THE *QUERCUS GARRYANA* FORESTS OF THE WILLAMETTE VALLEY, OREGON

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Abstract. *Quercus garryana* forests, prominent at low elevations throughout the Willamette Valley, Oregon, have developed from oak savanna subsequent to settlement of the valley in the mid-nineteenth century. Interruption of the ground fires that were common in the pre-settlement environment probably caused the change. The understory of the oak forest is dominated by shrubs, and well-defined strata are present. Four plant communities occur: (1) *Quercus garryana/Corylus cornuta* var. *californica/Polystichum munitum* (most mesic); (2) *Quercus garryana/Prunus avium/Symphoricarpos albus;* (3) *Quercus garryana/Amelanchier alnifolia/Symphoricarpos albus;* and (4) *Quercus garryana/Rhus diversiloba* (most xeric). All are in seral condition because of their relatively recent development and because they have been disturbed throughout their existence by man's activities. The soils supporting the oak forest are generally deep and well drained and have developed profiles with illuvial horizons and acidic reaction. They are derived from sedimentary and basic igneous rocks and old valley-filling alluvium. Seven established soil series are present: Steiwer, Carlton, Peavine, Nekia, Dixonville, Olympic, and Amity. The Steiwer series and its catenary associate, Carlton, are the most common soils.

INTRODUCTION

Forests dominated by *Quercus garryana*[2] are a characteristic vegetation at low elevations throughout northwestern Oregon. Although the range of the species extends from southern Vancouver Island, British Columbia, to the coastal mountains south of San Francisco, California (Fig. 1), it attains its best development as a dominant tree on the cross-valley ranges and bordering foothills of the central Willamette Valley. In this region it forms almost pure, closed-canopy stands, occurs intermixed with conifers or other broadleaf trees, and grows as isolated trees in pastures, farmlands, and grassy foothill balds. This study describes the floristic composition, stand structure, physical environment, and successional status of plant communities where *Quercus garryana* is the major component of the overstory.

STUDY AREA

Geography and physiography

The Willamette Valley is located in western Oregon about 65 km inland from the Pacific Ocean. It extends southward from the Columbia River approximately 210 km and is bounded by the Oregon Coast Range on the west and the Cascade Mountains on the east. The width varies from 40 to 65 km. Average elevation of the valley floor is approximately 90 m. The northward-flowing Willamette River with its many tributaries is the major drainage system.

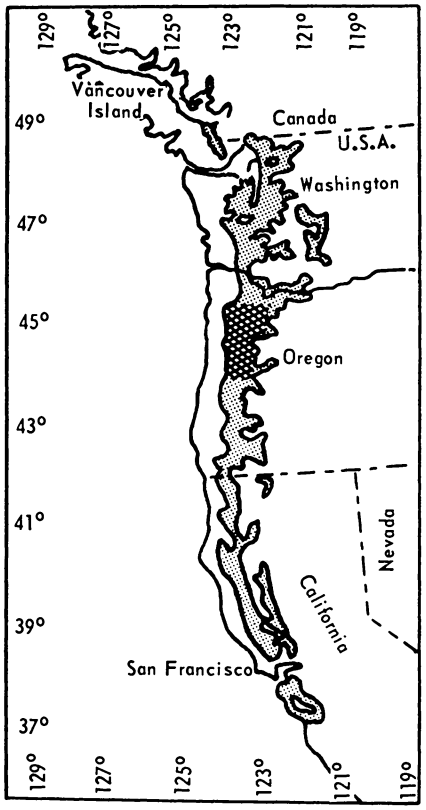

FIG. 1. Range of *Quercus garryana*. Study area indicated by crosshatching.

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[2] Where possible, scientific nomenclature follows Hitchcock et al. (1955–60). Otherwise, Peck (1961) has been used, except for Gramineae, where the authority is Hitchcock (1950).

