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The Biogeography of Oregon White Oak (*Quercus garryana*) in Central Oregon

Robert Allen Voeks
Portland State University

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AN ABSTRACT OF THE THESIS OF Robert Allen Voeks for the Master of
Science in Geography presented April, 1981.

Title: The Biogeography of Oregon White Oak (Quercus garryana)
in Central Oregon.

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

Larry Price, Chairman

Clarke Brooke

Robert Tinnin

ABSTRACT

Oregon white oak (Quercus garryana) is distributed along a north-south swath from British Columbia to central California, bounded on the west by the Coast Range and on the east by the Sierra/Cascade cordillera. It departs from this linear path near latitude 46°N, where it passes east through the Columbia River Gorge into central Oregon and Washington. Here it occupies a distinct eastern Cascade foothill zone between Douglas fir/ponderosa pine associations and juniper/sagebrush/grassland habitats. This thesis examines Q. garryana's range extension into this portion of north-central Oregon.

The study proceeded as follows: The distribution of Q. garryana was mapped through field reconnaissance. Annual rings from fifteen trees were counted in order to establish age versus trunk diameter ratios. This greatly simplified the dating of trees. Transects were then run through individual groves to determine population age structures. These age structures, along with Q. garryana's distribution patterns, were graphically compared with historic temperature, precipitation, and growing season data. The effect of livestock grazing on oak reproduction was examined. Potential vagility of the species was evaluated by estimating the potential for acorn dispersion by airfall, streams, vertebrates, and the human (aboriginal) population. Finally, pollen evidence was scrutinized in conjunction with acorn dispersal rates in order to determine the longer term history of Q. garryana in this portion of its range.

The age structure results indicate that Q. garryana is maintaining a stable population equilibrium: While it is neither expanding nor contracting its range, it is reproducing at an adequate pace to maintain its present range and numbers. Further, the data suggest that oak is a climax species in central Oregon, occupying an exclusive environment between the more mesic coniferous associations and the more xeric grassland/juniper/sagebrush communities.

Q. garryana's reproductive equilibrium at individual sites is largely a function of historic precipitation fluctuations. Thus, the 1930s drought favored increased oak reproduction at its moist (coniferous) frontier but decreased reproduction near its xeric border. Particularly moist spells contributed to a reversal of this trend. Q. garryana thus appears to be in constant flux between upslope or downslope migration in response to moisture availability.

Sites which are heavily grazed by livestock lack reproductive equilibrium; in some cases oak has not propagated in fifty years. Nevertheless, oak seedlings appear to be capable of quickly repopulating heavily grazed areas when the cattle are removed. Similar soil disturbances such as periodic ground fires, on the other hand, may play a beneficial role in oak seedling success through elimination of the thick organic mat.

In increasing order of importance, Douglas' squirrels (Tamiasciurus douglassi), Lewis' woodpeckers (Asyndesmus lewis), and Steller's jays (Cyanocitta stelleri) were found to be effective agents of acorn dispersal. Stellers jays, which usually carry

acorns upslope into nearby coniferous areas, contribute to the highest potential oak migration rate of 20 km per 1000 years. Lewis' woodpeckers, which often cache acorns in drier downslope areas, provide a potential population extension of 4 km per 1000 years. Indians were largely discounted as dispersers of viable acorns due to their practice of roasting acorns prior to transport. The action of Q. garryana acorns falling and rolling away from the seed tree is not an effective means of acorn dispersal. And due to their heavy weight, acorns are probably not transported by streams, although turbulent flood conditions might allow this to occur.

By applying the maximum calculated oak migration rate to the chronology of oak's presence (as established by pollen evidence) in the Pacific Northwest, it is shown that rather than migrating to its present position in post-Pleistocene times, Q. garryana must have survived Ice Age conditions at sporadic locations throughout the Willamette-Puget Trough.

Finally, Q. garryana's anomalous presence east of the Cascades is accounted for by either post-Missoula Flood migration from the Willamette Valley through the Columbia River Gorge or by its uninterrupted presence in central Oregon from previous interglacials or even earlier.

THE BIOGEOGRAPHY OF OREGON WHITE OAK (Quercus
garryana) IN CENTRAL OREGON

by

ROBERT ALLEN VOEKS

A thesis submitted in partial fulfillment of the
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TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

The members of the Committee approve the thesis of
Robert Allen Voeks presented April, 1981.

Larry Price, Chairman

Clarke Brooke

Robert Tinnin

APPROVED

Richard Lycan, Head, Department of Geography

Stanley E. Rauch, Dean, Graduate Studies and Research

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CHAPTER I

INTRODUCTION

Oregon white oak (Quercus garryana) occurs in the Pacific Northwest between the Cascade Mountains and the Coast Range, extending from latitude $49^{\circ}30'N$ in British Columbia south into central California at latitude $36^{\circ}N$. Its north-south distribution is interrupted by a small range extension eastward along the Columbia River Gorge into the semi-arid steppe region of central Oregon and Washington. The following thesis is an examination of Oregon white oak's location and status in central Oregon.

Plant geography involves the description and interpretation of plant distributions. Plants or their associations are depicted on maps and evaluated through various methods in order to establish their relation to the physical and biotic environment. An array of methods may be employed, including: climatic evaluation, field ecological and taxonomic study, pollen and fossil research, historical reference, cultural tradition and legend, and other methods. Through integration of these data, meaningful deductions about floral distribution and dynamics can be made.

Oregon white oak is the only member of the genus Quercus occurring north of southern Oregon in the western United States. It grows primarily in the deep alluvial soils, level to gently hilly terrain, and in a west coast marine climate characterized by cool, moist winters and warm, dry summers. Oak woodlands form the ecotone between the Douglas fir and grassland associations. The native grasslands, however, have been extirpated by agricultural expansion. Oregon white oak is like-

wise being replaced through human intervention, as well as by overtopping by Douglas fir, which has been invading oak woodlands since the 1850s.

The extension of oak through the Columbia River Gorge into central Oregon and Washington is a deviation from the normal conditions just depicted. The vegetation and soils change radically in a short distance from west to east in response to the transition from a west coast marine to a continental climatic regime characterized by increasing aridity and seasonal temperature extremes. The vegetation grades from coniferous forest to oak woodland to sagebrush-juniper-grasslands. The soils likewise change from deep alluvial to thin, desert soils.

It can be seen that the extension of Oregon white oak's range into central Oregon presents a unique biogeographic situation whereby a plant's distribution can be studied with respect to radically changing geographic factors in a small area. Processes and stages observed within this limited area may then be cautiously applied to Q. garryana's entire distribution.

Several methods of enquiry have been used in this study. Oak populations were field mapped on foot and by car on a 1:125000 topographic map. Age-structures were constructed for several oak stands and compared to population equilibrium curves. Variations from the curves, which indicate a fluctuating rate of regeneration, were dated and compared to the area's temperature and precipitation data for possible cause and effect relationships. Sites whose age-structures failed to correlate with climatic data were considered in light of livestock grazing pressure.

Probable modes of acorn dispersal resulting in oak population diffusion were also considered. Acorn transport away from the parent tree

by means of gravity, streams and wildlife were measured or estimated. The records of early explorers and settlers were consulted in order to determine the role of native Indians in the transport of acorns. The potential rates of oak population migration as calculated from these results were considered in respect to post-Pleistocene climatic change and oak's chronological position in the pollen record. From these data, the routes and timing of Oregon white oak's migration into the Willamette-Puget Trough and central Oregon are proposed.

CHAPTER II

LITERATURE REVIEW

PREVIOUS DISTRIBUTION OF OREGON WHITE OAK

The genus Quercus is represented in western North America by fossil and pollen evidence. It first appeared in Eocene (36-53 million years before present) floral assemblages characterized by subtropical families such as *Palmae* and *Moraceae*. As the climate cooled during the Oligocene (25-36 m.y.b.p.), subtropical taxa such as Metasequoia, Juglans, Betula, and the ancient relatives of Quercus migrated southward into what is now Montana (Axelrod, 1976; Chaney, 1948; Detling, 1968; Wolfe, 1969). During these epochs, the Pacific Northwest was dominated by shallow inland seas. With the dawn of the Miocene (7-25 m.y.b.p.), terrestrial environments supplanted the seas and the climate cooled and dried. Species diversity increased and later decreased during this epoch; Quercus was represented by at least 10 species (Wolfe, 1969). Notable among these taxa was Quercus pseudolyrata, a close relative of Q. kelloggii, which now occurs in southern Oregon.

During the Pliocene (2-7 m.y.b.p.), tectonic processes recontoured the western landscape. The leeward climates of Oregon, Washington, California, and Nevada were slowly desiccated by the emergence of the Cascade Mountains and the Sierra Nevada. The climate of Pliocene western America began to resemble present conditions (Wolfe, 1969).

The Deschutes River Pliocene flora, as reconstructed from locations near the present study site, reveal similar vegetation types to those found there today. Close relatives of Populus tricarpa, P.

tremuloides, and Acer negundo are well represented by fossils. Quercus fossils are not present in this formation but are recorded in the nearby Dalles formation. These fossils, however, are considered unlikely ancestors of Quercus garryana (Chaney, 1944).

The vegetation changes during the Quaternary Period (2 m.y.b.p. to present) have been considered in light of local pollen deposits. Unfortunately, this evidence is confined to the present interglacial period, reaching back little further than 15,000 years. Pollen profiles evaluated by Hansen (1938, 1940; 1941a, b; 1942; 1943a, b, c; 1947) and Heusser (1969; 1964) for the Willamette-Puget Trough reveal the following post-glacial succession: 1) early invasion by lodgepole pine (Pinus contorta) along with large numbers of Sitka spruce (Picea sitchensis) and fir (Abies ssp); 2) gradual replacement by Douglas fir (Pseudotsuga menziesii); encroachment by more xeric species including Oregon white oak and various grasses (Heusser, 1960); and re-emergent dominance by Douglas fir. This species is presently the numerical dominant, while ceding on cooler and moister sites to western hemlock (Tsuga heterophylla) and in drier areas to Oregon white oak.

The vegetational history east of the Cascades is more problematic, as conditions are less than optimal for pollen profile development. Pollen evidence from eastern Washington reveals oscillations between the sagebrush (Artemisia, ssp), western juniper (Juniperus occidentalis) and ponderosa pine (Pinus ponderosa) associations. Early in the post-glacial, lodgepole pine dominated much of the area. As the climate warmed, ponderosa pine largely replaced lodgepole pine. At the maximum of xerix conditions during the Hypsitherm (Deevey, 1957) grasses and chenopods (Chenopodiaceae) increased relative to ponderosa pine. Post-

Hypsithermal climatic cooling has led to an increase in **p**onderosa pine east of the Cascades (Hansen, 1947).

The Hypsitherm figures prominently in the vegetational history of the Pacific Northwest, particularly in regards to Q. garryana. Detling (1961) set limits on the temperature and precipitation changes necessary to account for the multiplication of xeric species during this period, including: a decrease of 230 mm of precipitation per year; a rise in the winter mean temperature of 1.0°C ; and an increase in summer mean temperatures of at least 5.0°C .

Oregon white oak is thought to have penetrated central Oregon during the Hypsitherm. Detling (1958, 1961, 1966, 1968) discussed the relict status of both boreal and chaparral species at various Oregon locations. He located several pockets of endemic boreal flora at low elevations which he attributed to down-slope migration during a glacial advance and later retreat upslope during a warmer inter-glacial, thus stranding disjunct islands of flora. He further identified several floral associates of the California-Oregon chaparral formation (including Oregon white oak) at scattered sites throughout the Northwest; he considered these to be xeric island relicts of the Hypsithermal vegetation advance. Thus, the northern California chaparral formation migrated into the Klamath Basin during the climatic maximum, followed the Willamette-Puget Trough north and

...under less xeric conditions, the Garry Oak Woodland invaded the area [Columbia River Gorge] east from the west. (Detling, 1961, p. 356)

Detling bases this assumption on his conclusion that oak could not have tolerated Pleistocene conditions north of the Klamath highlands and thus must have migrated to its present position after the last glacial ad-

vance (Detling, 1968). Ross (1975), however, implies that oak may have weathered Ice Age conditions in favorable microhabitats.

Hickman (1968) also evaluated disjunct xeric species in the Willamette Valley and considered two alternatives to account for their distribution: they were either vanguards of an expanding population or relicts of a retreating floral assemblage. Considering the continuity of species composition between several disjunct sites, Hickman agreed with Detling's hypothesis of Hypsithermal relicts.

PRESENT DISTRIBUTION OF OREGON WHITE OAK

Oregon white oak is presently distributed in a north-south swath through the states of California, Oregon, Washington, and in British Columbia (Figure 1). It is found tucked between the Cascade Mountains and the Coast Range. In California, it occurs at isolated sites as far south as Tulare County and in the Santa Cruz Mountains north of Monterey Bay. Oregon white oak becomes a conspicuous member of the oak woodland community in northern California. In Oregon and Washington, it follows the Willamette-Puget Trough north to Vancouver Island, deviating from this linear distribution in three places: 1) on the Chetko River on the seaward side of the Siskiyou Mountains; 2) in British Columbia along the Fraser River; and 3) in Oregon and Washington on both sides of the Columbia River Gorge and into central Oregon and Washington (USDA, 1965). The eastern extension of oak stops at the confluence of the Deschutes River, just as it did in 1804, as noted by the explorers Lewis and Clark (Thwaites, 1904).

Figure 1. The distribution of *Quercus garryana* (U.S.D.A, 1965)

ECOLOGICAL RELATIONSHIPS

The ecology of the genus Quercus involves the interaction of plant growth and reproduction relative to a host of factors, including: climate, fire, soil, grazing, interspecific competition, wood production, and acorn utilization. Since little work has been done on Q. garryana specifically, much of the following information is inferred from studies of closely related species.

Oak is ultimately dependent upon carbohydrate production and absorption of organic and inorganic nutrients. Water is the medium of transport both from soil to root and from root throughout the tree, as well as being necessary in the photosynthetic process. Critical temperatures must be maintained at the root and stem levels to ensure favorable metabolism. Oak maintenance is thus essentially a function of moisture, temperature and insolation (Kozlowski, 1962).

Little is known about Oregon white oak's climatic requirements aside from those interpreted from its current range. Comparison of its distribution to Koppen's climatic regions places oak largely in a marine west coast regime, with cool wet winters and warm summers with a distinct summer drought (Visher, 1954). Its range is delimited by a 600-1000 mm mean annual isohyet, although its distribution more closely correlates with a 100-200 mm April through September growing season isohyet. Low temperatures, snowfall, and early or late frosts are apparently not limiting to Q. garryana's growth or reproduction (USDA, 1965).

