may have differed to some degree from that in the Coast Range and the leeward valleys. Its climate was certainly tempered by its proximity to the ocean. *Picea sitchensis* was dominant from the glacial maximum and *Pinus contorta* was present in considerable quantity as they are now. The coastal bog plants today are the same ones which were present in the Willamette valley during the period we are considering and were undoubtedly common along the coast at that time. Except for *Ledum* we have no direct evidence that the shrubs listed above as forming the understory of the valley and Coast Range forest were present in the coast strip forest. However, several of the herbaceous species of the foregoing list were present in at least some parts of the coastal strip, e.g., *Xerophyllum tenax, Saxifraga* spp., *Valeriana sitchensis* and *Montia parvifolia flagellaris*.

The Boreal Forest may have occupied the plateau south of the continental ice sheet east of the Cascade Range at least as far as the northern Great Basin if we can interpret the distribution of a number of typical boreal species ordinarily occurring today either in the Cascades or the Blue-Rocky massif, or frequently in both, as evidence of such an occupation. They are also found on one or more of the higher mountains of the northern Great Basin, the widely dispersed peaks of the Steens, Hart, Warner, Pueblo and Mahogany Mountains, Gearhart Butte, Drake's Peak and Abert Rim, all separated by many miles of arid plateau in southeastern Oregon. Occurring at elevations of 6000-9000 feet on these peaks we find:

Agoseris aurantiaca
Arctostaphylos nevadensis
Caltha leptosepala
Cryptogramma acrostichoides
Epilobium alpinum
Habenaria dilatata leucostachys
Hulsea nana
Kalmia polifolia microphylla
Lupinus lepidus lyalli
Mitella pentandra
Oxyria digyna
Penstemon davidsonii
Phleum alpinum
Phyllodoce empetriformis
Pinus albicaulis
Polemonium elegans
Polygonum bistortoides
Populus tremuloides
Salix barclayi
Sibbaldia procumbens
Sorbus scopulina
Thermopsis montana montana
Veratrum viride

This distribution pattern gives evidence of a former more or less continuous range of the Boreal Forest at plateau level at least as far south as southeastern Oregon.

The bog pollen profiles from eastern Washington and Oregon and northern Idaho show that while *Pinus contorta* was the dominant arboreal species, *P. monticola* and *P. ponderosa* were significantly present from the beginning within a short distance of the face of the ice. The same is true of the grasses, composites and chenopods. These more xeric species and genera were the ones which replaced *Pinus contorta* as the glaciers retreated, and not *Pseudotsuga* or *Tsuga* as was the case west of the Cascades.

As the Boreal Forest retreated northward and to higher elevations, it was succeeeded first by the Mesic Conifer Forest, and this in turn by a series of xeric austral vegetation types which included the Pine-oak Forest, and the woodlan and chaparral types.

We have already noted the origin of these communities as a part of the Madro-Tertiary Geoflora early in the Tertiary and their culmination during the middle Pliocene. Although some elements of this flora probably persisted in the Rogue basin through the cooler and moister period of the Pleistocene, as shown by the abundance of yellow pine at the beginning of the glacial retreat (Hansen 1947), it is doubtful that the more extremely xeric elements such as the chaparral and pure oak woodland would have withstood the conditions north of the Klamath highlands during that period. However, they were present throughout this time in northern and central California (Axelrod 1958).

Evidences of the northward advance of the more extremely xeric types following the retreat of the continental glaciers, however, are to be found not only in the fossil pollen record but also, at least west of the Cascades, in a number of relict islands of this xeric vegetation.

During the last few years the writer has made detailed studies of the distribution, floral constitution and ecological relations of some of these relicts (Detling 1953, 1954). The islands that have been studied occupy special habitats consisting of exposed mountain tops or ridges, with shallow soil in which the more deeply-rooted trees or shrubs have probably never gained a foothold and thus have not entered into serious competition with the low-growing xeric species. They occur at elevations of from 2000 to 6000 feet, mostly along the west slopes of the Cascades or rising from the floor of the Puget trough. The only one seen and studied in the Coast Range is on Marys Peak in Benton-Lincoln Counties, Oregon. Those studied by the writer were all in Oregon, although others occur as far north as Puget Sound. In most cases the islands are bounded below by the Mesic Conifer Forest; a few of the higher ones are bounded by a belt of Boreal Forest.

The most striking of the islands from the standpoint of numbers of xeric species supported are those on Bohemia-Fairview Mountain, Rebel Peak and Horsepasture Mountain, all in eastern Lane County. Others of significant importance are on Spencer Butte and the Coburg Hills, both near Eugene.

In one of the studies the writer analyzed the distribution patterns of the species associated specifically with chaparral, while in the other he was concerned with the relict distribution of Rogue basin xeric species in general. In the present discussion of the post-Pleistocene migrations of Madro-Tertiary elements in our flora, no advantage would be gained by distinguishing among the various associations of the xeric flora. Many chaparral associates occur also in the oak and pine woodlands of southwestern Oregon, and while chaparral is a distinct vegetation type, it responds to climatic changes in the same way as do the other types comprising the xeric flora.

As the writer pointed out in the earlier paper on xeric islands, the most significant feature of a vegetation area is not its boundaries but rather its environmental center, the point about which its environmental (in this case climatic) extremes are concentrated, which point functions as a center of influence for the whole area. In most cases, and certainly in the Pacific Northwest, the positions of the environmental centers are determined by the topography of the region. Since our topography has not been appreciably altered since the close of the Pleistocene we may reasonably assume that the centers of climatic extremes, and therefore of vegetation areas, have also remained unchanged. What changes is the intensity of influence of the combined climatic extremes at the environmental center. If the climate of the Pacific Northwest were to undergo a trend toward increased warmth and dryness the influence of the warm and dry extremes in such areas as the Rogue and the Deschutes would be intensified, and the floras of those areas would spread progressively away from the centers at the expense of the floras of areas such as the South Cascade and Siskiyou which have had a cool-humid combination of extremes. In the case of the Rogue Area, the xeric yellow pine-oak type under such conditions would migrate northward and to higher elevations around the Rogue basin, followed by the more xeric chaparral and finally, if the climatic trend continued, by grassland types.

It is difficult or impossible to trace through the xeric islands the former distribution of the shrubby species so characteristic of the chaparral. Their absence from the xeric sites probably is due largely to the shallowness of the soil, although other limiting factors may also play a part. *Rhus diversiloba,* while abundant in the chaparral, is so widespread in the Pine-oak Forest west of the Cascades and even in the drier phases of the Mesic Conifer Forest, that its value in determining the former range of its chaparral associates is negligible. Relict stands of *Ceanothus cuneatus* occur in the deeper soils of the Puget Area as far north as the Columbia River, especially on well drained sites such as those underlain by old gravel bars. *Garrya fremontii,* a common chaparral species in the Rogue Area, occurs occasionally as far north in the Puget Area as the McKenzie River, and again in the Columbia Gorge. *Chrysothamnus nauseosus albicaulis,* less typical as a chaparral species but still a member of the association, occurs in several of the Puget xeric islands. These four are the only chaparral shrubs known to the writer to extend northward from the Rogue basin. All other chaparral associates found relict north of this area are herbaceous.

While a considerable number of Madro-Tertiary genera are found on both sides of the Cascade axis, the number of species that are generally distributed at present both east and west of the range is not large. More numerous are those species which have a fairly wide distribution, but on one side only of the Cascades. Examples of such species west of the mountains are *Quercus garryana, Arbutus menziesii, Corylus cornuta, Phacelia heterophylla, Ceanothus sanguineus, Erysimum capitatum* and *Godetia amoena.* Widespread east of the mountains are *Purshia tridentata, Artemisia tridentata, Cercocarpus ledifolius, Ceanothus velutinus, Descurainia pinnata* and *Lupinus laxiflorus.*

Another group of xeric species, however, is much more closely restricted to one or sometimes two areas today, and we find no evidence of their ever having spread beyond the confines of their present limits. Such are: *Quercus chrysolepis, Arctostaphylos viscida, A. canescens, Eriodictyon californicum, Chlorogalum pomeridianum* and *Fritillaria recurva,* restricted to the Rogue Area and California west of the Sierra Nevada; *Asclepias cordifolia, Cercocarpus betuloides, Convolvulus polymorphus, Lomatium californicum, Mahonia piperiana, Micropus californicus* and *Rhus trilobata,* occurring typically in the Rogue Area but extending at least into the Klamath basin portion of the Washoe Area (Fig. 3).