The valley is a structural depression with hills of moderate relief separating wide alluvial flats. It is divided east and west by a low range of hills (Salem-Eola Hills) about halfway down its length. South of these hills it is relatively broad to the vicinity of the city of Eugene, Oregon. Isolated basaltic buttes are a prominent physiographic feature in the southern valley.

Geology

The geology of the Willamette Valley is complex. Both sedimentary and volcanic geologic materials are present and often intermixed. Quaternary gravels, sands, and silts cover most of the lower portions of the valley. To the west the foothills of the Oregon Coast Range consist of sandstones and shales of Eocene and Miocene age. The Cascade Mountain foothills along the eastern side of the valley are predominantly Columbia River basalts. The valley itself was never glaciated, but has been inundated several times during interglacial periods by meltwater floods from the Columbia River. The last of these, the Missoula flood, is reported to have covered the valley to a depth of over 120 m above sea level (Baldwin 1959).

Climate

In Thornthwaite's (1931) climatic scheme, the Willamette Valley region is classed as a humid, microthermal climate with a deficiency of summer precipitation. Average yearly precipitation is about 1,220 mm, occurring mostly as rain between the months of November and May. Snow is not uncommon during the winter, but rarely remains on the ground for long periods. Very little precipitation occurs during the summer months. Temperature extremes are rare as high summer temperatures are moderated by an afternoon ocean breeze that occurs almost daily. Winter temperatures are moderated by warm-moist southwesterly oceanic winds. Mean winter temperature is about 5°C; spring temperatures average 10°C; summer temperatures, 21°C; and fall temperatures, 12°C.

Historical Aspects

The first detailed account of the vegetation of the Willamette Valley was given by David Douglas (1914). In 1826 he described the northwestern portion of the valley as, "Country undulating, soil rich, light with beautiful solitary oak and pine [*Pseudotsuga menziesii*] interspersed through it." Further south, he described the appearance of the vegetation as ". . . oaks more abundant and pines [*Pseudotsuga*] scarcer and more diminutive in growth."

Douglas also emphasized the burned-over nature of the country and stated he was told by the Indians burning was for ". . . urging the deer to frequent certain parts, to feed, which they [Indians] leave unburned, and of course they [deer] are easily killed," and ". . . that they [Indians] might better find wild honey and grasshoppers, which both serve as articles of winter food."

In the report of the Wilkes Expedition of 1838–42 (Wilkes 1845), rolling uplands in the vicinity of Tualatin, Oregon, were described as ". . . destitute of trees, except scattered oak; these look more like orchards of fruit trees, planted by the hand of man, than groves of natural growth." The minor effect of fire on mature oak trees was noted in the report: "The country had been overrun by fire, which had destroyed all the vegetation except the oak trees, which appeared to be uninjured." Fires set by Indians were described as the causal agent in keeping down the undergrowth beneath the oaks, and the comment made, ". . . since the white have had possession of the country the undergrowth is coming rapidly up in places." This was in 1840.

By 1852 ". . . the hills and prairies had commenced to grow up with a young growth of firs [*Pseudotsuga*] and oaks, because the Calapooias [local Indian tribe] were no longer there to burn off the face of the country" (Clarke 1927). Much of the land once "oak prairie" was covered by a heavy growth of "oakgrubs" and young trees of other species in the late 1870's (Nash 1882).

Large numbers of immigrants were starting to move into the Willamette Valley by 1845. Because of the abundance of native grasses, livestock raising became one of the major occupations of the settlers. Wheat farming replaced livestock production as the major land use during the 1870's, and lands covered with dense stands of "oakgrubs" were cleared for planting. By the mid-1880's wheat production declined because of high crop losses from disease and competition from other areas, and many abandoned fields reverted to oak scrub.

These reports of the vegetation of the Willamette Valley indicate that coniferous species did not dominate the vegetation at low elevations in the valley itself, although *Pseudotsuga menziesii* was present even in the savannas.