Oregon white oak may be a successional species in the Willamette Valley, able to historically fend off invasion by its rival Douglas fir only through its tolerance of fire. Prior to white settlement, the Valley vegetation graded from riparian forests to prairies punctuated

by broad, savanna-form oaks to oak openings and Douglas fir forests in the foothills. As a result of grass fires - set by Indians to improve deer hunting - Douglas fir was excluded from much of the valley floor and immediate hinterlands. Oak, however, due to its fire tolerance and coppice sprouting ability, withstood these low intensity fires at scattered locations. With the cessation of burning after 1850, oak and Douglas fir quickly invaded oak openings and prairies not given over to cultivation. Douglas fir has subsequently overtopped oak in many of these areas (Habeck, 1961; Johannessen, et al., 1971; Sprague, 1946); thus oak's widespread presence in the Willamette Valley may be considered a cultural phenomena related to periodic burning.

Oak regeneration is most sensitive to atmospheric conditions during seed maturation and germination. Acorns mature in one season, germinating in September or October. The acorn contains carbohydrates and water for the initial radicle growth, although additional water is needed immediately after the radicle penetrates the soil (Korstian, 1927). Leaf litter or some other protection from dessication is imperative for the young acorn. Under experimental conditions, it was found that Quercus alba, an eastern white oak, had the following survival rates when planted at various depths: 37% survival at 10 cm; 57% survival at 5 cm; 73% survival at 1.5 cm; and 5% survival on the bare soil (Korstian, 1927). Further, since Q. garryana germinates in the autumn and young radicles are susceptible to frost damage, early frost could be damaging, especially under the more continental climatic conditions of the study site.

The soils that support oak stands vary greatly. Although soil moisture is a necessity, under saturated conditions oxygen deficiency

may be a limiting factor (Kramer, 1960). Oregon white oak grows on several soil types, from stoney and gravelly to dense clayey soils (USDA, 1965). In the Willamette Valley, Thilenius (1968) found oak populations ranging from well-drained acidic illuviated soils to poorly drained clayey soils in the valley bottoms.

Plant consumption and the accompanying soil disturbance by large domestic herbivores is an important factor in tree reproduction. Weaver (1950) felt that grazing by domestic livestock indirectly increased ponderosa pine seedling survival through soil disturbance. Oregon white oak may also benefit from ungulate grazing:

As most of these sites are being grazed, competition from other species is lessened and the acorns from the Quercus trees are able to germinate and seedlings can grow...there are generally enough young Quercus trees on these sites for replacement. (Thilenius, 1964, p. 115)

In Wisconsin, however, grazing by livestock was found to compact soils, as well as to reduce the nitrogen and phosphorous levels (Steinbrenner, 1951).

Shoot consumption is deleterious to red and white oak reproduction in the Midwest and the eastern United States (Steinbrenner, 1951). Den Uhl (1954) found that while oak leaves and buds are unpalatable to cattle, they will readily eat them when other forage is not available. He also found over-grazing to have a potentially irreversible impact on oak forests. Holland (1976) noted the lack of reproduction in a California white oak species, Quercus douglasii, and correlated this trend with heavy grazing of young shoots by cattle and sheep. Griffin (1977) summarized the lack of regeneration in California white oaks relative to live oaks and suggested differential palatability of these species to livestock and perhaps pocket gophers. Regardless, oak shoots contain

little nutritional value (Smith, 1957) and Hall (1956) found little forage available in Q. garryana woodlots.

Over-grazing by sheep and cattle has been widespread in the Pacific Northwest since the middle to late 19th century (Galbraith, 1971). Due to the elimination of open range by the Bureau of Land Management, this problem has considerably decreased since the early 20th century (Cholis, 1952). Cattle are known to consume oak leaves - heavy snowfall in 1861-62 forced farmers to cut down many oaks in the Willamette Valley as fodder for livestock (Thilenius, 1964) - but nothing is known about the direct effect of grazing on Q. garryana regeneration.

Acorns are readily consumed by mammals, birds, and insects. The following animals eat Q. garryana acorns: western gray squirrel, Douglas' squirrel, racoon, black bear, porcupine, deer, elk, Steller's jay, acorn woodpecker, Lewis' woodpecker, scrub jay, common flicker, and wild turkey (Bakker, 1971; Horn, 1977; Ingles, 1965; Larrison, 1976).

Korstian (1927) found that 90-100% of a year's mast production may be eaten by wildlife. He also observed few examples of acorns being stored and not later recovered. Verme (1953) noted that acorn consumption by wildlife had a deleterious effect on oak reproduction.

Oregon white oak leaves and bark are attacked by several insect species, including the western oak looper (Lambdina fiscellaria somnaria), several tent caterpillars, and numerous gall wasps. None, however, are considered serious pests (USDA, 1965). Verme (1953) noted a 78-100% rate of insect infestation in acorns.

Oregon white oak is not a valuable forest product. In pioneer days, it was fashioned into wagon rims, fenceposts, chairs, doors, and

used for general millwork (Gibson, 1913; Hanzlik, 1928). It is currently cut for firewood (Hall, 1956).

Another factor in plant ecology is vagility. The dynamics of the environment require that even sessile species periodically migrate or perish. And rooted organisms, which produce progeny only at their doorstep, invite intense intraspecific competition (Janzen, 1970). Hence selective pressures operate for effective seed dispersal mechanisms. Organisms which produce microscopic spores in large quantities have little problem distributing their progeny hither and thither, and are often broadly distributed, e.g. certain fungi (Elton, 1958). Acorns, while large and heavy, have several potentials of dispersal, including: falling off the tree and bouncing or rolling downslope; dropping in a stream and floating to a safe site; or being carried by an animal to a safe location. The first possibility only occurs on slopes. Verme (1953) noted that the majority of acorns are produced around the periphery of the crown, thus ensuring that they will fall the maximum distance from the parent tree. It would be of further advantage if open crown or border trees produced more seeds than interior trees. While this does occur in some species (Kramer, 1960), it is not always the case in oaks (Verme, 1953).

Transport by flotation is probably not very important. Crocker (1953) noted that acorns have a low longevity; while some can withstand prolonged soaking, most die quickly (Kramer, 1960). In addition, white oak acorns do not float well due to a high specific gravity (Korstian, 1927). Ridley (1930), however, believes that acorn flotation is a viable means of dispersal in rivers, but not in the ocean.

Animal transport is probably the most effective mode of acorn

dispersal. The nut is selectively carried for some distance and deposited in a similar habitat which is frequently conducive to seed germination (Cruden, 1966). In North Carolina, animals tend to carry viable rather than infested acorns. As noted, however, this value may be negated by animals with a high rate of seed retrieval (Koristan, 1927). In California, scrub jays are important vectors of acorn dispersal:

The Scrub Jay...taking the role of the competent nurseryman as he places the acorns in the substrate most suitable for their germination, mineral soil under duff. (Bakker, 1971, p. 118).

Squirrels also place acorns in safe sites:

Gray squirrels are important and beneficial animals in reforestation in the Valley Oak Association... (Ingles, 1956, p. 157).

The role of humans in the distribution of acorns is not documented. The high correlation in eastern Oregon and Washington of Indian camps located within oak stands, however, has been noted as a possible cause and effect relationship (Ross, 1975).

CHAPTER III

SITE DESCRIPTION

The study is limited to Wasco and Hood River Counties in Oregon (Figure 2) and is found within "The Dalles" United States Geological Survey quadrangle. The oak population grades from the mesic plant associations of the Columbia River Gorge east to the borders of the central Oregon desert. Either or both sides of the Columbia River could have been chosen for this study; the Oregon side was selected for convenience.

GEOLOGY

The study area is found at the junction of the Deschutes-Umatilla Plateau and the Cascade Mountains. It is dominated by 1600 m deep Miocene-Pliocene flows of Columbia River basalt which has weathered little in this arid climate (McKee, 1972). Overlying these basalt layers are Pliocene-aged alluvial deposits of silt, sandstone and conglomerates. These occur linearly along the Columbia River, occurring sporadically throughout the study area. At the western edge of the Dalles Formation occur the recent (Pliocene-Holocene) Cascade lavas, which consist of volcanic flows and a single cinder cone within the study area (Baldwin, 1959; Newcomb, 1969).

CLIMATE

The climate changes dramatically as one passes through the Columbia River Gorge from west to east. Annual precipitation plunges from over 1900 mm in the Cascades to less than 240 mm at sites in Wasco County.

Figure 2. The distribution of Oregon white oak in north-central Oregon. The numbers represent the location of study sites (Table 1).

The rainfall regime moves from a definite winter maximum to a more uniform seasonal precipitation regime. Temperatures can be intensely hot in the summer and bitterly cold in the winter. Basically, the climatic shift is from a west coast marine climate to a more continental climatic regime.

VEGETATION

Detling (1958, 1960) studied the vegetation associations within the Columbia River Gorge. He found that the north facing (Oregon) side of the Gorge changes from a mesic, coniferous forest on the western slopes of the Cascades to a xeric vegetation association in the east. The mesic association includes such dominants as Douglas fir (Pseudotsuga menziesii), western hemlock (Tsuga heterophylla) and western red cedar (Thuja plicata). The eastern assemblage dominants consist of western juniper (Juniperus occidentalis), big sagebrush (Artemisia tridentata) and many species of native and introduced grasses, such as blue-bunch wheat grass (Agropyron spicatum) and Russian cheatgrass (Bromus tectorum). The Quercus garryana association, including such species as snowberry (Symphoricarpos albus) and poison oak (Rhus diversiloba), is a member of and forms an ecotone between these converging associations (see Figure 3).

LAND USE

The land use of this area has changed considerably since white settlement. Before 1850, the Wasco-Wishram Indians gained their livelihood from salmon fishing and trading along the Columbia River. After their displacement in the 1850s, cattle grazing quickly spread through-

Figure 3. Oregon white oak forms pure stands between Douglas fir/ponderosa pine and sagebrush/juniper/grassland associations.

out eastern Oregon. With the arrival of sheep ranching operations, conflicts over grazing rights inevitably led to range wars. Wheat farming, which was introduced in the 1860s, remained a small contributor to the economy until railroads opened up inexpensive freight transport to Portland in the 1880s. Currently, wheat farming, cattle grazing, and forestry dominate the economic landscape east of the Cascades (Brogan, 1964).

CHAPTER IV

METHODOLOGY

The first step in distribution synthesis is accurate mapping. This information was garnered by driving and walking over much of Wasco and Hood River Counties. Populations of oak were plotted on a 1:125,000 topographic map (Figure 2). Q. garryana stands were found to be sporadically distributed over the area. Thus sites within the designated oak range may be devoid of individual trees.

I attempted to use Soil Conservation Service air photos to map the distribution of oaks. The available scale, however, was too small to discriminate oaks from other deciduous trees.

In order to calculate the age of oak size-classes, fifteen oaks were cored with a hand increment corer*. The cores were inserted into plastic straws, labeled with site characteristics and the tree diameter, later mounted on flat pieces of wood, and finally sanded and coated with linseed oil to bring out the tree rings. Annual secondary xylem additions were counted with the aid of a dissecting microscope.

The age of each tree was then plotted against its diameter on a simple scattergram. The resultant line of positive regression was evaluated for statistical significance. Then, in order to predict the age of tree size-classes and individual trees, inverse predictions - interpreting abscissa points from ordinate points - were calculated, including 95% confidence limits.

*Q. garryana contracts heart rot after an unspecified age, thus rendering tree ring counting impossible, and was found to tenaciously resist penetration by an increment corer.

The size-structures of fifteen sites were determined by line-quadrat analyses. Both pure and mixed stands of Oregon white oak and conifers were surveyed. The starting point for each transect was randomly chosen using a table of random numbers or numbered slips of paper picked from a hat. If the population was small, the line intersecting the greatest part of the stand was chosen. In one particularly small stand, each tree was measured. By cueing on a distant object as a reference point, a fairly straight line could be maintained with a Brunton Compass. Circular quadrats were spaced every 10 m along this line. Stakes with a 3-5 m length of attached rope were inserted into the ground. The rope was stretched from the stake and walked around the periphery of its length, thus enclosing a 6-10 m diameter circle. Each tree was measured with a dbh (diameter at breast height) tape which converted the circumference to a diameter-in-centimeters figure. Any tree trunk that touched the circulated rope was counted in; consequently, density estimates should run slightly high. Dead trees and stumps were not counted.

The afore-mentioned method was used throughout the study, with the exception of one site which was surveyed using a grid quadrat method (see site 3). In this case, 200 m were marked off in 20 m intervals in a north-south direction; then 100 m in 10 m intervals in an east-west direction. Using a table of random numbers, stakes were placed at the intersection of selected grid lines. Circular quadrats were then applied and the size-structure data were gathered.

Trunk measurements were made at 0.7 m up from the ground. The decision as to whether the growth represented one or more trees was sometimes arbitrary due to oak's habit of separating into 2 or more

trunks. Trees less than 2 cm in diameter were counted as seedlings, with no reflection of genesis intended (often, regeneration is stump rather than seed generated).

Historic climatic data were extracted from the U.S. Climatological Register for 4 stations in the study area. Temperature and precipitation figures are plotted as running mean fluctuations about the mean (0) line for comparison to the oak size-structures.

Plant identification follows Hitchcock and Cronquist's Flora of the Pacific Northwest. Flowering had passed in most species, making positive identification difficult. Thus, only easily identified plants were recorded (see Appendix I).

In order to measure the distances traveled by falling acorns, an oak was selected in November 1977 and as many living acorns as could be reached were painted with silver nitrate (AgNO_3). This compound, however, did not visibly stain the acorns. Another tree was chosen and its acorns were painted with red spray paint. The following spring, the painted acorns were relocated and mapped relative to the parent tree.

In order to determine the effectiveness of animals as vectors of seed dispersal, the distances acorns were carried before being dropped, stored, or eaten were roughly calculated for birds and mammals. Potential rates of oak population migration were estimated from these results. A cursory bird survey was also conducted (see Appendix II).

CHAPTER V

OREGON WHITE OAK'S POPULATION STATUS

INTRODUCTION

In natural populations, more organisms are produced than can be expected to reach maturity. Annual mast production in oaks is thus quickly decimated by physical intolerance and predation. As a consequence, the number of individuals surviving from one age-class to the next decreases at a fairly constant rate. This phenomena is visually demonstrated by separating the members of a population into successive age-classes and graphing the data as a simple regression. Such a representation will conform to a gently sloping "reverse J curve" if the population is in a state of reproductive equilibrium. If reproduction is relatively high or low for a period, however, the regression curve should exhibit an aberration from the norm. It should be possible, then, to estimate the reproductive status of a population and, further, where gross reproductive changes are evident, to identify the chief environmental factors responsible (Hett, 1971; Hett and Louks, 1971; Johnson and Risser, 1975; Leak, 1965).