Between these extremes of wide diffusion and restricted distribution is a large group of species which are much more pertinent to our study because of their present-day distribution and their occurrence in the relict islands of xeric species. The distributions of most of these involve the Rogue Area, and when they do they usually continue southward through the warm canyons of the Klamath Mountains and the foothills of the interior valleys of central California. Many of them are chaparral associates, either typically or more or less incidentally.

The simplest distribution pattern of this group, and a very common one, consists of the Rogue Area with outlying stations in the xeric islands or other isolated xeric sites of the Puget Area. Examples of this pattern are seen in *Ceanothus cuneatus, Erigeron foliosus confinis, Hieracium cynoglossoides nudicaulis* and *Si-*

dalcea asprella. A relatively small number of species with this basic distribution occurs also in the Klamath basin, but apparently no farther north east of the Cascades. *Castilleja pruinosa* and *Viola sheltonii* are examples.

A significant variation of this pattern is one in which typical Rogue species appear in the xeric islands (rarely more extensively) of the Puget Area and also in that portion of the Columbia Area contiguous with the east end of the Columbia Gorge. A few of these Rogue species may occur in the Klamath basin but are not found farther north on the east side of the Cascades. This distributional variant is represented by such species as *Eriogonum compositum pilicaule, Sisyrinchium douglasii, Quercus garryana, Dentaria tenella pulcherrima, Lupinus bicolor, L. micranthus, Tonella tenella, Linanthus bolanderi, Orthocarpus attenuatus, Pectocarya pusilla* and *Plagiobothrys nothofulvus.* One of the most interesting of these examples is afforded by *Eriogonum compositum.* The typical variety of this species (nomenclatorially), with glabrous scapes and peduncles, occurs commonly east of the Cascades except in the Columbia Area (Fig. 3). The variety *pilicaule,* characterized by pubescent scapes and peduncles, replaces this in the Rogue and Siskiyou Areas and in the Columbia Area at the head of the Columbia Gorge, and is the form which is always found on the xeric islands of the Puget Area where it occurs with considerable frequency.

A lesser number of xeric island species are typical of arid vegetation areas east of the Cascades, namely one or more of the Washoe, Deschutes or Columbia Areas (Fig. 3). They may or may not occur also in the Rogue Area. They include such species as *Chrysothamnus nauseosus albicaulis, Phacelia linearis, Artemisia tridentata, Gila aggregata, Collomia linearis, Penstemon deustus, Lupinus lepidus medius, Arenaria formosa, Bromus polyanthus, Arnica parryi* and *Sanicula graveolens.* The most interesting refugium of this group of species is probably the rather extensive colony of *Artemisia tridentata* which occurs on Rebel Peak in eastern Lane County at an altitude of 5384 feet, associated with about twenty other xeric species normally found in the Rogue or Deschutes Areas, or both. This is the only occurrence of sagebrush so far reported from west of the Cascade crest.

From the evidence of the relict distributions summarized in the foregoing paragraphs we can infer the movements of the xeric flora in the Pacific Northwest with the return of the warmer and drier climate following the retreat of the continental glaciers.

The migration was merely the resumption and continuation of the northward spread of the Madro-Tertiary Geoflora that was temporarily interrupted by the cold-humid period of the late Pliocene and Pleistocene. In this region it involved any species that might have survived in the Rogue basin during the generally changed conditions, and those species that had reached and remained in northern and central California and the central areas of the Great Basin.

The high elevation of the Sierra-Cascade axis prevented any general east-west interchange of the flora until late in the xerothermic trend. Exceptions may have been the Klamath River Gap between the Central Valley of California and the Klamath basin, the Columbia Gorge, and most probably the Fraser River Gap in southern British Columbia.

West of the Cascades the first Madro-Tertiary species to migrate northward with the advent of warmer and drier conditions were undoubtedly the pine-oak associates that had persisted in the Rogue basin. With increasing warmth and aridity the low cross ranges such as the Wolf Creek and Calapooya Mountains became less effective as barriers, and the xeric flora moved north and attained dominance through the Puget trough as far as Vancouver Island and the lowlands of mainland southwestern British Columbia.

The continuing xerothermic trend brought new genera and species over the Klamath Mountains from northern California, and the chaparral type became established in the

Rogue basin. This moved northward at lower elevations as the earlier migrants into the Puget trough moved to higher elevations in the Cascades and the Coast Range.

Xeric species occupied extensive warm open slopes and ridges in the Cascades to an elevation of 6000 feet, and at this stage must have mixed with an ascending xeric flora from the east slopes of the range to form such communities as that on Rebel Peak. Boreal conditions in the strip along the Cascade summit were least effective as a barrier at this stage.

Meanwhile the xeric flora that had reached the lower Willamette valley, made up of *Quercus garryana* and its associates, was migrating eastward through the Columbia Gorge, and having reached the upper end, spread out over the warm valleys of the Deschutes, John Day and Yakima Rivers and such moderate uplands as the Simcoe Mountains. Later migrations through the Columbia Gorge included some of the herbaceous typical chaparral associates.

On the east slope of the Coast Range, bordering the Willamette valley, the early migrants of the xeric flora ascended at their maximum to an elevation of 4000 feet. On a few of the higher peaks they mingled with but failed to supplant a relief boreal flora persisting from the glacial maximum. This presumably explains the occurrence today on Marys Peak of the xeric *Allium crenulatum*, *Eriogonum umbellatum* and *Silene douglasii* alongside the boreal *Abies procera*, *Erythronium grandiflorum pallidum*, *Lomatium angustatum flavum*, *Lupinus lepidus lyallii*, *Phleum alpinum* and *Polygonum bistortoides*, and on Saddle Mountain, *Allium crenulatum*, *Festuca howellii*, *F. pacifica*, *Poa secunda*, *Senecio fastigiatus* and *Silene douglasii* associated with such boreal species as *Abies procera*, *Acer glabrum douglasii*, *Anemone globosa*, *Cladothamnus pyrolaeflorus*, *Lewisia columbiana rupicola*, *Rudbeckia occidentalis*, *Saxifraga bronchialis vespertina* and *Vaccinium scoparium*.

On the basis of precipitation and temperature data selected from recording stations in the Shasta River valley and Rogue basin chaparral belt, and from others in the transverse ranges and areas where chaparral relicts occur today, as well as from Klamath Falls and The Dalles, the writer has postulated that for the more xeric phases of the Madro-Tertiary Flora to cross the ecologic barriers interposed by the higher ridges of the Siskiyou Mountains and the transverse ranges to the north it would require that the mean annual rainfall west of the Cascades be decreased by about 230 mm below that prevailing at present with not more than twenty-seven per cent occurring during the six driest months of the year. At the same time a general increase in the July mean maximum temperatures of 5.0° C over that of today would be required. An increase of only 1.0° C in the January mean minimum temperatures would have favored the invasion of the Klamath basin and the Columbia Area above the Columbia Gorge by chaparral of its present associates (Detling 1961).

The general aridity just cited as part of the requirement for the elimination of the ecologic barriers to the northward progress of chaparral undoubtedly decreased rainfall in the broader valleys to a figure below the 250 mm which Cooper (1922) found to be the minimum required by chaparral in California. As a consequence, during the xerothermic maximum chaparral probably was replaced by grassland in the lowlands of the Rogue, Umpqua and Willamette valleys and in the area about The Dalles.

As pointed out earlier, bog pollen profiles indicate that the xerothermic trend was initiated about 13,000 years ago (Heusser 1960), at which time the postglacial northward migration of the Rogue River Madro-Tertiary Geoflora got well under way. By the same source of evidence the xerothermic maximum was reached about 6000 years ago, the time at which the xeric vegetation reached its greatest northward advance and greatest altitudinal distribution, and had spread into the area east of the Columbia Gorge and into the Klamath basin. Much of the floor of the basins west of the Cascades was probably covered by grassland, and near-desert conditions may have obtained along the Columbia River from near the head of the gorge eastward to its confluence with the Snake River.