Methods

Investigations were confined to closed-canopy stands 4 ha or more in area where *Quercus garryana* was the major component of the overstory. Basal area, frequency, and density of overstory trees were determined on twenty 0.004-ha circular plots spaced at 9-m intervals in four rows parallel to the slope contour. Density was re-

corded in four classes: saplings (< 10 cm dbh); poles (11–40 cm dbh); mature (41–100 cm dbh); and relict (> 100 cm dbh). The maximum height of trees on each plot was measured with an optical rangefinder. Age-diameter relationships of *Quercus garryana* were obtained from increment cores and ring counts of cut stumps.

Frequency and percentage crown coverage of shrub and herbaceous species were recorded on sixty 0.2-m^2 quadrats spaced at 3-m intervals in four rows coincident with the rows of 0.004-ha plots. Very low crown coverage was recorded as trace and arbitrarily assigned a value of 0.5% for calculation purposes. Above trace, the intervals were 1% and 5%. Coverage greater than 5% was estimated to the nearest 10%. Density of shrub and herbaceous species was not determined because of the high numbers present and the frequent impossibility of distinguishing an individual plant.

Physical site attributes (elevation, position on slope, slope angle, slope orientation) were recorded, and a complete soil description was made for each macroplot (U. S. Soil Survey Staff 1951).

The phytosociological importance of each species in the tree stratum was determined by summing its percentage basal area, percentage total density, and percentage frequency. In the subordinate strata (tall shrub, low shrub, herbaceous) percentage crown coverage and percentage frequency were added to determine species importance. Species were arranged by strata in descending order of importance in each macroplot, and the macroplot data serially tabulated in a releve. Physical site attributes, soil features, and disturbance factors were also listed on the releve for each macroplot. The releve was rearranged according to similarities in species composition, importance ranks, and environmental attributes.

The groupings formed are the basis for the plant communities designated. The term "plant communities" is used to indicate a geographically repeated assemblage of plants of relatively uniform species composition and structural characteristics. The dominant species in the tree and shrub strata are used to designate the communities. It should be emphasized that most species are not confined to any one plant community. There are changes, however, in species dominance, distribution, vigor, and growth form between communities that gives each a recognizable physiognomy.

Vegetation

Four plant communities have been distinguished. The *Quercus garryana/Corylus cornuta* var. *californica/Polystichum munitum* community is found on moderate to steep, sheltered slopes. More exposed slopes and ridges are occupied by the *Quercus garryana/Amelanchier alnifolia/Symphoricarpos albus* community. The *Quercus garryana/Prunus avium/Symphoricarpos albus* community is found on both level and sloping sites on a variety of aspects. The most exposed sites in the oak forest are occupied by the *Quercus garryana/Rhus diversiloba* community which does not have a well-developed tall shrub stratum. Only the generic names will be used hereafter.

Tree stratum

At present *Quercus garryana* is dominant in the tree stratum of all communities (Table 1). Two growth forms of *Quercus garryana* occur. The majority of the trees have developed under forest conditions. These "forest-form" trees are relatively tall, seldom exceed 60 cm dbh, and have ascending branches clustered near the crown. Their crowns form a closed canopy. Mean density of forest-form *Quercus garryana* is 1,054 trees/ha. The average age of mature forest-form trees is 90 years with a range of 47–135 years.

Scattered through the forest are a few large relict *Quercus garryana* apparently developed under nonforested conditions. These "savanna-form" trees generally exceed 1 m dbh and their boles are short in relation to the total height of the tree. They have massive branches and spreading crowns and are usually spaced so the crowns do not touch. There is an average of 17 savanna-form *Quercus garryana* per hectare. Annual growth rings from a small sample of freshly cut trees indicated a mean age of 283 years, with a range of 257–308 years, for trees 76–94 cm dbh. Fowells (1965) indicates *Quercus garryana* may live over 500 years and reaches 90 cm dbh at 250 years.