The reproductive equilibrium method of population evaluation must be applied cautiously. Only climax species will conform to a reverse J curve; a seral species such as Douglas fir, which cannot reproduce under its own canopy, will not conform to this model. Oregon white oak will be temporarily treated as a climax species in the study area, although it may be a successional species in other parts of its range. Its climax status will be further considered in light of the size-structure results.

Another potential problem is that the negative regression slope will naturally vary between different species. Whereas organisms with short life spans require copious annual reproduction in order to survive, long-lived species may be adapted to less frequent and abundant productions of progeny. Thus, the evaluation of size-structure anomalies in a long-lived tree like Q. garryana must be limited to lengthy or radical perturbations from the norm.

Finally, subtle accumulative changes in the environment, while increasingly depressing reproduction in an organism, may not be revealed in a size-structure evaluation. Since there is no standard regression for comparison, populations on the road to extirpation may appear to be healthy.

OAK SIZE-STRUCTURE DATA

In order to discern the reproductive status of the central Oregon Q. garryana population, circular quadrats on line transects were used to sample tree diameters at fifteen sites. The site characteristics are recorded in Table I, the tree diameters divided into size-classes in Table II, and graphed in Figures 4-25.

DISCUSSION

Oregon white oak's population status appears to be blurred rather than clarified by the greatly varying size-structure data. This is because the results include data from both the arid and moist limits of oak's range. Thus, changing environmental conditions, which elicit opposite regeneration responses from sites at the Douglas fir ecotone and the juniper/sagebrush ecotone, are expected to produce contrasting

TABLE I
FEATURES OF STUDY SITES

Site #	Location	Elevation (m)	Slope Aspect and Inclination	Dominant Vegetation	Evidence of fire	Evidence of live- stock grazing	Acorn Sprout- ing	Coppice Sprout- ing
1	McCubbins Gulch	900	N facing - 4° S facing - 14°	N facing - Douglas fir, ponderosa pine S facing - oak, bit-terbrush, manzanita	Yes	No	Low	High
2	White River Canyon	750	N facing - not noted S facing - 33°	N facing - Douglas fir S facing - oak, grasses Level area - oak, pine	No	No	None	High
3	Laughlin Hills	800	Level	oak, incense cedar, pine, Douglas fir, manzanita	Yes	No	Low	High
4	Oak Springs	500	NW facing - 30°	oak, juniper, birch, sagebrush	No	Yes	None	None
5	Butler Canyon	550	N facing - not noted S facing - 25°	oak, snowberry, grasses	No	No	Low	High
6	Badger Creek	550	N facing - 15° S facing - 25°	N facing - oak S facing - oak, pine	No	No	None	High
7	Jordan Creek	750	N facing - 12°-27° S facing - 12°	N facing - pine, oak S facing - pine, oak	No	No	Low	High

TABLE I (Continued)

FEATURES OF STUDY SITES

Site #	Location	Elevation (m)	Slope Aspect and Inclination	Dominant Vegetation	Evidence of fire	Evidence of live- stock grazing	Acorn Sprout- ing	Coppice Sprout- ing
8	Oakbrook Canyon(1)	350	Level	oak, sagebrush	No	Yes	None	None
9	Oakbrook Canyon(2)	350	SE facing - 30° NW facing - 33°	oak	No	Yes	None	None
10	Dry Creek	550	Level	oak	No	No	None	None
11	Japanese Hollow	550	Level	oak	Yes	No	None	High
12	The Dalles(1)	200	NE facing - not noted	oak, poison oak	No	No	Low	Low
13	West Fork Mosier Creek	350	E facing - 16°	oak	No	No	Low	High
14	Mosier Creek	700	E facing - 12°	oak	No	No	Low	High
15	The Dalles(2)	250	Level	oak, grasses	No	No	High	Low

Figure 4. *Q. garryana*'s population size-structure at site #1.

Figure 5. *P. menziesii*'s population size-structure at site #1.

Figure 6. *P. ponderosa*'s population size-structure at site #1.

Figure 7. *Q. garryana*'s population size-structure at site #2.

Figure 8. *P. menziesii*'s population size-structure at site #2.

Figure 9. *Q. garryana*'s population size-structure at site #3.

Figure 10. *P. menziesii*'s population size-structure at site #3.

Figure 11. *P. ponderosa*'s population size-structure at site #3.

Figure 12. *Q. garryana*'s population size-structure at site #4.

Figure 13. *Q. garryana*'s population size-structure at site #5.

Figure 14. *Q. garryana*'s population size-structure at site #6.

Figure 15. *P. ponderosa*'s population size-structure at site #6.

Figure 16. *Q. garryana*'s population size-structure at site #7.

Figure 17. *P. ponderosa*'s population size-structure at site #8.

Figure 18. *Q. garryana*'s population size-structure at site #8.

Figure 19. *Q. garryana*'s population size-structure at site #9.

Figure 20. *Q. garryana*'s population size-structure at site #10.

Figure 21. *Q. garryana*'s population size-structure at site #11.

Figure 22. *Q. garryana*'s population size-structure at site #12.

Figure 23. *Q. garryana*'s population size-structure at site #13.

Figure 24. *Q. garryana*'s population size-structure at site #14.

Figure 25. *Q. garryana*'s population size-structure at site #15.

size-structure results.

Field observations revealed that differences in slope aspect were a major factor in oak distribution. Oak populations on south facing slopes, due to reduced effective precipitation and greater temperature variation, reveal very different size-structures than adjacent north facing slopes. In order to later evaluate this factor, the data for sites on north and south facing slopes are separated in Table III and graphed in Figures 26 and 27.

The overall picture of oak's population status is revealed by graphing the summed size-class data for all of the sites (Table III and Figure 28). The size-structure conforms to a reverse J curve; thus Oregon white oak's total central Oregon population is in reproductive equilibrium.

There is no evidence to indicate that oak is expanding its range. In order for this to occur, it is necessary for acorns to be transported to a safe site and germinate beyond oak's present range. No young populations of Q. garryana were located, nor does oak seem to be regenerating by acorns at this time. As noted in Table I, regeneration is being largely accomplished through coppice sprouting, an adaption to stress, especially fire. The causes of this lack of seed regeneration are not immediately evident, as there seems to be sporadically abundant mast production.

There is some indication that oak is being reduced in extent at its arid periphery. Figures 12, 18, and 19 describe disjunct, arid frontier populations exhibiting no recent regeneration. This situation, however, appears to be a by-product of human land use practices rather than environmental change and will be discussed later.

TABLE III:

SIZE-CLASS DATA TOTALS

No. of Indivi- duals:	dbh (cm)														
	0-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75 76-80
North															
Facing Slopes	249	18	37	15	6	2	2	2	0	0	0	0	0	0	0
South															
Facing Slopes	227	18	9	11	7	2	3	2	1	0	1	0	0	0	0
Totals for all Sites	1174	101	88	55	40	31	22	14	6	7	8	0	0	2	1 1

Figure 26. *Q. garryana*'s population size-structure for sites located on north-facing slopes.

Figure 27. *Q. garryana*'s population size-structure for sites located on south-facing slopes.

Figure 28. Summed *Q. garryana* population size-structure results for sites 1-15.

Finally, oak was found to occupy a separate geographic area between the colliding Douglas fir/Ponderosa pine and western juniper/sagebrush/grassland associations. While this ecological zone is made narrow by the rapidly changing environmental conditions resulting from the ascending Cascades, it appears nonetheless distinct. This situation, in addition to oak's relatively stable population structure (Figure 28), qualifies Q. garryana as a climatic climax species within its central Oregon range.

In order to more fully understand Oregon white oak's ecological situation, its distribution and size-structure results will be compared to climatic data in the following chapter. In addition, oak's response to climatic change, as well as the effects of differing slope aspect, will be discussed.

CHAPTER VI

THE EFFECTS OF CLIMATE ON OREGON WHITE OAK

INTRODUCTION

While climate is recognized as the most important factor in plant maintenance and reproduction, separating its effects from those of other variables is a difficult task. Ideally, both experimental and comparative data are used. In the case of long-lived species of little economic value, such as Q. garryana, only the latter types of interpretation are available.

In the following evaluation, Oregon white oak's distribution is superimposed on average frost-free days and isohyet maps in order to reveal climatic limiting factors. Aberrations in the population size-structure are dated using a tree age versus diameter correlation and compared to temperature and precipitation changes for possible causes and effects. And the response to climatic change by oak populations inhabiting north and south-facing slopes are contrasted.

GENERAL CLIMATIC CONSIDERATIONS

The dominant factor defining the rapid vegetation change from the Columbia River Gorge into central Oregon is increasing aridity. As shown in Figures 29-32, the precipitation changes in both quantity and seasonality. The mean annual precipitation drops from 750 mm at Hood River to 350 mm at The Dalles in a short 35 km. And while Hood River receives over 85% of its precipitation in the dormant months between October and March, Madras, which is 100 km to the southeast, receives

only 60% of its moisture during this same period.

The distribution of Oregon white oak is noted to fall between the 625 and 1000 mm mean annual isohyet (U.S.D.A., 1965). Figure 33, however, shows that oak occurs well outside of these limits, from 300-1500 mm of precipitation. While the comparison of these data is useful in determining oak's precipitation requirements, favorable microhabitats, such as provided by drainage water-tables (see Figure 2), natural springs (Oakbrook Canyon and Oak Springs), rocky soils (Mosier Creek), and favorable slope aspects (White River Canyon) contribute to spreading oak out beyond its precipitation limits.

Many plant species are limited by the length of the frost-free season, through flower, fruit, and seedling damage. In order to test this hypothesis on Q. garryana, its distribution is plotted on a map of the annual frost-free season for the study area (Figure 34). Oak is seen to occur in areas varying from over 200 to less than 80 frost-free days. While it is tempting to pin oak's southerly range cessation on this factor, such a conclusion seems overly-ambitious without better knowledge of the exact mechanisms involved.

TEMPERATURE AND PRECIPITATION FLUCTUATIONS

Climatic data were evaluated for 4 towns within the study area: Hood River, The Dalles, Dufur and Madras (Tables IV-VII).

Running means, as represented in Figures 35-40, were calculated in the following manner: a grand mean for the data was computed for the entire time interval, e.g. 1911-1975; this figure was subtracted from each individual datum; these results were added in 5-year intervals; and this figure was divided by 5 (e.g. $\frac{(10-10)+(11-10)+(9-10)+\dots}{5}$).

Figure 29. Mean monthly precipitation for Hood River, Oregon.

Figure 30. Mean monthly precipitation for The Dalles, Oregon.

Figure 32. Mean monthly precipitation for Madras, Oregon.

Figure 31. Mean monthly precipitation for Dufur, Oregon.

Figure 33. North-central Oregon's mean annual precipitation (cm) is superimposed on a map of Oregon white oak's distribution (precipitation data from Tables IV-VII).

Figure 34. Average number of frost-free days per year is superimposed on a map of Oregon white oak's distribution (from Highsmith, 1968).

TABLE IV

MEAN TEMPERATURE AND PRECIPITATION DATA: HOOD RIVER

Year	Mean Annual Precip.(in)	Mean Annual Temp.(°F)	Mean Temp. Apr.-May (°F)	Mean Temp. Oct.-Nov. (°F)	Mean Precip. Apr.- May(in)	Mean Precip. Oct.-Nov. (in)
1911	18.6	50	47	45	2.7	2.3
1913	22.5	50	53	52	2.4	8.3
1915	30.2	52	54	48	3.6	11.2
1917	32.2	50	49	48	4.0	4.3
1919	35.2	48	53	44	3.1	8.4
1921	37.9	50	53	46	1.9	15.3
1923	----	51	52	48	---	3.5
1925	24.2	52	55	45	3.7	4.4
1927	30.2	51	52	49	1.9	8.8
1929	19.0	49	52	47	2.3	.3
1931	29	50	56	45	1.6	7.4
1933	35.7	50	51	49	1.5	5.0
1935	16.6	49	51	43	1.8	2.5
1937	37.0	50	52	50	4.3	8.7
1939	18.5	52	54	48	1.2	1.3
1941	24.8	52	55	47	3.0	5.9
1943	27.1	49	53	46	2.9	8.8
1945	32.1	50	53	46	4.5	9.3
1947	29.6	52	57	48	1.7	10.3
1949	28.5	50	55	47	5.6	12.7
1951	34.5	50	54	40	1.7	10.5
1953	34.6	52	51	49	5.6	6.1
1955	34.7	49	49	42	3.8	12.4
1957	31.6	50	55	46	2.3	5.3
1959	24.0	51	52	46	1.9	5.3
1961	38.0	51	52	44	2.9	7.0
1963	26.0	50	51	48	3.6	7.8
1965	24.2	51	52	49	3.0	6.4
1967	24.3	53	51	48	1.5	8.0
1969	26.5	50	54	46	2.1	3.4
1971	32.6	50	52	45	2.2	6.9
1973	35.0	51	54	45	1.2	13.7
1975	36.6	--	49	46	.9	10.3
mean	29.1	50.5	52.5	46.7	2.6	7.3

TABLE V

MEAN TEMPERATURE AND PRECIPITATION DATA: THE DALLIES

Year	Mean Annual Precip.(in)	Mean Annual Temp. (°F)	Mean Temp. Apr.-May (°F)	Mean Temp. Oct.-Nov. (°F)	Mean Precip. Apr.- May(in)	Mean Precip. Oct.-Nov. (in)
1911	9.0	52	54	47	1.0	1.5
1913	----	--	57	47	1.6	3.9
1915	15.9	55	59	48	2.1	4.6
1917	12.5	54	54	50	2.4	2.5
1919	15.2	52	57	47	1.1	3.5
1921	21.7	54	57	50	1.0	9.9
1923	16.2	56	60	51	1.5	1.6
1925	13.2	56	60	49	2.3	2.0
1927	15.9	54	55	51	.4	3.8
1929	8.6	53	56	49	.4	.3
1931	11.6	53	58	46	.5	2.6
1933	13.1	53	54	50	1.3	2.1
1935	6.9	53	55	43	.5	1.2
1937	19.3	52	56	51	1.2	3.7
1939	6.4	56	57	50	.3	.2
1941	11.7	56	59	50	1.3	3.3
1943	16.2	--	57	48	1.8	5.3
1945	14.5	55	58	50	2.6	4.0
1947	14.4	56	62	51	1.0	4.8
1949	10.0	54	60	49	.6	3.0
1951	18.0	55	57	49	1.1	4.3
1953	19.0	56	55	52	2.2	3.2
1955	16.5	53	54	47	1.6	6.0
1957	15.2	54	61	49	.9	2.7
1959	9.0	55	57	49	.4	1.7
1961	18.3	56	57	47	1.9	3.6
1963	11.5	55	57	52	1.7	3.0
1965	10.9	56	58	54	1.3	2.6
1967	----	--	56	--	1.3	--
1969	10.9	53	57	48	1.2	1.1
1971	13.9	53	55	47	.8	2.7
1973	17.5	54	58	47	.7	6.4
1975	----	--	55	47	1.1	4.0
mean	13.8	54.3	57.2	48.9	1.2	3.3