The trend toward a cooler and more humid climate since the xerothermic maximum has witnessed the reversal of the vegetational migrations. The increasingly more mesic types, pine and pine-oak woodlands and Mesic Conifer Forest, moving southward in the basins and downward from the mountains replaced the grassland and chaparral. Only in especially favorable sites have a few of the xeric species persisted, and some of these colonies may have been reduced to actual "islands" only within the last one or two thousand years.

East of the Cascades the postglacial migrations of the Great Basin flora followed the same general pattern as that of the Rogue. While we have nothing from xeric refugia upon which to base this statement, Hansen's pollen studies on bogs east of the mountains bear out such a conclusion. We have already pointed out in this connection that at the end of the Pleistocene the Boreal Forest occupied at least the uplands as far south as the northern Great Basin, with yellow pine occupying the lower slopes and grasses and chenopods on the plateau. We may recall also that Axelrod has shown that by middle Pliocene, when the Madro-Tertiary Geoflora reached its farthest north pre-Pleistocene extension, the northern Great Basin was occupied largely by grassland and by arboreal genera of northern rather than southern origin.

Judging then by these sources of evidence it seems extremely likely that a major northward migration of Great Basin Madro-Tertiary Geoflora was initiated at the end of the Pleistocene and kept pace with the advance of the Californian species of the same flora from the Rogue basin.

Yellow pine woodland as a phase of the more southern and western Pine-oak Forest extends at present as far north as Kamloops Lake in central British Columbia, and is well represented along the Thompson River between Lytton and Kamloops, and in adjacent valleys such as that of the Nicola River. Mingled with the woodland in several of the valleys are areas of well developed sagebrush type. Within these mingled types occurs an association of species of austral origin common in the pine or Juniper-sagebrush Woodland to the south. These are the species that moved north with the xerothermic trend, reaching the southern margin of the Fraser Plateau by the time of its maximum. Included in the association are:

Amelanchier alnifolia cusickii
Artemisia tridentata
Astragalus beckwithii
Astragalus purshii
Astragalus stenophyllus
Balsamorhiza careyana
Balsamorhiza sagittata
Castilleja thompsonii
Chaenactis douglasii
Chrysopsis villosa hispida
Chrysothamnus nauseosus albicaulis
Chrysothamnus viscidiflorus
Cirsium undulatum
Clematis ligusticifolia
Delphinium bicolor
Descurainia pinnata filipes
Erigeron filifolius
Erigeron pumilus
Erigeron speciosus
Eriogonum heracleoides
Eriogonum niveum
Fragaria vesca bracteata
Gaillardia aristata
Gilia aggregata
Heuchera cylindrica
Juniperus scopulorum
Lithospermum ruderale
Lomatium dissectum multifidum
Mahonia repens
Mentzelia laevicaulis parviflora
Opuntia fragilis
Orobanche fasciculata
Phacelia hastata leucophylla
Phacelia linearis
Prunus virginiana melanocarpa
Purshia tridentata
Rhus radicans

Ribes cereum
Senecio canus
Sieversia ciliata
Symphoricarpos albus laevigatus
Zygadenus venenosus

RECENT

As the climate became warmer and drier in the wake of the receding continental ice, the Boreal Forest flora retreated northward and upward in the mountain ranges. This movement was more clear-cut in areas removed from oceanic influence. Along the narrow coastal strip it was modified to the extent that while there is evidence that many boreal species did move northward, at the same time many persisted at sea level. In the Coast Range south of the Olympic Mountains the mild climate of the low, more inland mountains resulted in the elimination of the boreal flora except in a few restricted localities such as the summits of Saddle Mountain, Mount Hebo and Marys Peak (Fig. 1).

The final result of the migration was the establishment of a broad zone of boreal flora extending northward from central British Columbia and reaching from the coast to the Rocky Mountains, with three fingerlike extensions of the same flora extending southward down the coastal strip, the Cascades and the Blue-Rocky Mountain massifs (Fig. 4).

It is not known to what extent the British Columbia boreal zone was repopulated by the flora that moved north from below the ice limit, and to what extent from refugia that may have existed within the glaciated region. Various authors have pointed out that ice-free areas did exist during the Wisconsin phase of the ice age in the Canadian Rockies as well as in northern British Columbia and the Yukon (Hultén 1937, Hansen 1947, 1950, 1953, 1955). Be that as it may, it is certain that all vegetation was eliminated from a broad strip for many miles behind the ice front, extending from the Puget Sound area to the Rockies and beyond, and that this strip was apparently repopulated largely by the boreal species that occupied the terrain contiguous to the ice front at the beginning of its recession.

With the amelioration of the climate many of the species have persisted in more than one of the southerly extensions of the boreal flora in Canada (Fig. 4). The following list is representative of this group of species. The occurrence of each species in the various fingers south of glaciation is shown by the symbols C (coastal strip), Cas (Cascade Range), B (Blue Mountains) and R (Rocky Mountains). An asterisk following a symbol indicates that the species occurs only a very short distance south of the limit of glaciation.

Abies amabilis C—Cas
Abies lasiocarpa Cas—B—R
Acer glabrum douglasii Cas—B—R
Agoseris aurantiaca Cas—B—R
Alnus sinuata C—Cas—B—R
Anemone occidentalis C—Cas—B—R
Antennaria racemosa C—Cas—B—R
Arctostaphylos uva-ursi C—Cas—B—R
Arnica latifolia Cas—B—R
Betula glandulosa Cas—B—R
Betula papyrifera occidentalis Cas*—R*
Caltha leptosepala Cas—B—R
Cardamine bellidifolia Cas—R
Cassiope mertensiana Cas—R*
Cornus canadensis C—Cas—R
Crepis nana Cas—B—R
Cryptogramma acrostichoides C—Cas—R
Empetrum nigrum C—Cas*
Epilobium alpinum Cas—B—R
Epilobium latifolium C—Cas—B—R
Eriophorum chamissonis C—R*
Eriophorum gracile Cas—B—R
Erythronium grandiflorum C—Cas—B—R
  chrysandrum R
  grandiflorum Cas—B—R
  pallidum C—Cas—B—R
Gaultheria humifusa C—Cas—B—R
Gaultheria ovatifolia Cas—B—R
Habenaria dilatata C—Cas—B—R
Heuchera glabra C—Cas
Hieracium gracile Cas—B—R
  densifloccum B—R
  detonsum Cas

Juniperus communis montana C—Cas—B—R
Kalmia polifolia C—Cas—B—R
microphylla Cas—B—R
polifolia C—Cas
Ledum glandulosum C—Cas—B—R
columbianum C
glandulosum Cas—B—R
Ledum palustre groenlandicum C—R*
Leptarrhena pyrolaeflora C—Cas—R*
Lonicera involucrata C—Cas—B—R
involucrata C—Cas—B—R
ledebourii C—Cas—B—R
Luetkea pectinata Cas—B—R
Maianthemum dilatatum C—Cas—R*
Mitella breweri C—Cas—R*
Mitella pentandra C—Cas—B—R
Mitella trifida C—Cas—B—R
Myrica gale C
Oxyria digyna C—Cas—B—R
Penstemon davidsonii C—Cas
davidsonii Cas
menziesii C—Cas
Petasites frigidus Cas
Petasites sagittatus R
Phleum alpinum C—Cas—B—R
Phyllodoce empetriformis C—Cas—B—R
Phyllodoce glanduliflora Cas—B—R
Picea engelmannii Cas—B—R
Picea sitchensis C
Pinus albicaulis Cas—B—R
Pinus contorta C—Cas—B—R
contorta C
murrayana Cas—B—R
Polygonum bistortoides C—Cas—B—R
Pyrola secunda C—Cas—B—R
Rhododendron albiflorum C—Cas—B—R
Rubus nivalis C—Cas—R*
Rubus pedatus C—Cas—R*
Saxifraga bronchialis C—Cas—B—R
austromontana Cas—B—R
vespertina C—Cas
Saxifraga caespitosa C—Cas—R
emarginata C—Cas*
minima R
subgemmifera C—Cas
Saxifraga ferruginea C—Cas—R*
Saxifraga oppositifolia C—Cas*—B—R
Saxifraga punctata cascadensis C—Cas
Saxifraga tolmiei C—Cas—R*
Senecio triangularis C—Cas—B—R
angustifolius C
triangularis C—Cas—B—R
Shepherdia canadensis B—R
Sibbaldia procumbens Cas—B—R
Sorbus scopulina C—Cas—B—R
cascadensis C—Cas
scopulina C—Cas—B—R
Sorbus sitchensis C—Cas—R
grayi C—Cas
sitchensis C—Cas—R*
Stenanthium occidentale C—Cas—R
Trientalis arctica C—Cas—R*
Tsuga mertensiana C—Cas—B—R
Vaccinium caespitosum C—Cas—R
Vaccinium ovalifolium C—Cas—B—R
Vaccinium scoparium Cas—B—R
Vaccinium uliginosum C—Cas—R
Veratrum viride Cas—B—R
Viola sempervirens orbiculata Cas—B—R
Xerophyllum tenax C—Cas—R