There are some distinct differences in the phytosociological attributes of *Quercus garryana* between the four communities. Large forest-form trees—a tree with a tall, generally undivided trunk and small, ascending branches—are most numerous and tallest and the basal area of *Quercus garryana* is greatest in the *Quercus/Corylus/Polystichum* community. Basal area and maximum height of *Quercus garryana* decrease in the *Quercus/Prunus/Symphoricarpos* and *Quercus/Amelanchier/Symphoricarpos* communities and are least in the *Quercus/Rhus* community. Savanna-form *Quercus garryana* are least numerous in the *Quercus/Rhus* community, averaging only three per hectare, but sapling and pole-size *Quercus garryana* are more numerous and density of *Quer-*

TABLE 1. Phytosociological attributes of major species in the tree stratum

Plant community and species	Constancy (%)	Average frequency (%)	Average basal area (m^2/ha)	Average denstity/ha				Maximum height (m)
				Saplings (<10cm dbh)	Poles (11-40cm dbh)	Mature (41-100cm dbh)	Relict (>100cm dbh)	
Quercus/Corylus/Polystichum								
Quercus garryana	100	92	75.6	200	675	156	10	25
Acer macrophyllum	79	24	2.0	126	13	1	1	21
Pseudotsuga menziesii	63	17	1.6	96	10	1	1	30
Rhamnus purshiana	84	23	0.2	77	1			9
Prunus avium	16	15	0.2	111	1			11
Quercus/Prunus/Symphoricarpos								
Quercus garryana	100	96	66.3	166	613	92	15	22
Prunus avium	100	77	10.4	3912	74	3		12
Pseudotsuga menziesii	100	20	1.7	52	22	3		19
Acer macrophyllum	60	26	1.4	133	20	3		12
Rhamnus purshiana	60	7	<0.1	25				4
Cornus nuttallii	40	3	<0.1	10				9
Quercus/Amelanchier/Symphoricarpos								
Quercus garryana	100	94	48.5	232	603	96	3	22
Prunus avium	77	9	<0.1	30	1			10
Pseudotsuga menziesii	54	3	<0.1	15	1			23
Acer macrophyllum	46	2	<0.1	7	1			15
Rhamnus purshiana	46	7	0.2	104				9
Quercus/Rhus								
Quercus garryana	100	97	41.3	580	783	55	3	18
Arbutus menziesii	30	15	1.3	5	17	3		18
Pseudotsuga menziesii	50	19	0.2	59	5			15
Acer macrophyllum	50	6	<0.1	15				14
Rhamnus purshiana	50	1	<0.1	7				4

cus garryana is greatest in this community (Table 1).

There are 15 other species in the tree stratum, but only seven are overstory trees. The most important are *Acer macrophyllum* and *Pseudotsuga menziesii*. Both are most numerous in the *Quercus/Corylus/Polystichum* and *Quercus/Prunus/Symphoricarpos* communities (Table 1). *Acer macrophyllum* is most common on concave microrelief and along the edges, or near the heads of watercourses. *Pseudotsuga menziesii* grows on convex slopes and ridges as well as along watercourses. Large, usually solitary trees occasionally are present in the oak forest. These exceed 1 m dbh and 30 m in height and have branches the full length of their trunks. They appear to have developed under nonforest conditions and are probably contemporaries of the savanna-form *Quercus garryana*.

The third species to enter the overstory with *Quercus garryana* is *Prunus avium*. It was introduced into the Willamette Valley to provide disease-resistant rootstock for commercial cherry orchards (Horticulture Department, Oregon State University, *personal communication*) and has become established in the oak forests. It now occurs mainly as a tall shrub, but trees equal in height to the dominant *Quercus garryana* are present. An increment core from a 40-cm dbh tree had 70 rings and larger trees occur. *Prunus avium* grows well under the *Quercus garryana* canopy and produces an abundance of fruit.

Other trees that may enter the overstory canopy are *Arbutus menziesii, Pinus ponderosa, Libocedrus decurrens,* and *Abies grandis*. *Arbutus menziesii* is more common near the southern end of the Willamette Valley where it is codominant with *Quercus garryana* in some stands. Scattered trees are found throughout the oak forests, but the species is most abundant on sites occupied by the *Quercus/Rhus* community. *Pinus ponderosa* and *Libocedrus decurrens* both occurred in a single stand located in the Cascade Mountain foothills in the southeastern part of the Willamette Valley. *Abies grandis* is found only in the *Quercus/Corylus/Polystichum* community and is rare even there.