TABLE VI

MEAN TEMPERATURE AND PRECIPITATION DATA: DUFUR

<u>Year</u>	<u>Mean Annual Precip.(in)</u>	<u>Mean Annual Temp. (°F)</u>	<u>Mean Temp. Apr. - May (°F)</u>	<u>Mean Temp. Oct.-Nov. (°F)</u>	<u>Mean Precip. Apr.- May(in)</u>	<u>Mean Precip. Oct.-Nov. (in)</u>
1919	17.4	46	49	42	1.2	2.7
1921	17.5	47	48	45	1.4	7/3
1923	14.9	47	49	45	1.6	1.8
1925	10.7	49	51	43	3.1	2.0
1927	14.7	47	47	46	.3	3.7
1929	7.8	48	50	46	.7	.2
1931	10.3	50	55	43	.4	1.2
1933	9.6	49	49	48	1.2	1.3
1935	5.1	49	51	42	.5	1.0
1937	15.5	49	50	48	1.5	3.6
1939	6.2	55	54	47	.3	.2
1941	11.2	51	54	46	1.6	3.5
1943	12.5	49	52	46	1.6	2.0
1945	----	--	52	48	3.0	2.8
1947	13.0	51	57	47	1.1	5.5
1949	8.2	49	57	46	.6	2.3
1951	14.0	50	53	44	1.6	3.1
1953	14.7	51	50	48	2.5	2.5
1955	13.6	48	49	42	2.1	4.0
1957	13.4	49	55	40	1.8	2.1
1959	8.9	50	51	45	.7	1.1
1961	14.7	52	52	43	2.1	2.2
1963	12.2	--	51	45	2.1	2.2
1965	10.2	50.0	51	48	1.5	2.8
1967	7.1	51	49	46	1.7	2.4
1969	10.9	48	53	44	2.4	1.2
1971	10.9	48	50	42	1.6	1.9
1973	13.7	49	52	44	.6	6.0
1975	13.7	48	47	44	1.2	2.7
mean	11.9	49.0	51.3	44.9	1.4	2.6

TABLE VII

MEAN TEMPERATURE AND PRECIPITATION DATA: MADRAS

<u>Year</u>	<u>Mean Annual Precip.(in)</u>	<u>Mean Annual Temp. (°F)</u>	<u>Mean Temp. Apr.-May (°F)</u>	<u>Mean Temp. Oct.-Nov. (°F)</u>	<u>Mean Precip. Apr.- May(in)</u>	<u>Mean Precip. Oct.-Nov. (in)</u>
1921	10.1	48	48	45	2.3	3.1
1923	9.5	48	49	44	2.1	1.7
1925	8.9	49	52	42	4.0	1.2
1927	10.8	47	47	46	.4	1.6
1929	7.9	45	48	41	1.9	1.1
1931	7.0	48	52	39	.7	1.1
1933	5.4	48	47	44	1.8	.7
1935	6.6	46	47	39	1.4	1.1
1937	14.5	47	54	46	1.8	4.0
1939	5.0	49	51	43	.4	.4
1941	12.2	48	49	44	2.0	2.9
1943	8.8	46	47	43	1.8	2.3
1945	10.9	48	49	44	3.2	2.5
1947	10.5	49	53	46	.9	3.3
1949	4.1	47	52	41	.5	2.1
1951	9.7	47	49	42	1.6	2.6
1953	12.2	49	47	46	1.7	2.5
1955	9.8	46	45	42	1.7	2.4
1957	12.8	46	51	40	3.7	1.1
1959	----	--	47	--	1.2	---
1961	12.9	50	49	41	1.7	3.5
1963	11.3	48	49	46	2.7	2.4
1965	9.6	49	50	47	1.4	2.6
1967	5.9	--	48	45	1.8	1.0
1969	13.6	--	--	44	1.4	1.2
1971	9.0	49	50	44	1.7	1.6
1973	11.0	--	50	44	.7	4.2
1975	10.7	--	--	45	1.1	1.7
mean	9.7	47.7	49.2	43.4	1.7	2.1

These computations are graphed as variations about the mean (0) line for ease of comparison between stations.

Six types of data were compiled in Tables IV-VII: mean annual precipitation and temperature; mean temperature and precipitation for October and November; and mean temperature and precipitation for April and May. The 2-month interval results represent the period of most effective precipitation for Q. garryana. In the fall, oak germinates and quickly takes root if soil conditions are favorable; temperature and precipitation extremes during this period should be critical factors in survival of seedlings. The timing of spring rainfall and temperature increases are important to the survival of the previous year's seedlings.

The climatic trends exhibited in Figures 35-40 are discussed and compared to the size-structure data. A point worth noting is that a well-documented arid cycle, known variously as the "dust bowl years" or simply the "1930s drought", occurred on a global scale. Climatic records (Page, 1937) and tree ring data (Fritts, 1966) indicate that extremely dry conditions prevailed throughout the western United States from the late 1920s to the late 1930s. On a local level, Keen's (1937) tree ring evaluation revealed that the drought of 1917-1935 was the most severe that central Oregon had perserved for the last 650 years. Thus, if oak's regeneration is sensitive to climatic change, this period should serve as a good index of response.

In general, the precipitation graphs elicit a more cyclical sequence of above and below-normal figures than the temperature data, which seems more randomly distributed. The correlation between annual and fall precipitation is particularly close. The 1930s drought stands out, spanning the late 1920s into the late 1930s. The temperature variations,

Figure 35. Annual precipitation running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur and Madras, Oregon.

Figure 36. Annual temperature running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur and Madras, Oregon.

Figure 37. Spring (April-May) precipitation running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur and Madras, Oregon.

Figure 38. Autumn (October-November) precipitation running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur, and Madras, Oregon.

Figure 39. Spring (April-May) temperature running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur, and Madras, Oregon.

Figure 40. Autumn (October-November) temperature running-mean variations from the grand mean for climatological stations in Hood River, The Dalles, Dufur and Madras, Oregon.

however, show little seasonal or annual correlation.

COMPARISON OF OAK SIZE-STRUCTURES TO CLIMATIC CHANGE

Q. garryana size-structures, as shown in Figures 4-25, exhibit periods of relatively higher or lower reproduction. In order to link these variations to possible climatic causative factors, chronological values were assigned to the successive size-classes. A small group of oaks were cored, their diameters measured (Table VIII), and a linear correlation was established for these 2 variables (Figure 41). An evaluation of variation around the line-of-best-fit showed the linear function to be statistically significant (Appendix III, Table I). Using the estimation of x-coordinates from y-coordinates, ages were assigned to each potential oak size-class (Appendix III, Table II).

The following is a discussion of dated size-class variations from the expected reverse J curve reproductive curve in relation to the climatic fluctuations derived from Figures 35-40. The sites are divided into two groups: those which show anticipated responses to climatic variations and those which do not. These divisions were based on Q. garryana's reproductive response to wetter or drier conditions considered in respect to the population's location at either the arid or moist frontier of its range. Oak stands which were inhabited by Douglas fir or ponderosa were considered to be at their upper moisture limits; those sharing their site with junipers, desert shrubs, and grasses were classified to be at their arid limits. Oak's response at its arid limits to the 1930s drought should be reduced reproduction; at its upper precipitation limits, periods of drought should favor oak reproduc-

TABLE VIII

OREGON WHITE OAK TREE RING DATA

<u>Tree Number</u>	<u>Diameter (cm)</u>	<u>Age (Years)</u>
1	19.9	56
2	7.6	28
3	15.3	56
4	29.0	49
5	16.8	48
6	19.1	52
7	9.2	36
8	9.2	41
9	25.2	63
10	17.5	36
11	8.4	35
12	15.3	53
13	6.1	33
14	10.7	32
15	39.0	84

Figure 41. Age and diameter-at-breast-height for a stand of Oregon white oak trees.

tion over Douglas fir or ponderosa pine. Moist periods should elicit opposite reproductive responses.

SITES WITH A POSITIVE SIZE-STRUCTURE VERSUS CLIMATIC CORRELATION

The population at site 2 (Figure 7) shows a rapid drop in numbers of individuals below 17 cm dbh, or near 1928*. Regeneration resumed in the 5 cm dbh class, or since about 1951. This gap in reproduction between 1928 and 1950 correlates with the drought as depicted in Figures 35 and 38. The resumption of reproduction after 1951 may be a result of increased precipitation. Most of the young oaks, however, are of coppice origin, indicating that some other factor may have restrained oak regeneration after the drought.

The oaks at site 3 (Figure 9) exhibited excellent correlation to precipitation variations. The oldest individual - 14 cm dbh - sprouted in approximately 1934 in the middle of the drought (Figures 35 and 38). Oak reproduced successfully after this time, while reproduction in Douglas fir and ponderosa pine was greatly reduced (Figures 10-11). These species were out-competed by Oregon white oak during this drought. Oak is normally only a subordinate member of plant communities at this elevation (800 m) due to overtopping by conifers. The drought, however, provided the drier conditions under which oak could temporarily stifle its mesic associates. The return of wetter conditions should have signaled the cessation of oak dominance, although the size-structure does not reveal this. Many oaks, however, were visually noted to be

*The chronology of each size-class, as taken from Appendix III, is estimated by subtracting the age for the size-class from the study year, 1976. Thus 5 cm = 25.0 years; subtracting this figure from 1976 yields the date of oak germination: $1976 - 25.0 = 1951$.

dead or dying due to overtopping by faster-growing ponderosa pines. In addition, many of the dying oaks were coppice sprouting, which accounts for the bulk of recent oak regeneration.

The oak size-structure at site 5 (Figure 13) conforms to the expected reverse J curve with the exception of the 6-10 cm dbh class. The cessation of regeneration occurs at 12 cm, or near 1938, and correlates with the termination of drought conditions. The continued lack of regeneration after this period, however, is unaccounted for in the climatic data. The large number of sprouts is misleading in that over 90% were in tight clumps, probably of coppice origin (see Figure 42). Thus, while the drought seems to account for the initial reduction in regeneration, something else is causing the lack of recent reproduction.

The Q. garryana population at site 6 exhibits excellent correlation to the reverse J curve (Figure 14). Most of the oaks sprouted after 1932 (15 cm dbh) during the 1930s drought. Ponderosa pine, which also inhabits this site, appears to be in the process of being replaced by oak; the complete lack of pine regeneration (Figure 15) coincides with the upsurge in oak reproduction. It is not immediately obvious, however, why pine is not currently replacing oak.

The oak size-structure for site 7 (Figure 16) fits the reverse J curve with the exception of a reproductive gap during a moist period from 1902-1924 (19-30 cm dbh). Thus oak reproduction decreased during a period of abundant precipitation and increased during the drought. This probably resulted from competition with ponderosa pine during the moist period, followed by less competition during the dry spell (Figure 17). Such an interpretation is confused, however, by ponderosa pine's apparent release from fire pressure during the 1930s drought (Weaver,

Figure 42. This north-facing slope in Butler Canyon (site #5) exhibits abundant coppice regeneration (note right foreground)

1950), resulting in steadily increasing reproduction until recent times. Thus, while oak's reproduction here fits a climatic model, fire may be an equally important factor.

Site 14 exhibits excellent conformity to the reverse J curve (Figure 24). Neither severe drought nor precipitation increases seem to be manifested in size-class variations. The single older individual, propagated in approximately 1881, is outside of possible climatic comparison.

The size-structure for site 15 exhibits good correlation with the reverse J curve (Figure 25) with the exception of the class between 12 and 18 cm dbh, or from 1925 to 1937. This gap in regeneration correlates with the 1930s drought. The presence of healthy Agropyron spicatum bordering this small oak stand signifies that oak is at the arid periphery of its range. Thus, the drought worked against oak regeneration, while earlier and later moisture surpluses favored it.

SITES WITH A NEGATIVE SIZE-STRUCTURE VERSUS CLIMATIC CORRELATION

Oak's size-structure at site 1 (Figure 4) shows complete cessation of regeneration after the 5 cm dbh class. Estimating the recovery (or invasion) of oaks at 5 cm (1951), this period correlates with resumption of normal and above-normal rainfall after the 1930s drought (Figures 35 and 38). Precipitation averaged 75-100 mm above normal at this time. It is improbable, however, that climate alone would have completely eliminated such a drought-resistant species as oak. In light of the accompanying size-structure success during this period for Douglas fir and ponderosa pine (Figures 5-6), both of which are less drought-tolerant species than Q. garryana, some other factor, such as fire must have

taken its course during this period. This site did, however, show strong slope-aspect vegetational differences; the more mesic species occurring on the north facing slope while oak and grasses dominated the south facing slope.

The disjunct population of Oregon white oak at site 4 (Figure 12) demonstrates a pronounced departure from the reverse J curve at the 25-30 cm dbh class. The precise termination of regeneration occurred at 31 cm, or near 1902. The climatic records do not extend back this far. Regeneration, however, has not taken place since the turn of the century, while the population appeared stable prior to this period. The indication, then, is that a continuous restraint other than climatic change has affected the population since 1902.

The oaks at site 8 (Figure 18) exhibit a sporadic size-structure. This population is dominated by the presence of some very old trees and a total lack of regeneration after the 20 cm dbh size class, or near 1923. Since regeneration did not take place during the 1930s drought, nor during the earlier or later drier periods, some other factor is obviously overriding the climate-plant relationship.

The transect at site 9 sampled another section of the oak population found at site 8. The size-structure is again characterized by an erratic distribution of size-classes (Figure 19) culminating in the total lack of regeneration after 19 cm dbh, or near 1924. These fluctuations do not correlate with either above or below-average precipitation. As in the previous case, climate does not appear to be the overriding factor at this site.

The size-structure of site 10 shows two distinct periods of limited regeneration (Figure 20). One occurs at 23 cm dbh, or near 1917,

the other at 15 cm dbh, or near 1932. The 1917 variation agrees with a period of copious precipitation (Figures 35 and 38), while the 1932 variation correlates with the 1930s drought. Considering the low elevation - 550 m - and the surrounding grassland habitat, the drop in regeneration associated with the 1930s drought would seem reasonable. In order to associate a surplus of precipitation with a drop in oak regeneration, however, some other arboreal species, either Douglas fir or ponderosa pine, would need to be competing with oak; neither of these trees occurs at the site. Thus, another factor other than climate was operative in order to account for the cessation of regeneration near 1917.