A lesser number of species apparently did not follow in the wake of the retreating ice front but have been stranded instead in one or more of the boreal fingers, and have maintained no connection in the north. Examples of this type of distribution are shown in the following list:

Arctostaphylos nevadensis Cas—B
Bolandra oregana Cas—B
imnahensis B
oregana Cas
Calochortus lobbii Cas
Chamaecyparis nootkatensis C—Cas—B
Cladothamnus pyrolaeflorus C
Claytonia megarhiza Cas—B—R
bellidifolia B
megarhiza R
nivalis Cas
Collomia debilis C—Cas—B—R
debilis Cas—B—R
larsenii C—Cas
Dodecatheon dentatum Cas—R
Douglasia laevigata Cas

ciliolata Cas
laevigata Cas (Columbia Gorge)
Draba aureola Cas
Erigeron howellii Cas
Erigeron oreganus Cas
Hieracium longiberbe Cas
Hulsea algida B—R
Hulsea nana Cas
Lewisia columbiana C—Cas—B
columbiana Cas
rupicola C—Cas
wallowensis B
Lomatium martindalei C—Cas
angustatum C—Cas
flavum C
martindalei Cas
Lupinus lepidus lyallii C—Cas—B—R
Microseris alpestris Cas
Penstemon rupicola Cas
Polemonium elegans Cas—B
Polemonium viscosum B—R
Polygonum newberryi C—Cas
Polygonum phytolaccaefolium Cas—B—R
Rubus lasiococcus C—Cas
Salix hookeriana C
Saxifraga tolmiei C—Cas—R
Suksdorfia violacea Cas—R
Sullivantia oregana Cas
Synthyris missurica B—R
Synthyris schizantha C—Cas
Synthyris stellata Cas
Vaccinium deliciosum C—Cas
Vaccinium membranaceum C—Cas—B—R
Vaccinium occidentale Cas—B—R
Vaccinium ovatum C

The significance for evolution of the partial or complete isolation of population fragments in the mountain or coastal fingers is obvious. Gene mutations occurring in one fragment have been separated by such great distances from the rest of the population that in numerous cases divergent evolution has proceeded to the point where separate subspecies or even separate but closely related species now occupy one or more distinct fingers. Such undoubtedly has been the origin of the subspecific differentiation noted in the two preceding plant lists.

The climatic trend of the last 4000 years, toward cooler and moister conditions (Hansen 1947, Heusser 1960), has brought the Pacific Northwest flora to its present status. With possible temporary unrecorded reversals the Mesic Conifer Forest has again become dominant over much of the western portion of the region. It has largely replaced the xeric Rogue flora except for numerous refugia where soil conditions have probably hindered its competitors. Many Madro-Tertiary species have been sufficiently adaptable to become incorporated into the mesic forest where we find them, especially in its drier phases. On the valley floors the mesic forest has not taken complete possession; the chaparral has retreated southward, but considerable areas are occupied by oak woodland, and occasional stands of ponderosa pine persist.

Judging by the vestiges of Madro-Tertiary associations remaining in the high mountains, the Boreal Forest has increased in area along the crest of the Cascades, descending the western slopes by 1000 feet or more, and widening the strip it occupies to the point where the vegetation types on either side are now far separated.

The coastal strip of Boreal Forest was probably the least affected by the xerothermic trend of any of our types. No evidence of the Madro-Tertiary invasion is to be seen north of the central Oregon coast, and although the Mesic Conifer Forest encroached greatly upon it from the landward side during the warm period it has maintained itself intact, including the numerous bog associations that have persisted since the glacial period.

East of the Cascades, even with the relative increase in humidity and lowering of temperatures in the last 4000 years, the region is still one of actual aridity. Consequently the Madro-Tertiary elements still dominate except at higher elevations, as in the mountains of southern British Columbia and the Blue Mountains. The only change over the period has been a migration down slopes and out on to the plateau of the yellow pine forest at the expense of sagebrush and grassland.

Certain genera and families in the Madro-Tertiary Geoflora have undergone marked evolutionary development during their adjustment to the changing Tertiary climate, and have given rise to specially adapted forms appearing in different vegetation types. This seems to account for the presence in the more northern Mesic Conifer and Boreal Forests of members of typically drought-adapted genera. The more recently derived northern species are usually taller plants with larger leaves, mesophytic structure and surfaces. Some of the outstanding examples of this species evolution and adaptation are the following:

a) *Ceanothus cuneatus* and *C. cordulatus* in the chaparral, replaced by *C. velutinus* in the Pine-oak Forest, especially east of the Cascades, and by *C. thyrsiflorus* and *C. integerrimus* in the drier phases of the Mesic Conifer Forest.

b) *Arctostaphylos viscida* and *A. canescens* in the chaparral, represented by *A. patula* in the Pine-oak Forest and by *A. columbiana* in the coastal Boreal Forest.

c) *Rhamnus crocea* in the chaparral, and *R. purshiana* in the Mesic Conifer Forest and coastal Boreal Forest.

d) *Mahonia repens* in the Pine-oak Forest east of the Cascades, replaced by *M. aquifolia* in dry phases of the Mesic Conifer Forest. *M. nervosa* apparently is of more ancient origin and is related to East Asian species and has probably come into the Mesic Conifer Forest from the north.

e) *Holodiscus glabrescens* of the arid Pine-oak and Juniper Woodlands, and *H. discolor* of dry situations in the Mesic Conifer Forest.

f) *Cercocarpus ledifolius* and *C. betuloides* of the Juniper Woodland and Chaparral Formations, respectively.

g) *Garrya fremontii* of the chaparral and *G. elliptica* of the coastal Boreal Forest.

h) *Rhus trilobata* in the chaparral, represented in both chaparral and dry phases of the Mesic Conifer Forest by *R. diversiloba* and in the Juniper Woodland by *R. toxicodendron.*

It is of interest to note that in several of the genera drought-adapted species in arid formations are replaced by morphologically more mesic species or subspecies in the Mesic Conifer or Boreal Forests. They are represented in Mexico by similarly mesic forms (taller plants with mesophytic foliage, etc.). These features are displayed by such Mexican species as *Ceanothus coeruleus*, *Arctostaphylos pungens* and *Mahonia fascicularis.*

VEGETATION AREAS IN WESTERN MEXICO

(The following section consists of brief and incomplete notes dealing with work done in Mexico in connection with the geologic history of the Northwest flora. Most of the plant collections are as yet unidentified.)

According to paleobotanical studies (Axelrod 1938, 1950a), a large part of the xeric flora of western United States developed in response to warm dry climates in the Tertiary, evolving from a subtropical flora that already existed in northwest Mexico. The closest present relatives of this Madro-Tertiary Geoflora are centered in the western Sierra Madre of Mexico (Fig. 6). Since there are several closely related vegetation types in that region through which evolutionary lines from subtropical to desert can be traced, it is of considerable interest and value to determine these pathways from their origins eventually to their contributions to our present western United States flora.