Subordinate trees are *Rhamnus purshiana, Cornus nuttallii, Fraxinus latifolia, Pyrus fusca, Pyrus malus, Pyrus communis, Acer glabrum, Acer circinatum,* and *Prunus virginiana*. Of these, *Rhamnus purshiana* is the most common. It occurs as a sub-

ordinate tree in all communities, but is most numerous in the *Quercus/Amelanchier/Symphoricarpos* and *Quercus/Corylus/Polystichum* communities (Table 1). *Cornus nuttallii* is less abundant than *Rhamnus purshiana* and does not occur in the *Quercus/Rhus* community. *Fraxinus latifolia* is most common on poorly drained sites. The indigenous *Pyrus fusca* and the introduced *Pyrus malus* and *Pyrus communis* are minor trees. *Acer glabrum, Acer circinatum,* and *Prunus virginiana* each occurred only in a single stand and are very rare.

Tall shrub stratum

The understory of the oak forest has very well-developed shrub strata which give the communities their recognizable appearance. However, of the 12 tall shrub species recorded, only three are physiognomic dominants.

The clustered, arching stems of *Corylus cornuta* var. *californica* may grow 6 m or more high and on some sites form an almost closed secondary canopy. More often, the species occurs as well-distributed, individual plants. Average coverage

TABLE 2. Mean cover (%) and frequency (%) of major species in the shrub and herb strata according to plant community

Species	*Quercus/ Corylus/ Polystichum*		*Quercus/ Prunus/ Symhoricarpos*		*Quercus/ Amelanchier/ Symphoricarpos*		*Quercus/ Rhus*	
	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)
Tall shrub stratum								
Corylus cornuta var. *californica*	20	29	11	17	2	3	×[b]	
Prunus avium[a]	4	8	55	63	3	4	1	1
Amelanchier alnifolia	3	8	9	18	23	41	1	6
Osmaronia cerasiformis	3	5	3	7	1	3	×	
Holodiscus discolor	6	11			1	1	×	
Low shrub stratum								
Polystichum munitum	34	61	13	29	4	9	1	2
Symphoricarpos albus	25	60	23	54	46	75	2	8
Rhus diversiloba	23	64	15	29	32	76	40	76
Rubus ursinus	13	47	11	37	10	22	2	11
Rosa eglanteria[a]	2	10	1	3	2	7	5	17
Rosa gymnocarpa	1	6	1	5	2	10	×	
Rosa nutkana	×		2	9	2	13	×	
Pteridium aquilinum var. *lanuginosum*	2	5	×		1	3	×	
Rubus parviflorus	4	10						
Dryopteris arguta	2	4						
Herb stratum								
Forbs								
Ligusticum apiifolium	2	12	1	2	1	10	×	
Tellima grandiflora	1	12	1	2	1	10	×	
Galium spp.	1	24	1	17	2	36	1	22
Osmorhiza chilensis	1	4	1	4	2	11	1	15
Satejura douglasii	1	3	1	3	1	3	1	9
Vicia americana	×		×		1	5	1	11
Hypericum perforatum[a]	1	2	1	3	1	4	1	11
Torilis arvensis[a]	1	6	1	5	2	13	2	37
Circaea pacifica	1	9	×		1	5		
Grasses								
Holcus lanatus[a]	2	4	×		1	5	2	22
Bromus laevipes	1	5	1	10	1	6	1	9
Elymus glaucus	1	2	1	3	1	4	1	16
Poa pratensis[a]	×		×		1	1	5	33
Agrostis spp.	1	2	×		1	2	2	33
Festuca rubra	×		1	3	1	2	2	9
Dactylis glomerata	×		×		×		3	11
Cynosurus echinatus[a]							1	11
Danthonia californica							1	9
Festuca californica							1	2
Tree seedlings								
Quercus garryana	1	4	1	4	3	13	6	46
Acer macrophyllum	3	6	4	9	2	4	1	5
Pseudotsuga menziesii	2	5	×		×		×	
Rhamnus purshiana	2	5	1	1	1	2	×	