The size-structure graph for site 11 elicits two variations from the expected reverse J curve (Figure 21). First, while only one individual in the 36-40 cm dbh class occurred in the transect (36 cm, or near 1892), other equally old trees were seen scattered sparsely throughout the area, especially in the draws. While the climatic data does not reach this period, the lack of oak regeneration for a full 25 years after this time precludes a purely climatic explanation.

Second, the renewal of reproduction occurred in the 10-22 cm dbh class, or between 1919 and 1942. This time span covers both the 1930s drought and the period of precipitation surplus preceding it. There are not nearby pines or Douglas fir to compete with the oaks; thus, the oak reproductive increase during the moisture surplus is more expected than during the drought. Likewise, a lack of regeneration occurred under moister conditions from 5-10 cm dbh (or approximately 1942 to 1951). Without competition from more mesic species, this drop in regeneration is not explained by simple climatic corre-

lation.

The size-structure of site 12 (Figure 22) resembles that of Figures 18-19. The only difference is the presence of recent regeneration at site 12. The immediate cessation of regeneration of reproduction at 15 cm dbh, or in 1932, correlates with the 1930s drought. Since the population is on the arid periphery of oak's range, the regenerative reduction during the long period of drought is anticipated. What is not explained is the lack of regeneration after the drought up until recent times. Another factor must be dominating the climatic factor during this latter period.

The size-structure of site 13 fits the reverse J curve (Figure 23) with the exception of oaks that are younger than 6 cm dbh, or since 1949. This correlates with a period of above-average precipitation (Figure 35). Since there are not other competing trees, this regeneration reduction is not explained by the climate graphs.

A situation not made apparent by the size-structures at site 13 is the great density of oak, especially in the 6-19 cm dbh class (see Figure 43). This abundance resembles that noted at site 7 for ponderosa pine. Weaver (1950) related this situation to removal of fire from the ponderosa pine ecosystem, and it is possible that this same situation applies to Q. garryana.

COMBINED SIZE-STRUCTURE DATA VERSUS CLIMATIC CORRELATION

Figure 28 represents the summed oak size-class results for all of the sampled sites. Two aberrations from the reverse J curve are apparent: one at 45 cm dbh (approximately 1875) and the other between 3 and 11 cm dbh (from 1940 - 1965). The first variation is beyond the

Figure 43. Scrubby Oregon white oak stands are punctuated by sporadic Douglas fir near Mosier Creek.

scope of climatic comparison while the second covers too long of a time span to be explained by any single climatic variation. The data, however, covers both the arid and moist periphery of oak's range; thus, opposite reproductive responses would be expected to cancel out any meaningful variations from totally summed results.

SLOPE ASPECT VERSUS CLIMATIC CORRELATION

The size-structure data are separated into north and south facing slope results in Table III and graphed in Figures 26-27. On each graph, only one size-class varies from the expected reverse J curve. On the north facing slopes (Figure 26), the 6-10 cm dbh size-class, or from 1942 - 1950, shows an appreciable drop in reproduction. This correlates with the increase in precipitation during the 1940s, especially fall precipitation figures (Figure 38), which are important to fall germinating species such as Q. garryana. This situation is consistent with the interspecific competition expected from Douglas fir and ponderosa pine on the mesic habitats during moist periods. Likewise, oak regeneration is relatively more active during the drought when more mesic species are apt to suffer from drought stress (Figure 44).

The summation of south facing slope size-class data in Figure 27 reveals a different situation. The size-classes from 6-10 and 16-20 cm dbh, covering 1943 - 1950 and 1922 - 1930, both show good reproductive rates and correlate with periods of above-average precipitation. Due to the increased aridity on south facing slopes, oaks exist on the tenuous edge of environmental exclusion. Thus, any increase in mean precipitation would result in increased oak regeneration. The size-class 11-15 cm dbh, covering 1932 - 1940, shows a good reduction in the

Figure 44. During the 1977 drought, Douglas fir trees frequently died while surrounding oaks survived.

number of individuals, which correlates with the 1930s drought. Thus, the moisture stress in this austere environment becomes a limiting factor to oak regeneration during times of below-normal rainfall.

SUMMARY

The size-structure data for Oregon white oak correlates to some extent with climatic data. Oak occurs between the 300 mm mean annual isohyet at its arid frontier and the 1500 mm isohyet at its moist periphery. This great range in tolerance is partly a result of climatic amelioration resulting from topographic heterogeneity.

Climatic fluctuations correlate with some transect data but not with others. At the moist edge of its range, interspecific competition from Douglas fir and ponderosa pine is apparently limiting oak's growth and reproduction during wet periods, while arid periods favor oak reproduction. At its arid border, competition for the dwindling moisture resource forces oak to yield to xerophytic species during times of drought, while moister periods favor its reproduction. Thus Oregon white oak's population is constantly jockeying for reproductive dominance with its two plant association adversaries.

In the following chapter, those size-structures which did not exhibit good climatic correlation will be considered in light of grazing pressure in central Oregon.

CHAPTER VII

EFFECTS OF GRAZING ON OREGON WHITE OAK

INTRODUCTION

Grazing is an integral process in most natural ecosystems. Photosynthetic energy is shuffled through the food chain via plants to herbivores, carnivores, and ultimately reduced through microbes to nutrients for plants. Thousands of years of co-evolution between the members of these communities has resulted in smoothly operating, mutually dependent systems, whereby grazing is reciprocally necessary for both the plant and the animal (Gilbert, 1980).

Man has altered the natural producer-consumer relationships of many areas by the introduction of domestic livestock. In natural ecosystems, the vertebrate grazers can move to other habitats, or perhaps enter a state of torpor when preferred forage becomes scarce. When grazing is controlled, as in farm woodlots or pastures, however, domestic livestock may be forced to continue grazing after the more palatable plants have been exhausted. Under such conditions, those plant species which are intolerant of these pressures will be reduced or eliminated, leaving a less diverse plant community of more tolerant elements. Continued heavy grazing will eliminate all but the weedier species, which are frequently exotics. Finally, continued grazing may result in the elimination of even these aliens, leaving the site stripped clean of vegetation and with a potentially serious erosion problem (Whittaker, 1975).

In the study area, domestic livestock grazing reached its maximum

intensity around the turn of the century. The extension of widespread private ownership through the Homestead Act soon afterward brought an end to the open range (Galbraith, 1971). By this time, however, there were serious overgrazing problems in central Oregon (Cholis, 1952; Cotton, 1904).

It is difficult to determine the functional importance of specific herbivores in oak habitats. Griffin (1976), working in a California oak woodland which was free of livestock grazing, constructed both deer and gopher exclosures for this purpose. Several herbivores were found to seriously limit regeneration in Quercus lobata, but no one of them was found to be primarily responsible.

GRAZING OBSERVATIONS

Several vertebrates were observed transporting, burying, or consuming acorns in central Oregon (Table IX).

TABLE IX

ANIMALS OBSERVED CARRYING OR EATING ACORNS

<u>Species</u>	<u>Number of Observations</u>	<u>Activity</u>
Douglas' Squirrel	2	Burying acorns
Western Gray Squirrel	2	Carrying acorns
Blue Jay	2	Carrying acorns from seed tree to another oak and consuming the acorns
Steller's Jay	17	Carrying acorns from seed tree to another tree (often conifer) and eating or occasionally dropping acorns.

TABLE IX (Continued)

ANIMALS OBSERVED CARRYING OR EATING ACORNS

<u>Species</u>	<u>Number of Observations</u>	<u>Activity</u>
Lewis' Woodpecker	9	Carrying acorns from seed tree to another tree and: 1) eating acorns; 2) dropping acorns; 3) cramming acorns into tree cracks.
Deer	6	Browsing under oak trees.

In addition, the terminal buds and bark of oak sprouts and saplings were found on occasion to be nibbled off.

Insects also graze in Oregon white oak communities. Oak galls bearing gall wasp larvae were commonly observed. In addition, a large percentage of the mast production found under oak canopies were infested by insect larvae, thus probably rendering them inviable.

Most or all of these herbivores were members of the Oregon white oak community during periods of both normal and abnormal reproduction, as depicted by the size-structure graphs (Figures 4-25). Records of variations in wildlife densities are, however, not available; their impacts on forest equilibrium are thus not known.

There is little doubt that selected vertebrate herbivores play an indispensable role in plant regeneration. Janzen (1970, 1971) notes that seeds accumulating under the canopy of the parent tree are rapidly consumed by animals, while those passively transported away by seed-storing vertebrates have a better chance of survival. It is plausible, then, that the actions of jays, woodpeckers, and squirrels may be an important element in Oregon white oak reproduction and diffusion.

Man may indirectly affect oak reproduction by the manipulation of native wildlife populations. In Oregon, many members of the upper trophic levels have been eliminated through hunting, predator control and toxic pesticide use. The grizzly bear, wolf, wolverine and various raptors have been either completely or largely extirpated. In many cases, this has released the predation on the herbivores, resulting in a rise in population densities. Increased grazing by these animals, in turn, may have resulted in increased acorn consumption and thus reduced oak regeneration.

The consumption of acorns, terminal buds, and leaves by livestock was not directly observed. Ranchers living in the area were divided on the question, one noting that:

Hell no, cattle won't eat any part of these oaks! They aren't good for anything.

while another said that:

Sure, they prefer oak shoots and acorns over the other shrubs. They love them!

It may be assumed, however, that livestock do graze on oaks, considering the abundance of incriminating evidence (DenUhl, 1945; Griffin, 1976, 1977; Holland, 1976; Smith, 1957; Steinbrenner, 1931).

Among the fifteen sites surveyed, several showed signs of heavy livestock pressure, such as browse lines on the trees, churned-up soil, and little or no herbaceous vegetation. Other sites showed no grazing evidence, while still others showed slight evidence. The division of sites based on grazing pressure is shown in Table X.

In order to relate the impact of livestock grazing pressure to Quercus reproduction, the grazing evidence is cross-matched with the climatic evidence, which is divided in Table XI between sites that did

TABLE X
OBSERVED EFFECTS OF GRAZING

	<u>Heavily Grazed</u>	<u>Lightly Grazed</u>	<u>Ungrazed</u>
Site #	4,8,9,10	5,11,12	1,2,3,6,7,13,14,15

or did not show positive correlation to the climatic data.

TABLE XI
COMPARISON OF CLIMATIC DATA TO SIZE-STRUCTURE

	<u>Correlation</u>	<u>No Correlation</u>
Site #	2,3,5,6,7,14,15	1,4,8,9,10,11,12,13

Comparison of Tables X and XI reveals a 75% overlap between the ungrazed sites and the sites showing positive climatic correlation. Only 25% of the ungrazed sites showed no climatic correlation. Further, among the sites exhibiting signs of heavy grazing, none showed good climatic correlation. This indicates that heavy livestock grazing is disruptive to the climate-plant reproductive relationship.

Closer scrutiny of the four heavily grazed sites reveals another common characteristic; all showed a complete absence of oak regeneration following a period of apparently healthy reproduction. The timing of this event was: site 4 - 1902; site 8 - 1923; site 9 - 1924; and site 10 - 1917. Whatever is stopping oak regeneration in these stands has been continuously operative for 50-75 years.

The soil condition and the herbaceous cover further reveals the effects of livestock grazing. All of the ungrazed sites exhibited soil profile development, except where trees grew directly out of bare basalt.

The heavily grazed sites, however, showed an undifferentiated soil profile which when wet became a pasty mud. Further, low-growing plants were not present at heavily grazed sites, while ungrazed sites were moderately to lushly vegetated.

The grazing history of the study area is incompletely known. Site 15, however, has not been grazed by livestock according to the land owner and shows excellent correlation to the precipitation data. Nearby is another parcel of oak woodland which is divided by a road, one side of which is inhabited by only old-growth oaks larger than 10 - 15 cm dbh. There are, however, many recently sprouted acorns, the ground being literally a carpet of young Quercus seedlings. The owner attests that this site is regularly used to pasture livestock, but that it had not been so used for several months. Thus, heavy livestock grazing appears to directly inhibit oak regeneration and, although the soil may be badly churned by the cattle's hooves, rapid acorn regeneration can take place if grazing pressure is removed. Weaver (1950) and Rumnel's (1951) suggestion that heavy livestock grazing could, by breaking up the sod layer, increase the chances of seedling survival, is in accordance with these findings.

At the same site, on the other side of the road, the oaks appear to have a stable size-structure, with both young and old individuals being present, and the shrub and herbaceous layers are luxuriant. According to the property owner, the land had not been grazed during his 20 years of ownership. Very little acorn regeneration is apparent. The sod layer is relatively tight and may be limiting the number of seedling radicles able to penetrate the solum. Thus, some disturbance to the

herbaceous layer may occasionally be necessary for extensive acorn regeneration to occur. Such a situation might have been created in the past by low intensity ground fires which, as recorded by Keen (1937), occurred every 7-12 years in central Oregon prior to man's fire-prevention efforts.

SUMMARY

Q. garryana communities are grazed by indigenous herbivores and domestic livestock. The functional role of native grazers is problematic, although it is reasonable to assume that acorn dispersal by vertebrates is important for oak reproduction and population movement.

Livestock grazing is strongly correlated with uneven size-structures in Oregon white oak communities. The consumption of seedlings apparently limits oak's ability to replace itself. The long-term effects of this practice may be the elimination of Quercus from these sites.

The accumulation of organic duff and the tight sod layer may have historically allowed only infrequent acorn regeneration. Acorn sprouts, however, were found to quickly take root in overgrazed areas when the livestock grazing pressure was removed. Such areas apparently provide easy access to the mineral layer for the seedling radicles. Before human fire-prevention activities, similar soil disturbances and hence productive seed-beds may have resulted from the low-intensity ground fires which periodically swept the area.

Many vertebrates transport acorns away from the seed tree as part of their grazing behavior, thus conceivably acting as vectors of seed dispersal. Inasmuch as plant species require some means of population mobility, particularly during periods of environmental stress, this ac-

tivity becomes an integral element in Oregon white oak's biogeography. The following chapter will explore the relative effectiveness of animals, physical processes, and man as agents of acorn movement.

CHAPTER VIII

VAGILITY OF OREGON WHITE OAK ACORNS

INTRODUCTION

In order to survive periods of radical environmental change, plants must possess the ability to either adapt to the new conditions or migrate away to suitable areas. Seeds, which provide the means for population movement, are as a normal course disseminated to both favorable and unfavorable habitats; those which survive may live to act as seed sources for diffusion into further amenable areas. Such a process, if carried on quickly enough to keep pace with changing conditions, will allow a population to migrate in the general direction of favorable environmental conditions and thus escape extirpation.

In Quercus, the adaptive value of acorn dispersal mechanism are manifold. Seed trees, which act as red flags for local herbivores, bequeth a slim chance of survival upon acorns that congregate under the tree canopy. Seeds that escape consumption here must further face a competitive battle with the mother tree, which would seldom tip in favor of the youthful aggressor. And subtle factors such as allelopathic inhibition, while not documented in Quercus, might further hinder the germination of acorns in the immediate vicinity.