We may distinguish six major vegetation types in western Mexico: Subtropical Forest, Xeric Matorral, Thorn Savanna, Desert Scrub, Pinyon-juniper Woodland and Pine-oak Forest. Degrees of relationship between major types may be shown by the relative number of genera (sometimes families) which they hold in common. Sometimes a genus (*e.g. Bombax, Ceiba*) may be represented by several species, all of which have remained typically subtropical in their distribution. On the other hand,

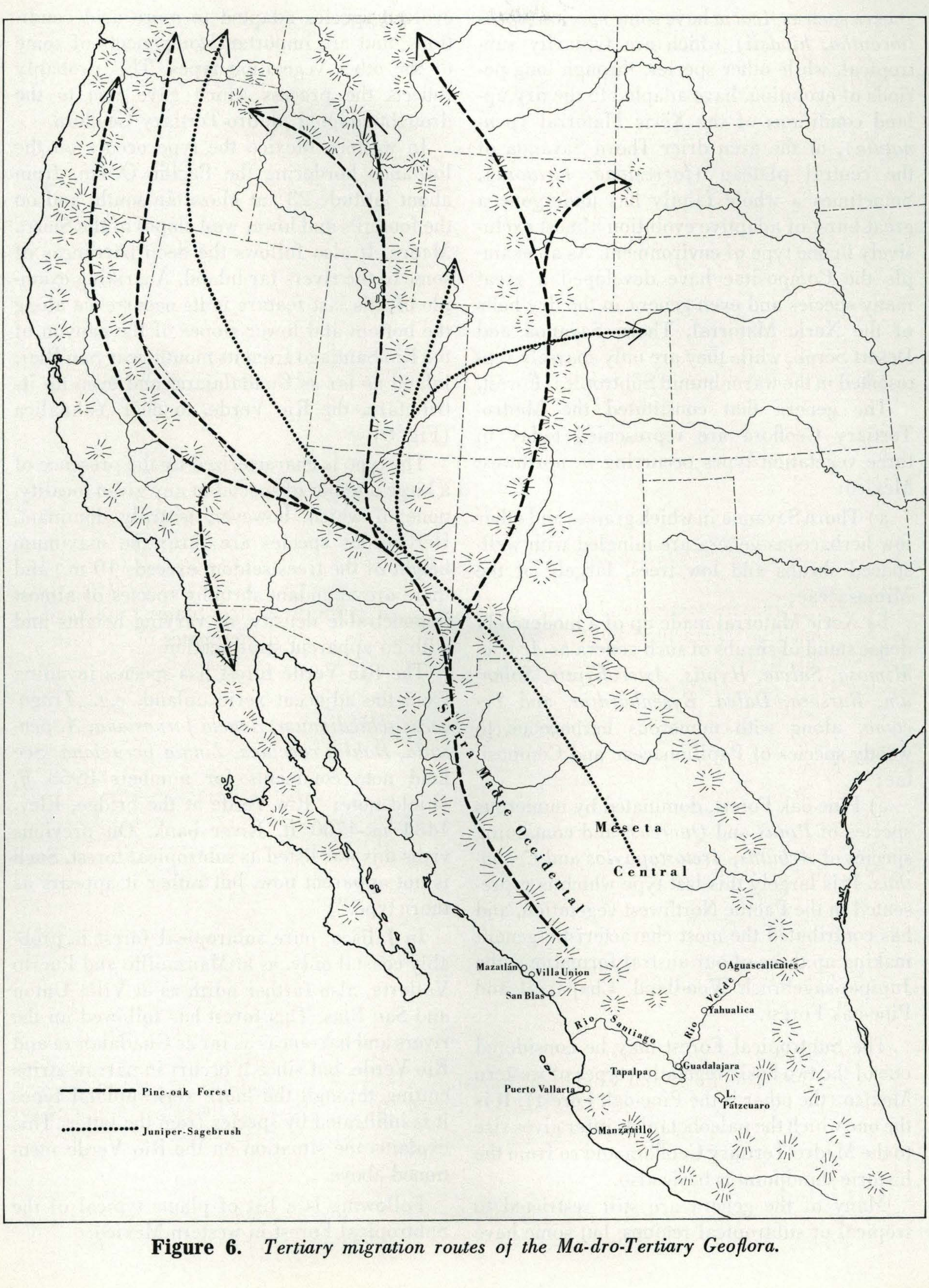


Figure 6. *Tertiary migration routes of the Ma-dro-Tertiary Geoflora.*

genera such as *Acacia* have some species (*cochliacantha, hindsii*) which are typically subtropical, while other species, through long periods of evolution, have adapted to the dry upland conditions of the Xeric Matorral (*pennatula*), or the even drier Thorn Savanna of the central plateau (*farvesiana, tortuosa*). Sometimes a whole family has undergone a great burst of adaptive evolution almost exclusively in one type of environment. As an example the Compositae have developed a great many species and even genera in the dry belts of the Xeric Matorral, Thorn Savanna and Desert Scrub, while they are only sparsely represented in the warm-humid Subtropical Forest.

The genera that constituted the Madro-Tertiary Geoflora are represented today in three vegetation types occurring in northwest Mexico:

a) Thorn Savanna in which grasses and other low herbaceous genera are mingled with well-spaced shrubs and low trees, largely of the Mimosaceae;

b) Xeric Matorral made up of a moderately dense stand of shrubs of such genera as *Acacia*, *Mimosa*, *Salvia*, *Hyptis*, *Asterohyptis*, *Solanum*, *Bursera*, *Dalea*, *Eysenhardtia*, and *Tecoma*, along with numerous herbaceous to woody species of Papilionaceae and Compositae;

c) Pine-oak Forest, dominated by numerous species of *Pinus* and *Quercus*, and containing species of *Arbutus*, *Arctostaphylos* and *Ceanothus*. It is largely this last type which is represented in the Pacific Northwest vegetation, and has contributed the most characteristic genera making up three of our austral formations, the Juniper-sagebrush Woodland, Chaparral and Pine-oak Forest.

The Subtropical Forest may be considered one of the two basic vegetation types of western Mexico (the other is the Pine-oak Forest). It is the one which the paleobotanists infer gives rise to the Madro-Tertiary Geoflora and so from the historic standpoint is basic also.

Many of the genera are still restricted to tropical or subtropical regions, but some have evolved species adapted to more arid conditions, and are important components of some of the other vegetation types. This probably reflects the process which gave rise to the drought-adapted Madro-Tertiary Geoflora.

In western Mexico the type occurs on the lowlands bordering the Pacific Ocean, from about latitude 23° at Mazatlán south, and on the foothills and lower west slopes of the Sierra Madre. It also follows the deep barrancas of some of the rivers far inland. A striking example of this last feature is its occurrence along the bottom and lower slopes of the canyon of the Rio Santiago from its mouth near San Blas, inland as far as Guadalajara, and even up its tributary, the Rio Verde, to near Yahualica (Fig. 6).

The type is characterized by the presence of a large number of species at any given locality, none of which, however, is truly dominant. Herbaceous species are rare; the maximum height of the trees seldom exceeds 10 m., and there are abundant shrubby species of almost impenetrable density, of varying heights and with no apparent stratification.

The Rio Verde forest has species invading from the adjacent xeric upland, *e.g.*, *Tragoceros schiedianum*, *Acacia farnesiana*, *A. penstula*, *Dahlia coccinea*, *Zinnia peruviana*. See field note comments for numbers 8953 *ff*. (Field note: "Rio Verde at the bridge, Elev. 1434 m.-4700 ft. River bank. On previous visits this was listed as subtropical forest. Such is not apparent now, but rather it appears as thorn type.")

In Jalisco, pure subtropical forest is probably coastal only, as at Manzanillo and Puerto Vallarta, also farther north as at Villa Union and San Blas. This forest has followed up the rivers and barrancas as far as Guadalajara and Rio Verde, but since it occurs in narrow strips cutting through the more xeric upland types it is infiltrated by species from the latter. This explains the situation on the Rio Verde mentioned above.