[a]Introduced species.
[b]×=less than 1% mean cover and frequency.

and frequency are greatest in the *Quercus/Corylus/Polystichum* community and decrease in the *Quercus/Prunus/Symphoricarpos* and *Quercus/Amelanchier/Symphoricarpos* communities. The species is rare in the *Quercus/Rhus* community (Table 2).

Amelanchier alnifolia is the second species to become a physiognomic dominant in the tall shrub stratum. Its density is often great enough to impede movement, and it normally forms a definite layer beneath the overstory canopy. Individual plants 15 cm dbh and over 9 m tall occur.

The high density of *Prunus avium* in the tall shrub stratum of the *Quercus/Prunus/Symphoricarpos* community gives it a characteristic two-layered appearance when seen from the outside. *Prunus avium* has the highest mean coverage and frequency of all species in the tall shrub stratum (Table 2), and even if it does not become an overstory tree in the future, it should remain an important tall shrub.

Osmaronia cerasiformis and *Holodiscus discolor* are the only other common tall shrubs. *Osmaronia cerasiformis* is present in all communities, but is never abundant. *Holodiscus discolor* occasionally forms small, dense thickets in the *Quercus/Corylus/Polystichum* community. It was not present in the stands of the *Quercus/Prunus/Symphoricarpos* community examined, but did occur in the other two communities.

Other tall shrubs present as minor species in all four communities are *Crataegus douglasii* and *Crataegus oxyacantha*. The latter is a garden escape. *Philadelphus lewisii* and *Ceanothus velutinus* var. *laevigatus* are rare members of the *Quercus/Corylus/Polystichum* community. *Physocarpus capitatus* was represented by one large individual shrub in one stand in the *Quercus/Prunus/Symphoricarpos* community. *Viburnum ellipticum* was similarly represented in one stand of the *Quercus/Corylus/Polystichum* community.

Low shrub stratum

The low shrub stratum is composed of 15 species of woody perennials and six species of ferns, but only three species are physiognomic dominants.

The woody fern *Polystichum munitum* is the dominant species in the low shrub stratum on many sites. Although its average coverage in the *Quercus/Corylus/Polystichum* community is 34%, coverage on the best sites is greater than 80% and the fronds exceed 1 m in height. In the other communities, coverage, frequency, and height of *Polystichum munitum* decline until in the *Quercus/Rhus* community it grows only as a sporadically distributed, depauperate plant.

Symphoricarpos albus dominates the low shrub stratum in the *Quercus/Prunus/Symphoricarpos* and *Quercus/Amelanchier/Symphoricarpos* communities and is abundant in the *Quercus/Corylus/Polystichum* community (Table 2). It is sparsely distributed in the *Quercus/Rhus* community. On some sites in the *Quercus/Amelanchier/Symphoricarpos* community it is particularly abundant and forms a dense, waist-high layer.

The ubiquity of *Rhus diversiloba* in the low shrub stratum of all communities is evident from Table 2. In the oak forest it grows as a liana and as a ground cover of single-stemmed plants 1.5–2 m tall. A maximum coverage of 80% with 100% frequency was recorded. The ground cover plants and the lianas are connected by a dense, shallow root system, and it is difficult to delimit an individual plant. *Rhus diversiloba* grows beyond the forest edge into adjoining openings and forms arborescent shrubs 3–4 m tall. The liana form is very evident in the *Quercus/Corylus/Polystichum* community where lianas with basal stems 15 cm or more in diameter are common.