Q. garryana cannot be considered a swiftly migrating species due to the bulky size and weight of its seeds. Spore producing life forms, which produce millions of wind dispersed propagules, enjoy wide distributions. Plants with sticky seeds or tasty fruits are adapted to dispersal by migrating birds and mammals. Acorns, however, are not wind

dispersed, can seldom be swallowed whole by birds, and do not cling innocuously to animal appendages. Oak seems to have sacrificed copious seed production and physical conveyance for increased nutritive value, physical protection, and specialized transport by a few vertebrate species. The endosperm, which makes up most of the seed, has a high content of protein and fats, thus supplying an ample reward for species adapted to their consumption.

Several means of acorn transport were examined within the study area. The effectiveness of gravity fall and hillside roll is considered, as well as flotation by running water. Particular attention is paid to the function of birds and mammals in acorn mobility. Finally, the role of humans in acorn transport is explored in an historical context.

GRAVITY FALL AND HILLSIDE ROLLING OF ACORNS

In order to measure the effectiveness of gravity fall and hillside roll as a dispersal mechanism, the acorns of an oak approximately 116 years old were painted in the fall. The following spring, a thorough search produced 41 acorns. The distances and directions of the seeds from the host tree, as well as calculations of the mean and maximum dispersal distance, either upslope or downslope, are listed in Table XII.

The results show that the majority of the retrieved acorns - almost 70% - fell and rolled downhill (Figure 45). The distance covered, however, was not dramatic, the maximum distance being 665 cm from the trunk. The tree canopy spread 460 cm in each direction from the trunk. Thus, the farthest dispersed acorn traveled just over 2 m beyond the tree canopy. The mean distance traveled places most of the propagules well within the limits of the canopy. The mean upslope distance covered

TABLE XII

DISTANCE (cm) AND DIRECTION OF MARKED ACORNS
FROM SEED TREE

<u>S</u>	<u>SSW</u>	<u>SW</u>	<u>WSW</u>	<u>W</u>	<u>WNW</u>	<u>NW</u>	<u>NNW</u>	<u>N</u>	<u>NNE</u>	<u>NE</u>	<u>ENE</u>	<u>E</u>	<u>ESE</u>	<u>SE</u>	<u>SSE</u>
15	64	360	317	363	294	260	250	252	390	113	368	4		325	
378			86	383	43	300	65	222	351	665		295		280	
345				41		165		165	490	52		92			
420						210		405	493						
235						365			602						
						413			160						

N = 41
 Mean = 270.6 cm
 Max. = 665 cm
 Mean Downslope = 288.9 cm
 Mean Upslope = 234.4 cm
 Total Downslope = 26 acorns
 Total Upslope = 12 acorns

Figure 45. The location - by percent of total - of recovered acorns under an Oregon white oak tree (see Table XII).

was 234.4 cm, while the mean downslope distance was 288.9 cm. The seeds moved downslope thus averaged over 50 cm farther from the trunk than those transported upslope. Considering predation by herbivores and competition with the seed tree, it seems safe to assume that few acorns simply fall to the ground and roll to a safe germination site, although downslope movement would be relatively more effective than upslope.

In order to calculate maximum potential dispersal rates by falling and rolling, an acorn will be hypothetically allowed to move the maximum noted distance of 665 cm from the mother tree, germinate, and grow into a seed-producing oak in approximately 25 years. If this sequence of events is repeated for 100 years (if the original tree is at the edge of the population, and if the acorns are carried directly away from the main population), the Oregon white oak population would have migrated 2.6 cm; if continued for 1000 years, this would account for a 226 m range extension. While differing canopy size, slope inclination, and a host of other factors could alter this rate somewhat, the fact remains that gravity fall and roll of acorns is a slow means of oak population migration.

It was further noted that eight of the forty-one acorns had been broken open and consumed. These propagules were located an average of 220 cm from the tree trunk, which is less than the overall mean and even the upslope mean. Thus, in this case, nearness of acorns to the seed tree seems to work to the detriment of seedling survival.

RUNNING WATER TRANSPORT

Three criteria must be met for running water to aid in acorn dispersal: 1) the seed tree must grow close enough to the stream course

for acorns to reach it; 2) the acorns must float or be dragged in the current for some distance without becoming waterlogged; and 3) the seed must be deposited at a safe site for germination.

In order for the first criterion to be consistently met, Oregon white oak would have to be a riparian species. While this is not generally the case, it does in some instances grow adjacent to drainages.

If the acorns are less dense than water, the stream would have little problem transporting them; if, however, they are heavier than water, the current would need to be swift enough to hold the seeds in suspension. This question was answered in a cursory manner by dropping 20 acorns into a creek; they immediately sank to the bottom. This was probably too small of a sample to positively disregard water flotation of acorns, and Ridley (1930) speculated that even a 4-8% rate of successful flotation in a European species of oak was sufficient to consider it a viable means of acorn transport. Generally, however, acorns are not able to tolerate long periods of water immersion, although Kramer (1960) found that the seeds of some oak species can remain submerged up to two months and still maintain viability.

The third criterion requires that floating acorns drift to a suitable site for germination and growth. The potential for this is not known, but considering the lack of oaks growing at streamside, it appears that Q. garryana may not be competitive in riparian habitats.

A severe flood might circumvent some of these limitations. A large volume of water traveling down a drainage system would reach and occasionally engulf oak trees. Acorns carried by a flood state volume of water would have the advantage of possibly being deposited on the lateral side of the levee. The scouring action of the flood, by removing stream-

side vegetation, might also be preparing a suitable seedbed. This, however, is purely speculative.

ANIMAL TRANSPORT OF ACORNS

The movement of acorns by animals is an important factor in oak migration. Several species were noted to cache or otherwise drop viable acorns, including: Steller's jays (Cyanocitta stelleri), blue jays, (Cyanocitta cristata), Lewis' woodpeckers (Asyndesmus lewis) and Douglas' squirrels (Tamiasciurus douglassi).

Douglas' squirrels were observed carrying acorns only twice and on both occasions they were carried approximately 8 m and buried. I retrieved these acorns and they appeared perfectly viable. They were buried about 2 cm deep, which should have greatly increased their potential for germination (Korstian, 1927). Thus, if Douglas' squirrels do occasionally fail to retrieve a cache, this would seem to be an effective mode of seed dispersal. It is not, however, a long distance means of dispersal.

Two blue jays were sighted at Oak Springs Fish Hatchery on 8 October, 1977. Although they were observed transporting acorns approximately 300 m, this species is not considered to be important in acorn dissemination, as it is considered an accidental species in this area.

Steller's jays were frequently seen carrying and dropping acorns. After grasping the seed in its beak, it commonly flies to a nearby conifer and eats or drops the seed. In addition, it often partook in a "musical chairs" type activity, whereby one jay would land in a tree, thus displacing the previous occupant, which in turn would fly to another tree and eject another jay, and so on; one or more seeds were dropped

in these exchanges. It is important in respect to progagule dissemination that Steller's jays did not retrieve fallen acorns.

It was also observed that Steller's jays would fly to either a Douglas fir or ponderosa pine to consume acorns; areas not inhabited by conifers as well as oaks were devoid of Steller's jays. Since conifers generally exist upslope relative to Oregon white oak, Steller's jays may be important vectors of upslope dispersal. Oak's linear extension up the south facing slopes of creek drainages into the Douglas fir zone may be dependent on this activity.

Lewis' woodpeckers, which do not participate in the typical woodpecker activity of hammering into tree bark seeking insects, seem to subsist on acorns and flight-captured insects (see Figure 46). They exhibit different behavior with respect to acorn consumption than do Steller's jays; they fly to oaks or western junipers as opposed to Douglas fir or ponderosa pine to eat acorns. This tree preference implies that Lewis' woodpeckers may be important modes of oak diffusion beyond the arid periphery of its range. Population extensions such as along Fifteen Mile Creek or Oak Brook Canyon may be the result of this activity.

Lewis' woodpeckers also cache large numbers of acorns in the crevices of trees and telephone poles (Figure 47). Viable-looking acorns were found lying on the ground under these seed storage areas.

Birds appear to be more effective agents of long distance dispersal than western gray squirrels. Lewis' woodpeckers were observed carrying acorns an average of 30-50 m, while Steller's jays transported them approximately 80-100 m. On several occasions, Steller's jays were seen moving acorns 300-400 m before landing. Utilizing the same method as was used to calculate the rate of population movement by gravity fall

Figure 46. Lewis' woodpeckers commonly carried acorns to other oak or juniper trees, where they cached or consumed them.

Figure 47. Lewis' woodpeckers stored viable acorns in the crevices of trees and telephone poles.

and roll, and by allowing Steller's jays a maximum of 500 m per carry, the swiftest rate of Oregon white oak expansion into a new habitat would be 2 km per 100 years, or 20 km per 1000 years. For Lewis' woodpeckers, given a maximum of 200 m per carry, the rate of migration would be 400 m per 100 years or 4 km per 1000 years. These figures will later be used to calculate potential post-Pleistocene migration rates.

MAN'S ROLE IN ACORN DISPERSAL

Humans have historically been active agents of plant dispersal. Transport methods have been as overt as the repeated attempts to introduce pheasant into North America, or as innocent as some insect introductions:

A friend of a friend of mine who had just returned from Europe was rather astonished when small beetles began to hatch out of his shirt buttons. These turned out to be made from the nuts of a kind of palm, and the larvae had gone on living in the stuff, having apparently passed through the manufacturing process without harm. (Elton, 1958, p. 3)

The Wasco-Wishram Indians, a Chinookan speaking group originally situated on the Columbia River within the study area, manufactured implements from oak wood and ate the acorns. Although of secondary importance to salmon, roots and seeds were gathered and consumed. And while acorns were popular food and trade items, it is stressed that:

The nuts [acorns] are not a staple, but were eaten at leisure moments, not at meals... (Spier and Sapir, 1930, p. 183).

Lewis and Clark's first observation of acorns came prior to the sighting of Oregon white oaks, about 25 km to the east of the John Day River:

We got from the people a few pounded roots, fish and acorns of white oak, those acorns they make use of as food

raw and roasted and inform us they procure them of the natives who live near the falls... (Thwaites, 1904, p. 143).

Acorns, then, were a trade item transported in both viable and non-viable condition. Roasted acorns were made into special standardized packages, along with huckleberries and hazel nuts, for trading purposes (Spier and Sapir, 1930).

For Indians to have been agents of dispersal, it was necessary for the seeds to be transported in raw form. Most ethnographic evidence, however, points to the non-viability of these trade items. Lee and Frost (1844, p. 181) record the following preparation of acorns:

Acorns, also, which are abundant some years, are used as an article of food. These are gathered and baked with heated stones - a method of preparing food common to both the Indians and the Pacific islanders. Heated stones are put into an excavation in the ground 3 feet across, and covered with leaves or grass so as to protect the articles to be cooked from burning. Then these are laid on and carefully covered in the same manner. Last of all earth is spread over the hole to keep in the heat, and the process of baking is done up in real native style. After the acorns are thus prepared, deep pits are dug near the water, where they remain through the winter; when they are taken up and eaten, much improved, it is supposed, by the soaking process.

The Wishram used a similar process, although they also added the seed of a wild mustard to the mud mixture for flavor (Spier and Sapri, 1930).

The leaching of bitter tannic acid would have rendered the acorns useless for germination. Neither process, however, explains Lewis and Clark's observation of "...raw..." acorns (Thwaites, 1904, p. 143).

Methods for preparing acorns, however, differed widely west of the Cascades. The Chehalis prepared them much like the Wascos (Gunther, 1945) as did the Kalapuyas (Peterson, 1975). The Cowlitz ripened the acorns in mud without cooking them, while the Klallam ate them fresh:

Acorns are eaten raw after the shell is cracked and the meat pounded on a rock. (Gunther, 1945, p. 28).

This is the only reference to the consumption of raw acorns.

SUMMARY

Plant species require the ability to migrate to favorable habitats during periods of environmental change. In Oregon white oak, large nutritious seeds, which are the preferred forage of several mobile vertebrates, provide the means of population movement through range extension. Douglas' squirrels, while burying acorns in suitable germination sites, do not carry acorns a great distance from the seed tree. Steller's jays, which act as vectors of seed dispersal into Douglas fir and ponderosa pine zones, carry acorns for several hundred meters. Lewis' woodpeckers, which transport acorns to more arid habitats, move acorns a shorter distance than Steller's jays. Through the actions of these two bird species, strategically placed propagules are ready to take advantage of varying climatic conditions.

Acorns fall from trees and roll a short distance. This mode of dispersal is probably not very effective due to heavy predation by herbivores, competition from the mother tree, and the slow potential rate of movement by this method, which may not allow the population to keep pace with a rapidly changing environment.

Due to their tendency to sink in water, stream transport of Q. garryana seeds probably seldom occurs. Flood conditions, however, might provide sufficient current and, through scouring action, an amenable seedbed for germination.

Although the Indians native to north-central Oregon - the Wasco-Wishram group - consumed and traded acorns, their practice of roasting them prior to transport probably precluded these people from being

active vectors of viable acorn dispersal. In the Willamette Valley, however, where at least one group is known to have eaten raw acorns, native groups may have been agents of acorn dissemination.

Oregon white oak has been shown to be a climax species in a state of reproductive equilibrium in central Oregon. Its disruption is climatically defined and its population status is in part a function of historic climatic changes and the introduction of livestock grazing. In addition, the different modes and potential rates of oak diffusion have been examined. In the following chapter, this information will be considered in conjunction with pollen evidence in order to shed light upon Q. garryana's post-Pleistocene migrational history in central Oregon and throughout the Pacific Northwest.

CHAPTER IX

MIGRATIONAL HISTORY OF OREGON WHITE OAK

INTRODUCTION

A plant's migrational pathway can be revealed by integrating the known temporal changes in climate of the area with a knowledge of the specie's climatic requirements, its historical presence in different areas, and its physical capacity to diffuse. In the following discussion, oak's migrational history will be proposed through consideration of its response to Hypsithermal warming, its entrance into the study area as determined by pollen evidence, and its intrinsic dispersal rates as calculated in Chapter VII.

HISTORY OF THE VEGETATION IN THE PACIFIC NORTHWEST

Hansen(1938; 1940; 1941a,b; 1942; 1943a,b,c; 1947; 1950) and Heusser (1960; 1964) surveyed the post-Pleistocene stratigraphy of the Pacific Northwest and reached much the same conclusion concerning the vegetational history of the area. At the close of the Wisconsin glaciation, the Willamette-Puget Trough was inhabited by lodgepole pine, Sitka spruce, and mountain hemlock. These forests were separated by patches of alpine vegetation(Detling,1958). As the glaciers receded, lodgepole pine quickly invaded the outwash plains, being replaced in time by western hemlock and Sitka spruce. The direction of migration was from south to north, although Pleistocene refugia for both Sitka spruce and western hem-

lock may have been provided by nunataks on Queen Charlotte Island (Hulten, 1937) thus providing northern centers of dispersal.