Following is a list of plants typical of the Subtropical Forest in western Mexico:

Acacia cochliacantha
Acacia hindsii
Adiantum princeps
Agdestis clematidea
Anona longiflora
Antigonon flavescens
Antigonon leptopus
Aristolochia sp.
Baukinia longiflora
Bravaisia integerrima
Bursera kerberi
Capparis verrucosa
Casearia pringlei
Cassia emarginata
Cissus sichyoides
Clematis dioica
Combretum farinosum
Conzattia multiflora
Corchorus siliquosus
Coria eleagnoides
Exogonium bracteatum
Guazuma tomentosa
Hamelia versicolor
Laguncularia racemosa
Lygodium venustum
Mimosa invisa
Mimosa pigra
Mimosa spirocarpa
Momordica charantia
Oxybaphus viscosus
Passiflora foetida gossypifolia
Peperomia campylotropa
Pluchea odorata
Pouzolzia palmeri
Randia armata
Rhus barclayi
Salix humboldtiana
Serjania mexicana
Solanum bicolor
Solanum umbellatum
Tournefortia hirsutissima
Xylosma velutinum

Under very xeric conditions oak occurs as a pure oak woodland, and then tends to be infiltrated by Xeric Matorral species. This is the case with the *Q. resinosa* woodland 34 km. west of Aguascalientes.

Pinus oocarpa is the most xeric of all the pines. Where it occurs as co-dominant with *Quercus* (as at 16-17 km. west of Guadalajara), it is associated with many Xeric Matorral species, just as in the pure oak woodland facies.

The genus *Dalea* is best developed in the Oak-Woodland facies or Oak-*P. oocarpa* woodland of the Pine-oak. It has two species in the Xeric Matorral of Ixtlahuacan. Probably the genus should be thought of as intermediate between these two xeric types. There are no *Dalea* in Subtropical Forest.

Following is a list of the Pine-oak Forest association:

Adiantum andicola
Adiantum patens
Adiantum poiretii
Alnus glabrata
Alnus jorullensis
Arbutus glandulosa
Arbutus xalapensis
Arctostaphylos pungens
Asphodelus fistulosus
Calliandra grandiflora (O-W facies)
Ceanothus coeruleus
Ceanothus durangoinus
Centaurium macranthum
Cheilanthes angustifolia
Cheilanthes kaulfessii
Cheilanthes pyramidalis
Clethra mexicana
Crataegus rosei
Cuphea aequipetala (O-W facies)
Dalea gracilis (O-W facies)
Dalea pectinata (w. *P. oocarpa*)
Dalea submontana (w. *P. oocarpa*)
Dalea tomentosa (O-W facies)
Dalea tuberculata (O-W facies)
Dodonaea viscosa (O-W facies)
Dryopteris patula (O-W facies)
Erigeron tenellus
Eupatorium areolare (O-W facies)
Hypoxis rugosperma
Hyptis oblongifolia (w. *P. oocarpa*)
Ipomoea heterophylla (O-W facies)
Mahonia fascicularis

Malaxis aurea
Malaxis pringlei
Oxalis decaphylla
Oxypappus seemannii (w. *P. oocarpa*)
Phaseolus coccineus (O-W facies)
Pinaropappus roseus (O-W facies)
Pinus cooperi
Pinus engelmannii
Pinus lumholtzii
Pinus michoacana
Pinus oocarpa
Pinus teocote
Prunus capuli
Pteridium aquilinum (w. *P. oocarpa*)
Quercus aristata
Quercus bolanyosensis (w. *P. oocarpa*)
Quercus coccolobaefolia
Quercus crassifolia
Quercus diversifolia (O-W facies)
Quercus durifolia
Quercus eduardii (O-W facies)
Quercus grisea
Quercus laxa
Quercus macrophylla (O-SF)
Quercus magnoliaefolia (O-SF)
Quercus mexicana
Quercus microphylla
Quercus omissa
Quercus praineana (O-W)
Quercus resinosa (O-W facies, or w. *P. oocarpa*)
Quercus rugosa
Quercus rugulosa (O-W facies)
Quercus transmontana (O-W facies)
Ranunculus petiolaris
Salix bonplandiana
Selaginella pallescens (O-W facies or Oak-SF)
Senecio stoechadiformis
Spiranthes velata
Tagetes lucida
Thalictrum tripeltiferum (O-W facies)
Triumfetta brevipes (O-W facies)
Trixis hyposericea (O-W facies)
Trixis longifolia (O-W facies)
Vaccinium geminiflorum
Vernonia jaliscana (O-W facies)
Vernonia mucronata (w. *P. oocarpa*)
Viola grahamii
Wigandia caracasana (O-W facies)
Yucca decipiens (O-W facies)

The Desert Scrub Formation is an edaphic phase of the Juniper Woodland dependent upon extreme saline (or otherwise basic) conditions. It is more common in Nevada and Utah, but in the Oregon portion of the Great Basin it occurs on the playas of ancient lakes or on surrounding lower slopes. The genera are austral in origin (except *Artemisia*, and this genus is probably of austral origin) and developed in the southwestern deserts during the Madro-Tertiary evolution and migrations.

Constituents of the Desert Scrub Formation:

Sarcobatus vermiculatus
Atriplex confertifolius
Grayia spinosa
Artemisa spinescens
Atriplex canescens
Tetradymia ?
Eurotia

All the ferns collected at Lake Pátzcuaro were along a (now) dry watercourse. Normally they would belong in the pine forest. Pátzcuaro is originally noted as a mixed pine-oak-thorn forest. See field notes 8481 *ff*.

The Chapalita district of Guadalajara is undoubtedly of thorn savanna type. This is attested by remnants of this type around the Politécnico, in the fields or roadsides just outside of town, Zapopan, etc., where such genera as *Prosopis* and *Pithecolobium* are common. However, a number of xeric matorral species are abundant in the vacant lots of Chapalita. The same is true of Zapopan. Does intensive land use in the savanna encourage the infiltration (development) of matorral?

Examine carefully the association on the slopes about 19 km. north of Tapalpa (Fig. 6). Now classified as Thorn Savanna, but they seem to be nearer Xeric Matorral because of some genera.

Axelrod refers to this as mesquite grassland (1958).

Constituents of the Thorn Savanna:

Acacia farnesiana
Acacia tortuosa
Anisacanthus thurberi
Argemone ochroleuca
Asclepias linaria
Aster tanacetifolius
Baccharis ramulosa
Bidens pilosa
Buddleia scordioides
Buddleia sessiliflora
Calliandra oaxacana
Clematis drummondii
Cynanchium kunthii
Desmondium sericophyllum
Ficus mexicana
Ficus petiolaris
Grindelia oxylepis
Haplopappus spinulosus scabrellus
Haplopappus venetus
Hyptis albida
Jatropha dioica
Karwinskia latifolia
Mimosa monancistra
Muhlenbergia rigida
Nicotiana glauca
Oenothera speciosa
Parthenium bipinnatifidium
Pellaea sagittata
Pigueria trinervia
Pithecolobium acatlense
Pithecolobium dulce
Prosopis juliflora
Psilactis brevilingulata
Psittocanthus calyculatus
Rhynchelytrum roseum
Sanvitalia procumbens
Senecio heracleifolius
Senecio salignus
Solanum eleagnifolium
Solanum madrense
Solanum torvum
Stevia jaliscensis
Tillandsia recurvata
Trixis angustifolia
Wigandia kunthii
Woodsia mollis (Pátzcuaro)