The genera *Rubus* and *Rosa* are well represented in the low shrub stratum. There are five species of each genera present. *Rubus ursinus* is common throughout the oak forests. *Rubus parviflorus* is confined to the *Quercus/Corylus/Polystichum* community and may dominate the low shrub stratum on some sites. The introduced species *Rubus laciniatus* and *Rubus procerus* are less common members of the low shrub stratum. *Rubus leucodermis* is rarely encountered. The most abundant rose is the introduced *Rosa eglanteria*. Although it grows in all communities, it is most abundant in the *Quercus/Rhus* community where the spreading, heavily armed stems of individual plants may cover an area 3–4 m in diameter. Native roses are *Rosa nutkana, Rosa gymnocarpa, Rosa pisocarpa,* and *Rosa durandii*. The first two species are rather common, but the last two are rare.

Other rare members of the low shrub stratum are *Berberis aquifolium, Ribes sanguineum, Spiraea betulifolia* var. *lucida, Cytisus scoparium,* and *Hedera helix*.

Several ferns besides *Polystichum munitum* are present in the low shrub stratum. *Dryopteris arguta* is a good indicator for the *Quercus/Corylus/Polystichum* community. *Pteridium aquilinum* var. *lanuginosum* grows in all communities, but is slightly more abundant in the *Quercus/Corylus/Polystichum* community. Less common ferns are *Athyrium filix-femina* and *Cystopteris fragilis*.

Tree seedlings have been tabulated in the low shrub stratum. Seedlings of *Quercus garryana*

are definitely more abundant in the *Quercus/Rhus* community, as are sapling and pole-size trees (Table 1). *Acer macrophyllum* seedlings are most abundant in the *Quercus/Prunus/Symphoricarpos* and *Quercus/Corylus/Polystichum* communities and least abundant in the *Quercus/Rhus* community. *Pseudotsuga menziesii* and *Rhamnus purshiana* have their greatest coverage and frequency in the *Quercus/Corylus/Polystichum* community. Seedlings of the other species are sporadically distributed or rare.

The most common epiphyte is *Polypodium vulgare* var. *occidentale*. It is ubiquitous in the oak forest. *Phoradendron villosum* occurs mainly in the southern Willamette Valley and is missing or very rare in the north. Common epiphytic cryptogams are *Camptothecium pinnatifidium* and *Orthotrichium speciosum*. The first is especially abundant and forms thick mats on the trunks of *Quercus garryana* and *Acer macrophyllum*.

Herb stratum

The herb stratum is relatively rich in species. One hundred thirty-eight species of grasses, sedges, rushes, and forbs were identified. Table 2 lists species with a mean frequency of 5% or more in at least one community and species confined to a single community. Several of the more important species are introduced.

Although most species are present throughout the oak forest, there is a general increase in the frequency and coverage as the shrub strata decrease in importance, and the herb stratum is best developed in the *Quercus/Rhus* community. Except for *Festuca californica*, the grasses and forbs confined to this community are also common in adjacent grasslands and hill pastures. *Actaea arguta* is found only in the *Quercus/Corylus/Polystichum* community. The most common indigenous herbs are *Galium* spp. (*G. boreale, G. triflorium*) and *Osmorhiza chilensis*.

Physical Environment

The oak forests tend to occur on north- and east-facing slopes (Table 3). This is especially true for the *Quercus/Corylus/Polystichum* and *Quercus/Amelanchier/Symphoricarpos* communities. On the other hand, the *Quercus/Rhus* community tends to occur on south and west aspects. The small sample of the *Quercus/Prunus/Symphoricarpos* community makes it difficult to draw conclusions.

Extremely steep slopes are rare in the bordering foothills and cross-valley ranges of the Willamette Valley. This is reflected in the gradients of the slopes on which the oak forest grows, the majority of which have a gradient of less than 30%. Only the *Quercus/Corylus/Polystichum* community has a tendency to occur on steeper slopes. Oak forests are most common on the upper (including ridgetops) and middle thirds of the slope.