As the climate warmed and dried, early invading species were replaced by more xeric trees, including Douglas fir and later Oregon white oak. When conditions reached their warmest and driest during the Hypsitherm, some 4000-8000 years b.p., Oregon white oak reached its greatest areal extent and density. Subsequent climatic cooling has led to a partial replacement of the xeric flora by more mesic species.

The anticipated replacement of the xeric flora was in part checked by the action of resident Indians. They burned large sections of the Willamette-Puget Trough which resulted in the retention of oak (due to fire tolerance) in many areas which otherwise would have been invaded by conifers. The elimination of burning in the Valley after the 1850s would have allowed much of the oak population to be supplanted by Douglas fir, had the land not been converted to agricultural and forestry land-use (Johannessen, et al., 1971).

POLLEN INTERPRETATION

The purpose of examining the pollen record is to pinpoint the chronology of Oregon white oak's migrational history. Puportedly, oak traveled in a northerly direction from California to British Columbia in response to the Hypsithermal warming period (Detling, 1961; 1968). Although most of the pollen work was done prior to C¹⁴ dating methods and the accuracy of the chronologies presented by early workers has been challenged (Mack, et al., 1976), the pollen profiles do contain a reliable reference point in the 6600 years b.p. Mt. Mazama ash layer (Fryxall, 1965; Rigg and Gould, 1957).

Using data from 412 bogs, Rigg and Gould (1957) established a correlation between the age of pollen strata and the depth within the profile. Bogs located within the Puget Sound till area were found to accumulate peat at a rate of 41 years per inch (16.4 years per cm); those outside of the area had a mean of 48.5 years per inch (19.4 years per cm) for layers above the Mazama ash layer. In order to date oak's entry into an area, as evidenced by its presence in the pollen profile, several pollen cores containing oak pollen were interpreted using this correlation (Table XIII). Years were added to or subtracted from 6600 years, depending upon whether oak pollen appeared above or below the ash layer. Oak pollen layers within cores not exhibiting an ash layer were calculated by applying the age-depth correlation from the top of the profile.

The pollen samples used in this interpretation are located from British Columbia to Oregon coastal areas and in the lowlands enveloped by the Olympic lobe of the Wisconsin ice sheet. The basin and pothole topography characteristic of the glaciated areas are particularly conducive to pollen stratification. More southerly areas in the Willamette Valley lack the necessary topography and, in addition, would have been thoroughly scoured out by the Missoula Flood of 13,000 b.p. (Allison, 1935; Bretz, 1925). Thus, much of Q. garryana's pollen record is translated from the northern reaches of its range.

The chronological sequence so derived does not support the south to north migration hypothesis. The oldest pollen date comes from the Parkland bog in the Puget Sound, followed by the cores from the Willamette Valley well to the south. Sites on Vancouver Island, at the northern periphery of oak's range, yield early Q. garryana pollen as do widely scattered sites. Younger oak pollen recordings branch out from the cen-

TABLE XIII
CHRONOLOGY OF POLLEN STRATIGRAPHY

Site	Depth Below Ash Layer (cm)	X	Depth/Age Multiplier	+/- Mazama Ash Age (yrs)	Total (yrs)
Parkland (a)	620	X	16.4	+ 6,600	16,798
Ronald (a)	220	X	16.4	+ 6,600	10,208
Malahat (b)	0	X	16.4	+ 6,600	6,600
Little Qualicum (b)	100*	X	16.4	0	1,640
Pangborn Lake (b)	150	X	16.4	6,600	9,060
Whidbey Island (b)	0	X	16.4	6,600	6,600
Ozette Lake (b)	200*	X	19.4	0	3,800
Seaview (b)	100*	X	19.4	0	1,940
Garrison Lake (b)	Radiocarbon dated			0	6,500
Black Creek (c)	210	X	16.4	6,600	10,044
Qualicum Beach (c)	230	X	16.4	6,600	10,372
Langford Lake (c)	320	X	16.4	6,600	11,848
Onion Flat (d)	325	X	19.4	6,600	12,905
Lake Labish I (d)	275	X	19.4	6,600	11,935
Lake Labish II (d)	300	X	19.4	6,600	12,420

Sources: (a) Hansen, 1938
 (b) Heusser, 1960
 (c) Hansen, 1950
 (d) Hansen, 1942

* Depth is below surface; Mazama ash was not present in the profile.

ter of oak's range toward coastal areas not presently inhabited. Thus, rather than incrementally moving northward with the improving post-Pleistocene climate, Oregon white oak appears to have been already inhabiting its current northern boundaries.

HYPsITHERMAL RELICTS

Another line of evidence for Q. garryana's migration comes from the existence of several disjunct "islands" of xeric vegetation (Detling, 1953). These isolated communities, which contain species commonly associated with more southerly regions, are considered to be reductional relicts of a once more liberally distributed association. The Hypsithermal warming and drying supplied an amenable climate for a northerly migration of these plant species, while the subsequent cooling of the last few thousand years has restricted this vegetation to a few favorable microhabitats.

Oregon white oak's presence in the Pacific Northwest is attributed to the aforementioned Hypsithermal conditions. For this hypothesis to be true, oak must have advanced from California north through the Willamette Puget-Trough to Vancouver Island. The Klamath-Siskiyou Mountains, which would have presented a formidable barrier, may have been circumvented by following the Klamath River to the coast and then entering the Willamette Valley via the Umpqua or Rogue River. Allowing this exodus to begin at Redding*, California, Oregon white oak must have traveled over 1000 km to have reached its present northern frontier.

The proposed pollen chronology (Table XIII), if considered in light

*Redding was chosen because if Detling (1968) is correct in assuming that Pleistocene conditions were too severe for oak to have wintered over to the north of the Klamath-Siskiyou Mountains, this northern tip of the Central Valley may have been the first southerly site of amenable conditions.

of the previously presented limitation of acorn dispersal rates, clearly show that Q. garryana did not migrate from California, as Detling (1953) has contended, during the Hypsitherm. Rather, if the maximum rate of acorn dispersal is 20 km per 1000 years as proposed (Chapter VIII), oak's post-glacial distribution must have closely paralleled its current northern reaches in order to have prospered so immediately after the Pleistocene. Over half of the sites contain oak pollen in the 10,000-12,000 years b.p. range, which is contemporaneous with the cessation of Ice Age conditions at about 12,000 years b.p.

It is of course possible that either or both of the rates of acorn dissemination and the pollen chronology are incorrect. In the former case, jays or woodpeckers may transport acorns farther than observed in the study area. For this to be the case, however, the average maximum rate of diffusion would need to be greatly increased (500 km per 1000 years for 2000 years as opposed to the projected 20 km per 1000 years) which would be equal to Stellers jays consistently carrying acorns 12.5 km per flight, which seems well beyond their capabilities.

Running water, which was relegated a minor role in acorn dispersal, may have been operative during the Missoula Flood, although this event could account for only a portion of the necessary acorn movement. This largest of all recorded deluges, dated at approximately 13,000 years b.p., burst through the Columbia Gorge from eastern Washington, carrying a mass of water and ice perhaps 300 m deep, raced up the Willamette Valley to near Eugene, depositing Rocky Mountain erratics up to the 100 m contour interval, and then continued westward into the Pacific Ocean. The flood could conceivably have carried acorns (not to mention entire forests) from the southern Willamette Valley and deposited them

along the Willamette and Columbia River's drainages, which might account for at least 200 km of northern range extension. Another, although unlikely, possibility is that acorns were rafted out to sea, followed the longshore currents north up the Oregon and Washington coast, and finally came to rest on the shores of Vancouver Island. The non-viability of acorns in salt water, however, makes this a remote possibility.

The role of Indians as agents of acorn dispersal may be underestimated. Although the Wasco-Wishram group was largely discounted as a seed disseminator, the tribes in the Willamette-Puget Trough may have been more effective at this enterprise. Gunther (1945), for example, noted that the Klallam group in Washington ate raw acorns. While it is therefore plausible that living acorns were traded and occasionally dropped in viable form, this process would not have accounted for 1000 km of diffusion in 2000 years.

It is also possible that the pollen record is being misinterpreted and that Rigg and Gould's (1957) correlation is not valid. Regardless, oak pollen shows up in the profile below the ash layer, and thus was present prior to 6600 years b.p. Application of the acorn dispersal rates even to the Mazama ash layer does not account for dispersal all the way from California.

It can thus be safely inferred that Oregon white oak was present in the Willamette-Puget Trough during one or more of the Pleistocene ice advances, and that it could not have migrated from California in the short period of time available during the Hypsitherm.

As a sideline, it is worth noting that while Q. garryana is the only representative of the genus Quercus in the Pacific Northwest, California black oak (Q. kelloggii) forms its northernmost stands along the

Umpqua River in southern Oregon. If the dispersal rates estimated for Q. garryana are applied to California black oak (starting again at Redding, California), 20 km per 1000 years for 12,000 years (post-Pleistocene period) yields a potential 240 km movement, which places Q. kelloggii quite near its present northernmost range. Although application of acorn dispersal rates to a different species of Quercus loses some validity, it is at least plausible and thus adds some credibility to the estimated dispersal rates.

CHRONOLOGY OF MIGRATION IN OREGON WHITE OAK

Although the topography and climate of the study area does not lend well to pollen profile accumulation, predictions can be made concerning Oregon white oak's migrational history using previously presented information. First, oak could not have colonized the area during a period drier than at present. Previous size-structure data have shown that at best Q. garryana is maintaining a stable population through its central range, and at the arid periphery of its range, it is limited by lack of precipitation. Thus, a period of increased aridity, such as the Hypsitherm, would have forced an upslope movement and general retreat of Oregon white oak from central Oregon. Rather than increasing numerically during the Hypsitherm, as was the case west of the Cascades, oak would have generally decreased in number.

Second, oak was apparently not present in the Columbia Gorge after the Missoula Flood. It is highly unlikely that oak could have survived in any number after this catastrophic event. Thus, if oak did use the Columbia Gorge as a migrational corridor, it must have done so after 13,000 years b.p.

Given these two conditions, two possible sequences of Oregon white oak's migration into the study area exist. Hypsithermal warming and drying, which lasted from approximately 4000-8000 years b.p., would have facilitated movement from the Willamette-Puget Trough through the Gorge by alleviating competition with Douglas fir and ponderosa pine. At the close of the Hypsitherm, with annual precipitation increasing east of the Cascades, oak could have moved south between the Cascades and the Deschutes River, thus arriving at its present position. Placing the initial migration into the Gorge at 13,000 years b.p., the application of maximum dispersal rates of 20 km per 1000 years yields an oak advance of 260 km, which exceeds the present southern extension of oak's range. Thus, this explanation is plausible if Q. garryana's center of distribution was the Willamette Valley.

An alternative explanation is that oak inhabited central Oregon throughout the Pleistocene, thus serving as a center of post-Pleistocene dispersal into western Oregon and Washington. The strength of this explanation rests in the climatic data referred to earlier, whereby Q. garryana was found to migrate upslope during dry periods and downslope into the sagebursh/juniper zone during moist periods. This area is thus open to plant migration during periods of environmental change and, once inhabiting such an area, Oregon white oak would be difficult to displace. The Willamette-Puget Trough, however, is a closed system for plant migration; it lacks an arid zone refuge which xeric species could inhabit during increasingly moister and cooler periods such as the Pleistocene. If oak did winter-over in the Willamette-Puget Trough in favorable microhabitats, as seems to be the case, it should have been even more capable of weathering conditions east of the Cascades, where conditions

were more amenable to xeric-type species.

SUMMARY

Oregon white oak was previously thought to have migrated north from California into its present position during the Hypsithermal maximum. The pollen record and acorn dispersal rates do not, however, substantiate this hypothesis; oak must have inhabited the Pacific Northwest well before the Hypsitherm. Application of acorn dispersal rates to Q. kelloggii infer that this species could have colonized its present northern frontier position during the Hypsitherm.

Two explanations are proposed for Q. garryana's occurrence in central Oregon: 1) it migrated east through the Columbia Gorge after the Missoula Flood, reaching its farthest southern and eastern extension during the recent moisture maximum; or 2) it was present in central Oregon throughout the Pleistocene, possibly back to Pliocene times.

CHAPTER X

MAJOR CONCLUSIONS

METHODOLOGICAL CONCLUSIONS

1. Size-structure evaluation is an effective means of establishing population equilibrium in tree species. If age-structures are found to statistically correlate with size-structures, aberrations from the expected regression curve can be compared to concurrent environmental changes in order to interpret possible cause and effects.

2. Q. garryana does not lend itself to increment core-dating due to progressive heart rot. Some other means of dating needs to be developed for individuals over 100 years of age.

3. Comparison of population dynamics to environmental factors is particularly fruitful if a radical change, such as the 1930s drought, is available as an index.

4. Acorns can be effectively marked with red spray paint for retrieval the following year. By plotting the position of retrieved acorns, an interpretation of oak's intrinsic dispersal capabilities can be made.

5. Acorns are adapted to dispersal by woodpeckers, jays and squirrels. While gross estimates of the distance carried can be made by simple observation, more accurate tracking of territorial characteristics would increase the reliability of these measurements. Through measurement of the average seed dispersal distances and with a knowledge of the time required from seed germination to tree maturity, estimates of potential rates of population movement can be made.

6. Ethnographic data can be used to either support or refute claims of human dispersal of seeds.

7. Pollen records can be used to date the colonization of an area by a plant species if a peat depth versus age relationship has been established for the area.

BIOGEOGRAPHIC CONCLUSIONS

1. Q. garryana is generally replacing itself in central Oregon.

2. There is no reliable evidence that oak is either expanding or retreating in its range. Youthful age-structures at the periphery of its range, which would indicate population expansion, were not found. While several sites exhibited unhealthy size-structures, these can largely be attributed to man's land-use activities.

3. Acorn sprouting is rare as a means of regeneration. This may be an adapted characteristic, since frequent regeneration in a long-lived species is not necessary. Thick sod or duff layers may also be inhibiting acorn germination. Coppice sprouting, however, is common in oak in central Oregon. Although this stress reaction would be an effective means of recolonization after fire, it could not aid in oak population diffusion.

4. Oregon white oak is a climax species throughout much of its north-central Oregon range. It exclusively occupies a narrow band between the sagebrush/grassland/juniper and the ponderosa pine/Douglas fir associations.

5. Oak is delimited by the 300 mm and 1500 mm isohyets. The microclimatic effects of differing slope aspect may help to account for this great range in moisture tolerance.