XERIC MATORRAL

Acacia pennatula
Asterohyptis mociniana
Bursera bipinnata
Bursera fagarioides
Canavallia villosa
Cassia stenocarpa
Cheilanthes myriophylla
Cosmos sulfureus
Crotalaria maypurensis
Crotalaria pumila
Crotalaria sagittalis
Croton morifolius
Cuphea llavea
Cuphea procumbens
Dalea diffusa
Dalea nutans
Desmodium procumbens
Dyssodia cancellata
Dyssodia tagetiflora
Eupatorium pulchellum
Eysenhardtia polystachya
Gomphrena decumbens
Gomphrena nana
Indigofera jaliscensis
Ipomoea intrapilosa
Lagascea decipiens
Leucaena esculenta
Loeselia mexicana
Lysiloma acapulcensis
Mandevilla foliosa
Manihot foetida
Mimosa albida
Montanoa myriocephala
Notholaena aurea
Notholaena sinuata
Perezia rigida
Phaseolus atropurpureus
Phaseolus heterophylla
Phorandendron carneum
Physalis nicandroides
Prunus ferruginea
Ptelea trifoliata
Rhus radicans
Salvia leptophylla
Salvia purpurea
Salvia tiliaefolia

Schkuhria anthemoidea
Solanum rostratum
Sprekelia formosisissima
Stevia rhombifolia
Tagetes filifolia
Tagetes micrantha
Tecoma stans
Thevetia ovata
Tithonia tubaeformis
Tragoceros schiefianum
Verbisina sphaerocephala
Vernonia serratuloides
Viguiera pachycephala
Viguiera quinqueradiata
Zinnia peruviana
Zornia diphylla

Xeric matorral may sometimes be a successional stage, as in Nayarit (numbers 8523 *ff.*) where it apparently came in after the clearing of an oak woodland.

Axelrod refers to this type as "arid subtropic scrub" (1958, p. 502).

PINON-JUNIPER WOODLAND

Cowania mexicana
Juniperus deppeana
Pinus cembroides
Populus arizonica

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APPENDIX

Following is a list of plants and their common names which are diagnostic of the vegetation areas of the Northwest discussed in this paper.

Abies amabalis—Amabalis or lovely fir
Abies concolor—White fir
Abies grandis—Giant or grand fir
Abies lasiocarpa—Alpine fir
Abies procera—Noble fir
Acer circinatum—Vine maple
Acer glabrum douglasii—Douglas maple
Acer macrophyllum—Big-leaf or Oregon maple
Achlys triphylla—Vanilla leaf
Aconitum spp.—Aconite, monkshood
Actaea spicata arguta—Baneberry
Adenocaulon bicolor—Trail plant
Agropyron inerme—Great Basin wheat-grass
Agropyron spicatum—Wheat bunchgrass
Allium crenulatum—Olympic onion
Allotropa virgata—Sugar stick
Alnus oregona—Oregon alder, red alder
Alnus sinuata—Sitka alder
Alnus tenuifolia—Mountain alder
Amelanchier spp.—Serviceberry
Anemone spp.—Anemone, wind flower
Anemone occidentalis—Mountain pasque flower
Antennaria racemosa—Slender everlasting
Aplopanax horridum—Devils club
Aquilegia formosa—Columbine
Arbutus menziesii—Madrone
Arctostaphylos canescens—Hoary manzanita
Arctostaphylos columbiana—Hairy manzanita
Arctostaphylos nevadensis—Pine mat manzanita
Arctostaphylos patula—Green-leaf manzanita
Arctostaphylos uva-ursi—Kinnikinnick
Arctostaphylos viscida—White-leaf manzanita
Arenaria formosa—Sandwort
Arnica latifolia—Broad-leaf arnica
Arnica parryi—Parry's arnica
Artemisia tridentata—Sagebrush
Aruncus sylvester acuminatus—Goat's beard
Asarum caudatum—Western wild ginger
Asclepias cordifolia—Purple milkweed
Astragalus spp.—Locoweed
Baccharis pilularis consanguineus—Chaparral broom
Balsamorhiza spp.—Balsam root
Betula glandulosa—Resin birch
Betula papyrifera—Paper birch
Bolandra oregana—Oregon bolandra
Boykinia major—Mountain boykinia
Bromus polyanthus—Bromegrass
Calochortus lobbii—Lobb's star tulip
Calochortus macrocarpus—Mariposa lily
Calochortus nuttallii—Sego lily
Calochortus tolmiei—Mariposa lily, Cat's ear
Caltha leptosepala—Marsh marigold
Calypso bulbosa—Lady's slipper
Campanula rotundifolia—Harebell, bluebell
Cardamine bellidifolia—Alpine bitter cress
Carex spp.—Sedges
Cassiope mertensiana—White heather
Castilleja spp.—Paint brush
Ceanothus cordulatus—Snow bush
Ceanothus cuneatus—Buck brush
Ceanothus integerrimus—Deer brush
Ceanothus prostratus—Squaw mat
Ceanothus sanguineus—Oregon tea tree
Ceanothus thyrsiflorus—Blue brush
Ceanothus velutinus—Sticky laurel, snow brush
Cercocarpus betuloides—Plume tree
Cercocarpus ledifolius—Mountain mahogany
Chaenactis douglasii—Hoary chaenactis
Chamaecyparis nootkatensis—Alaska cedar
Chimaphila umbellata—Prince's pine
Chlorogalum pomeridianum—Soap plant
Chrysopsis villosa hispida—Golden aster
Chrysothamnus spp.—Rabbit brush
Cimicifuga elata—Bugbane
Circaea pacifica—Enchanter's nightshade
Cirsium undulatum—Thistle
Cladothamnus pyrolaeflorum—Cladothamnus
Clarkia pulchella—Clarkia
Claytonia megarhiza—Spring beauty
Clematis hirsutissima—Leather flower
Clematis ligusticifolia—Clematis, virgin's bower
Clintonia uniflora—Queen cup
Collomia debilis—Alpine collomia
Collomia grandiflora—Large-flowered collomia
Convolvulus polymorphus—Morning-glory, bindweed
Coptis laciniata—Western gold-thread
Corallorhiza striata—Coral root
Cornus canadensis—Bunchberry
Cornus nuttallii—Western dogwood
Cornus stolonifera—American or red osier dogwood
Corydalis scouleri—Western corydalis
Corylus cornuta—Western hazel
Crepis nana—Hawksbeard
Cryptogramma acrostichoides—Parsley fern
Cynoglossum grande—Hound's tongue
Delphinium bicolor—Larkspur
Dentaria pulcherrima—Toothwort
Descurainia pinnata—Tansy-mustard
Dicentra formosa—Bleeding heart