6. The effect of climatic change on oak's population structure varies greatly. It was partially eliminated at its arid periphery during the 1930s drought, but recovered during moist periods, while at its coniferous frontier it yielded to evergreen competition during moist periods, but expanded into this area during the drought. The sum total of Oregon white oak's response to climatic change was retreat at one frontier and expansion at the other.

7. There was a direct correlation between precipitation variation and oak regeneration at sites not overly impacted by human activity.

8. Sites with unhealthy size-structures strongly correlated with the occurrence of heavy livestock grazing. This activity threatens to eliminate Q. garryana from these areas if given a long enough period of time.

9. Acorns quickly germinate in areas relieved of cattle grazing pressure, possibly in response to the elimination of competitive herbs and the tight sod layer.

10. Animals consume acorns and the terminal buds of oaks in natural ecosystems. The direct effects of native herbivory is not known, although a symbiotic relationship whereby Q. garryana and the herbivores exchange carbohydrate nutrition for acorn dispersal is indicated. Elimination of the upper trophic level elements, such as raptors and large mammals, may be expected to disrupt this balanced relationship, possibly resulting in increased predation on acorns and thus a drop in seed regeneration.

11. Gravity fall and roll is a slow means of acorn dispersal and, due to competition with the mother tree and heavy predation, not very effective.

12. The acorns of Oregon white oak are probably not disseminated by running water due to their weight and low-longevity, although flood stage conditions could conceivably negate these limitations.

13. Steller's jays are the most effective means of acorn dispersal, followed by Lewis' woodpeckers and Douglas' squirrels. A maximum acorn dispersal rate of 20 km per 1000 years for Steller's jays and 4 km per 1000 years for Lewis' woodpeckers was predicted.

14. The habit of roasting acorns prior to consumption precludes the early Wasco-Wishram Indians from acting as vectors of acorn dissemination in central Oregon. In the Willamette-Puget Trough, however, Indian dispersal of viable acorns may be a factor in oak distribution.

15. Q. garryana was present in the Willamette-Puget Trough during at least the Wisconsin glacial advance.

16. Two possibilities exist for Oregon white oak's presence in central Oregon: 1) it migrated from western Oregon through the Columbia Gorge immediately after the Missoula Flood; or 2) it inhabited central Oregon throughout the Pleistocene, migrating upslope and downslope as climatic conditions dictated.

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APPENDIX I

PLANTS IDENTIFIED IN THE STUDY AREA

Oregon White Oak	<u>Quercus garryana</u> Dougl.
Douglas Fir	<u>Pseudotsuga menziesii</u> (Mirb.) Franco
Ponderosa Pine	<u>Pinus ponderosa</u> Dougl. ex Loud
Incense Cedar	<u>Libocedrus decurrens</u> Torr.
Hairy Manzanita	<u>Arctostaphylos columbiana</u> Piper
Snowbrush	<u>Ceanothus velutinus</u> Dougl. ex Hook
Wild Rose	<u>Rose</u> ssp.
Bitterbrush	<u>Purshia tridentata</u> Pursh (DC)
Wild Strawberry	<u>Fragaria vesca</u> (L)
Horsetail	<u>Equisetum</u> ssp.
Arrowleaf Balsamroot	<u>Balsamorhiza deltoidea</u> Nutt
Compositae	?
Western Juniper	<u>Juniperus occidentalis</u> Hook
Oceanspray	<u>Holodiscus discolor</u> (Pursh) Maxim
Oregongrape	<u>Berberis nervosa</u> Pursh
Berry	<u>Rubus</u> ssp.
Sedge	<u>Carex</u> ssp.
Water Birch	<u>Betula occidentalis</u> Hook
Columbine	<u>Aquilegia formosa</u> Fisch.
Ninebark	<u>Physocarpus capitatus</u> (Pursh) Ktze.
Big Sagebrush	<u>Artemisia tridentata</u> Nutt
Cheatgrass	<u>Bromus tectorum</u> (L)
Lomatium	<u>Lomatium</u> ssp.

Snowberry	<u>Symphoricarpos albus</u> (L) Blake
Willow	<u>Salix</u> ssp.
Currant	<u>Ribes</u> ssp.
Rabbitbrush	<u>Chrysothamnus</u> ssp.
Yarrow	<u>Achillea millefolium</u> (L)
Grand Fir	<u>Abies grandis</u> (Dougl.) Lindl.
Blackberry	<u>Rubus ursinus</u> Cham and Schlecht.
Poison Oak	<u>Rhus diversiloba</u> T. and G.
Western Hazel	<u>Corylus cornuta</u> Marsh
Idaho Fescue	<u>Festuca idahoensis</u> Elm
Big Leaf Maple	<u>Acer macrophyllum</u> Pursh
Vine Maple	<u>Acer circinatum</u> Pursh
Bluebunch Wheatgrass	<u>Agropyron spicatum</u> (Pursh) Scirbn. and Smith
Serviceberry	<u>Amelanchier alnifolia</u> Nutt
Lupine	<u>Lupinus</u> ssp.
Pearly Everlasting	<u>Anaphalis margaritacea</u> (L) B. and H.
Western Hawthorn	<u>Crataegus douglasii</u> Lindl.

APPENDIX II

BIRDS IDENTIFIED IN THE STUDY AREA

Steller's Jay	(<u>Cyanocitta stelleri</u>)
Lewis' Woodpecker	(<u>Asyndesmus lewis</u>)
Mt. Chickadee	(<u>Parus gambeli</u>)
Chestnut-backed Chickadee	(<u>Parus rufescens</u>)
Western Meadowlark	(<u>Sturnella neglecta</u>)
Downy Woodpecker	(<u>Dendrocopos pubescens</u>)
Oregon Junco	(<u>Junco oreganus</u>)
Varied Thrush	(<u>Ixoreus naevius</u>)
Rufous-sided Towhee	(<u>Pipilo erythrophthalmus</u>)
Ruby-crowned Kinglet	(<u>Regulus calendula</u>)
Red-tailed Hawk	(<u>Buteo jamaicensis</u>)
Red-shafted Flicker	(<u>Colaptes cafer</u>)
Unidentified Buteo	(<u>Buteo</u> ssp.)
Unidentified Sparrow	(??)
Black-billed Magpie	(<u>Pica pica</u>)
Belted Kingfisher	(<u>Megaceryle alcyon</u>)
Common Crow	(<u>Corvus brachyrhynchos</u>)
Starling	(<u>Sturnus vulgaris</u>)
Great Blue Heron	(<u>Ardea herodias</u>)
Blue Jay	(<u>Cyanocitta cristata</u>)
Golden-crowned Kinglet	(<u>Regulus satrapa</u>)
Red-breasted Nuthatch	(<u>Sitta canadensis</u>)
California Quail	(<u>Lophortyx californicus</u>)

Rock Wren	(<u>Salpinctes obsoletus</u>)
Anna's Hummingbird	(<u>Calypte anna</u>)
Fox Sparrow	(<u>Passerella iliaca</u>)
Cedar Waxwing	(<u>Bombycilla garrula</u>)
Golden Eagle	(<u>Aquila chrusaetos</u>)
White-breasted Nuthatch	(<u>Sitta carolinensis</u>)
White-headed Woodpecker	(<u>Dendrocopos albolarvatus</u>)
Turkey Vulture	(<u>Cathartes aura</u>)

APPENDIX III

TABLE I

CALCULATION OF ANNUAL RING DATA

x	y	x ²	y ²	xy
28	10	784	100	280
32	14	1084	196	448
33	8	1089	64	264
35	11	1225	132	385
36	23	1296	529	828
38	12	1444	144	456
43	12	1849	144	516
48	23	2304	529	1104
49	38	2401	1444	1862
52	25	2704	625	1300
53	20	2809	400	1060
55	20	3025	400	1100
55	26	3136	676	1456
63	33	3969	1089	2079
84	51	7056	2601	4284
€705	€326	€36,175	€9073	€17,422

$$\bar{x} = 47.0 \quad \bar{y} = 21.7$$

Coefficient of Correlation

$$r = \frac{n(\epsilon xy) - (\epsilon x)(\epsilon y)}{\sqrt{n(\epsilon x^2) - (\epsilon x)^2} \cdot \sqrt{n(\epsilon y^2) - (\epsilon y)^2}}$$

$$r = \frac{31,500}{63615 \cdot 29819} = .723$$

- $n(15) = .514 < .723$
- there is linear correlation

Estimation of Sum of Squares (ss)

$$ss = \frac{(\epsilon y^2) - b_0(\epsilon y) - (b_1(\epsilon xy))}{n-2}$$

Estimation of Sum of Squares (continued)

$$ss = \frac{9073 + 3488.2 - 12021.2}{13}$$

$$ss = 41.5$$

$$\therefore ss_{b_1} = \frac{n(ss)}{n(\epsilon x^2) - (\epsilon x)^2} = 0.013$$

Linear Function

$$b_1 = \frac{n(\epsilon xy) - (\epsilon x)(\epsilon y)}{n(\epsilon x^2) - (\epsilon x)^2}$$

$$b_1 = \frac{31500}{45600} = .69$$

$$b_0 = y - b_1 x$$

$$= 21.7 - .69(47)$$

$$b_0 = -10.7$$

$$\hat{y} = -10.7 + .69x$$

Estimation of x from y (inverse prediction)

$$\hat{x} = \frac{(y - a)}{b_{y \cdot x}} \quad \text{This gives the } \hat{x} \text{ value}$$

For 95% confidence limits:

$$D = b^2_{y \cdot x} - t^2_{.05(n-2)} S^2_b$$

$$D = (.69)^2 - (2.16)^2 (.013)$$

$$D = .47 - .06 = .41$$

$$\text{Then } H = \frac{t_{.05(n-2)}}{D} \sqrt{S^2_{y \cdot x} \left[D(1 + 1/2) + \frac{(y_i - \bar{y})^2}{\epsilon x^2} \right]}$$

Then, with H for a particular y in question, the 95% confidence limits are set by:

$$L_1 = \bar{x} + \frac{by \cdot x(y_i - \bar{y})}{D} - H$$

$$L_2 = \bar{x} + \frac{by \cdot x(y_i - \bar{y})}{D} + H$$

To convert a particular DBH in centimeters to circumference in inches,

$$\frac{DBH \cdot \pi}{2.4} = \text{circumference in inches.}$$

TABLE II

INVERSE PREDICTIONS OF X (AGE) FROM Y (DBH)

dbh(cm)	(y) inches in circ.	H	X (age in years)	L ₁ (95% conf. limits	L ₂ 95% conf. limits
5	6.6	22.3	25.0	-1.0	43.8
6	7.8	22.3	26.8	1.3	45.9
7	9.2	22.3	28.8	3.7	48.3
8	10.5	22.3	30.7	5.8	50.4
9	11.8	22.2	32.6	8.1	52.5
10	13.0	22.2	34.3	10.1	54.6
11	14.4	22.2	36.4	12.5	56.9
12	15.7	22.2	38.3	14.7	59.1
13	17.0	22.2	40.1	16.9	61.3
14	18.3	22.2	42.0	19.1	63.5
15	19.6	22.2	43.9	21.3	65.6
16	20.9	22.2	45.8	23.4	67.8
17	22.2	22.2	47.7	25.6	70.0
18	23.6	22.2	49.7	28.0	72.4
19	24.9	22.2	51.6	30.2	74.6
20	26.2	22.2	53.5	32.4	76.7
21	27.5	22.2	55.4	34.6	79.0
22	28.8	22.2	57.2	36.7	81.1
23	30.1	22.2	59.1	38.9	83.3
24	31.4	22.2	61.0	41.1	85.5
25	32.7	22.3	62.9	43.2	87.8
26	34.0	22.3	64.8	45.4	90.0
27	35.3	22.3	66.7	47.6	92.2
28	36.6	22.3	68.5	49.8	94.4
29	38.0	22.3	70.6	52.1	96.7
30	39.2	22.4	72.3	54.3	98.6
31	40.6	22.4	74.3	56.4	101.2
32	41.9	22.5	76.2	58.5	103.5
33	43.2	22.5	78.1	60.7	105.7
34	44.5	22.5	80.0	62.9	107.9
35	45.8	22.5	81.9	65.0	110.0

TABLE II (continued)

dbh(cm)	(y) inches in circ.	H	X (age in years)	L ₁ (95% conf. limits	L ₂ (95% conf. limits
36	47.1	22.6	83.8	67.1	110.0
37	48.4	22.7	85.6	69.2	112.3
38	49.7	22.7	87.5	71.4	114.6
39	51.0	22.8	89.4	73.5	116.8
40	52.3	22.8	91.3	75.7	119.1
41	53.7	22.9	93.3	77.9	121.3
42	55.0	22.9	95.2	80.1	123.7
43	56.3	22.9	97.1	82.3	125.9
44	57.6	22.9	99.0	84.4	128.1
45	58.9	23.0	100.8	86.5	130.4
46	60.2	23.1	102.7	88.6	132.7
47	61.5	23.2	104.6	90.8	135.0
48	62.8	23.2	106.5	92.9	137.2
49	64.1	23.3	108.4	94.9	139.5
50	65.4	23.4	110.3	97.0	141.7
51	66.7	23.5	112.2	99.2	144.0
52	68.1	23.5	114.2	101.5	146.2
53	69.4	23.6	116.1	103.6	148.7
54	70.7	23.7	118.0	105.7	151.0
55	72.0	23.8	119.9	107.7	153.3
56	73.3	23.9	121.7	109.9	155.5
57	74.6	24.0	123.6	112.0	157.7
58	75.9	24.1	125.5	114.1	160.0
59	77.2	24.2	127.4	116.2	162.3
60	78.5	24.5	129.3	118.3	164.6
61	79.8	24.4	131.1	120.4	166.9
62	81.1	24.5	133.0	122.5	169.2
63	82.5	24.6	135.1	124.7	171.5
64	83.8	24.7	136.9	126.8	173.9
65	85.1	24.8	138.8	128.9	176.2
66	86.4	24.9	140.7	131.0	178.5
67	87.7	25.0	142.6	133.1	180.8
68	89.0	25.1	144.5	135.1	183.1
69	90.3	25.2	146.4	137.2	185.4
70	91.6	25.3	148.3	139.3	187.6
71	92.9	25.5	150.1	141.3	189.9
72	94.2	25.6	152.0	143.4	192.3
73	95.5	25.7	153.9	145.5	194.6
74	96.9	25.8	155.9	147.8	196.9
75	98.2	25.9	157.8	149.8	199.3
76	99.5	26.0	159.7	151.9	201.6
77	100.8	26.2	161.6	153.9	203.9
78	102.1	26.3	163.5	156.0	208.6
79	103.4	26.4	165.4	158.1	210.9
80	104.7	26.5	167.2	160.2	213.2