Disporum oreganum—Oregon fairy bells
Dodecatheon dentatum—Shooting star, bird's bill
Douglasia laevigata—Douglasia
Drosera rotundifolia—Sundew
Elymus glaucus—Western rye-grass
Empetrum nigrum—Crowberry
Epilobium spp.—Fireweed
Erigeron spp.—Wild daisy
Eriodictyon californicum—Yerba santa
Eriogonum spp.—Wild buckwheat
Eriophorum spp.—Cotton grass
Erysimum capitatum—Wallflower
Erythronium spp.—Lamb's tongue, fawn lily
Festuca spp.—Bunchgrass
Fragaria spp.—Wild strawberry
Fritillaria lanceolata—Mission bells, rice-root lily
Fritillaria pudica—Yellow bells
Fritillaria recurva—Scarlet fritillaria
Gaillardia aristata—Blanket flower
Galium spp.—Bedstraw
Garrya elliptica—Silk tassel bush
Garrya fremontii—Bear brush
Gaultheria humifusa—Alpine wintergreen
Gaultheria ovatifolia—Oregon spicy wintergreen
Gaultheria shallon —Salal
Geranium viscosissimum—Sticky geranium
Geum macrophyllum—Avens
Gilia aggregata—Scarlet gilia
Godetia amoena—Farewell-to-spring
Goodyera oblongifolia—Rattlesnake plantain
Habenaria dilatata—Boreal bog orchid
Haplopappus hallii—Hesperodoria
Helianthella uniflora—False sunflower
Heuchera spp.—Alum root
Hieracium spp.—Hawkweed
Holodiscus spp.—Ocean spray
Horkelia fusca—Dusky horkelia
Hulsea algida—Alpine hulsea
Hulsea nana—Dwarf hulsea
Hydrophyllum tenuipes—Waterleaf
Hypericum anagalloides—Tinker's penny
Hypopitys latisquama—Broad-leaved pinesap
Iris missouriensis—Western iris
Juniperus communis—Dwarf juniper
Juniperus occidentalis—Western juniper
Juniperus scopulorum—Rocky mountain juniper
Kalmia polifolia—Pale laurel
Kelloggia galioides—Kelloggia
Koeleria cristata—June grass
Ledum spp.—Labrador tea
Lathyrus polyphyllus—Leafy pea
Leptarrhena pyrolaeflora—False saxifrage
Leptodactylon pungens—Granite gilia
Lewisia columbiana rupicola—Columbia lewisia
Linanthus bolanderi—Bolander's linanthus
Linnaea borealis—Twinflower
Listera convallarioides—Broad-lipped twayblade
Listera cordata—Heart-leaved twayblade
Lithospermum ruderale—Western gromwell
Lomatium spp.—Desert parsley
Lonicera ciliosa—Orange honeysuckle
Lonicera interrupta—Chaparral honeysuckle
Lonicera involucrata—Black twinberry
Luetkea pectinata—Luetkea
Lupinus spp.—Lupine
Lysichitum americanum—Skunk cabbage
Mahonia spp.—Oregon grape
Maianthemum dilatatum—False lily-of-the-valley
Mentzelia albicaulis—White-stemmed mentzelia
Mentzelia laevicaulis parviflora—Great mentzelia
Menziesia ferruginea—Rustyleaf
Mertensia spp.—Lungwort
Micropus californicus—Cotton weed
Microseris alpestris—Microseris
Mimulus nanus—Purple monkey flower
Mitella spp.—Mitrewort
Monardella villosa—Coyote mint
Monotropa uniflora—Indian pipe
Montia parvifolia flagellaris—Miner's lettuce
Montia siberica—Spring beauty
Myrica californica—Western wax myrtle
Myrica gale—Sweet gale
Nemophila parviflora—Nemophila
Opuntia fragilis—Prickly pear
Orobanche fasciculata—Broom-rape
Orthocarpus attenuatus—Owl's clover
Osmaronia cerasiformis—Indian plum
Osmorhiza chilensis—Sweet cicely
Oxalis oregana—Wood sorrel
Oxyria digyna—Mountain sorrel
Pachystima myrsinites—Oregon boxwood
Paeonia brownii—Western peony
Pectocarya pusilla—Pectocarya
Pedicularis groenlandica—Elephant's head
Penstemon spp.—Beard-tongue
Petasites spp.—Coltsfoot
Phacelia spp.—Phacelia
Phleum alpinum—Mountain timothy
Phlox diffusa longistylis—Spreading phlox
Phlox hoodii—Gray phlox
Phyllodoce empetriformis—Rose heath
Phyllodoce glanduliflora—White heath
Physocarpus capitatus—Ninebark
Picea engelmannii—Engelmann spruce
Picea sitchensis—Sitka spruce
Pinus albicaulis—White bark pine
Pinus contorta—Beach pine, lodgepole pine
Pinus jeffreyi—Jeffrey pine
Pinus monticola—Western white pine
Pinus ponderosa—Western yellow or ponderosa pine
Plagiobothrys nothofulvus—Popcorn flower
Pleuricospora fimbriolata—Pinesap

Poa secunda—Bluegrass
Polemonium elegans—Slender polemonium
Polemonium viscosum—Skunk polemonium
Polygonum bistortoides—Mountain meadow knotweed
Polygonum newberryi—Newberry's knotweed
Polygonum phytolaccaefolium—Alpine knotweed
Polypodium vulgare columbianum—Licorice fern
Polystichum munitum—Western sword fern
Populus tremuloides—Quaking aspen
Populus trichocarpa—Poplar
Prunus emarginata—Bitter cherry
Prunus virginiana—Choke cherry
Pseudotsuga menziesii—Douglas fir
Pterospora andromedea—Pinedrops
Purshia tridentata—Bitter brush, antelope brush
Pyrola spp.—Wintergreen
Quercus chrysolepis—Canyon oak
Quercus garryana—Garry oak, Oregon oak
Quercus vaccinifolia—Huckleberry oak
Ranunculus spp.—Buttercup
Rhamnus californica—Coffee berry
Rhamnus crocea—Buckthorn
Rhamnus purshiana—Cascara
Rhododendron albiflorum—White-flowered rhododendron
Rhododendron macrophyllum—Rhododendron, rose bay
Rhododendron occidentale—Western azalea
Rhus diversiloba—Poison oak
Rhus glabra—Western sumac
Rhus radicans—Poison ivy
Rhus toxicodendron—Poison ivy
Rhus trilobata—Squaw bush
Ribes cereum—Squaw currant
Ribes viscosissimum—Sticky currant
Rosa spp.—Wild rose
Rubus lasiococcus—Dwarf bramble
Rubus nivalis—Snow bramble
Rubus parviflorus—Thimble berry
Rubus pedatus—Strawberry dwarf bramble
Rubus spectabilis—Salmon berry
Rudbeckia occidentalis—Western rudbeckia
Salix hookeriana—Hooker's willow
Sambucus glauca—Blue elderberry
Sanicula graveolens—Snakeroot
Satureja douglassii—Yerba buena
Saxifraga bronchialis—Matted saxifrage
Saxifraga caespitosa—Tufted saxifrage
Saxifraga ferruginea—Rusty saxifrage
Saxifraga oppositifolia—Purple saxifrage
Saxifraga punctata—Brook saxifrage
Saxifraga rudifula—Red-woolly saxifrage
Saxifraga tolmiei—Tolmie's saxifrage
Senecio canus—Gray senecio
Senecio fastigiatus—Clustered senecio
Senecio triangularis—Spear-headed senecio
Shepherdia canadensis—Buffalo berry
Sibbaldia procumbens—Sibbaldia
Sidalcia asprella—Harsh sidalcia
Sieversia ciliata—Prairie smoke
Silene douglasii—Campion
Sisyrinchium douglasii—Grass widow
Smilacina spp.—False Solomon's seal
Smilax californica—California smilax
Spiranthes romanzoffianum—Ladies' tresses
Sporobolus spp.—Dropseed
Stachys spp.—Hedge nettle
Stipa columbianus—Subalpine stipa
Stipa comata—Needle-and-thread grass
Suksdorfia violacea—Suksdorfia.
Sullivantia oregana—Oregon sullivantia
Symphoricarpos albus—Snowberry
Synthyris missurica—Western mountain syntheris
Synthyris reniformis—Syntheris
Synthyris schizantha—Fringed syntheris
Synthyris stellata—Columbia syntheris
Tellima grandiflora—Fringe cup
Thalictrum hexandra—Meadow rue
Thuja plicata—Western red cedar
Thysanocarpus radians—Lace pod
Tiarella unifoliata—Coolwort
Tolmiea menziesii—Bristle-flower
Tonella tenella—Small-flowered tonella
Townsendia florifer—Showy townsendia
Trautvetteria grandis—False bugbane
Trichostema lanceolatum—Vinegar weed
Trientalis spp.—Starflower
Trillium spp.—Trillium, wake-robin
Tsuga heterophylla—Western hemlock
Tsuga mertensiana—Mountain hemlock
Umbellularia californica—California laurel
Urtica spp.—Nettle
Vaccinium caespitosum—Dwarf huckleberry
Vaccinium deliciosum—Blue-leaved huckleberry
Vaccinium membranaceum—Thin-leaf huckleberry
Vaccinium occidentale—Western huckleberry
Vaccinium ovalifolium—Oval-leaved huckleberry
Vaccinium ovatum—Shot huckleberry
Vaccinium parvifolium—Red huckleberry
Vaccinium scoparium—Small-leaved huckleberry
Vaccinium uliginosum—Blueberry, bog huckleberry
Veratrum viride—Green false hellebore
Vicia americana—California vetch
Viola adunca—Western long-spurred violet
Viola glabella—Yellow violet
Viola sempervirens orbiculata—Evergreen violet
Viola sheltonii—Shelton's violet
Vitis californica—Western wild grape
Whipplea modesta—Yerba de selva, whipple vine
Wyethia amplexicaulis—Dwarf sunflower
Xerophyllum tenax—Bear grass, squaw grass
Zygadenus venenosus—Death camas

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