There are no great elevational differences in the oak forest, and most of the stands occur between

Table 3. Slope aspect, gradient, and position and elevation of stands in the four plant communities—expressed as percentage of number of stands

Environmental attribute	*Quercus/ Corylus/ Polystichum*	*Quercus/ Prunus/ Symphoricarpos*	*Quercus/ Amelanchier/ Symphoricarpos*	*Quercus/ Rhus*	All communities
Slope aspect					
North	47	20	54	10	33
East	37	40	38	10	32
South	5			50	13
West	11	40	8	30	22
Slope gradient (%)					
−10	21	40	46	40	34
11–20	21	20	31	40	28
21–20	21	40	8		15
+30	37		15	20	23
Slope position					
Top third	32	60	46	50	40
Middle third	47	20	38	50	45
Lower third	21	20	16		15
Elevation (m)					
>120	21	60	46	30	34
−180	53	20	46	40	45
−240	21	20	8	30	19
<240	5				2

TABLE 4. Percentage of stands on each soil series according to plant communities

Soil series	*Quercus/ Corylus/ Polystichum*	*Quercus/ Prunus/ Symphoricarpos*	*Quercus/ Amelanchier/ Symphoricarpos*	*Quercus/ Rhus*	All communities
Sedimentary soils					
Steiwer	53	80	37	30	46
Carlton	11	20	23		13
Peavine	5		8	40	13
Basic igneous soils					
Nekia	16		8		9
Dixonville	5		8	20	9
Olympia	5		8		4
Alluvial soil					
Amity	5		8	10	6

120 and 240 m. The lower elevation may be an artificial limit caused by clearing for agriculture. At the upper elevation the oak forests may grade into coniferous forest dominated by *Pseudotsuga menziesii*.

ASSOCIATED SOILS

Except for the alluvial soils of the floor of the Willamette Valley, soils are developed from parent materials residual to the underlying geological formations. These formations consist of two major types of materials: sedimentary rocks and basic igneous rocks (mainly basalts).

Sedimentary rocks are usually found at lower elevations than basic igneous rocks and are principally horizontally bedded sandstones and shales. The derived soils are deep and have profiles without eluvial horizons (A2), but with well-developed illuvial horizons (B2). Soil reactions are acidic, and brown hues (Munsell 10YR and 7.5YR) predominate. Drainage is generally good, although temporary high water tables caused by lateral water movement may be present during the wet season.

Sedimentary soils are the principal substrate of the oak woodlands (Table 4). Three series are present: Steiwer, Carlton, and Peavine. The Steiwer series is the most common soil. It occurred under approximately 46% of the oak stands sampled. Carlton series is found on lower slopes below areas of Steiwer and together form a catena. The Carlton-Steiwer catena was present under 59% of the stands examined. The Peavine series is limited to uplands on the western side of the Willamette Valley and is also related to the Steiwer series.

Basic igenous rocks are the parent materials for soils with brown (Munsell 10YR and 7.5YR) or reddish (Munsell 5YR) hues. These soils, are moderately deep and well drained, acidic, and have illuvial horizons, but not eluvial horizons. Weathered basalt fragments are often distributed throughout the solum.

Soil series derived from basic igneous rocks are Nekia, Dixonville, and Olympic. The Nekia series is a red soil typical of the rolling hills and buttes of the central Willamette Valley. Its catenary associate, the Dixonville series, is most common in the southern part of the Willamette Valley on the foothills of the Coast and Cascade Ranges. The Olympic series is found for the most part at higher elevations in the Coast and Cascade Ranges and on the basalt buttes that rise from the valley floor.

The soils of the valley floor are derived from alluvial deposits. Soils from alluvium are poorly drained and have mottled, compact, clayey subsurface horizons and grey brown hues (Munsell 2.5Y). The Amity series, which is derived from old consolidated alluvial deposits, is the only valley bottom soil supporting oak forest.

DISCUSSION

Development of the oak forest

Although the Willamette Valley is, in general, a forest environment, extensive, closed-canopy oak forests appear to have developed from oak savanna since the valley was settled in the mid-nineteenth century. The several historical references to "oak openings" or oak "orchards" are indicative of the growth habit of *Quercus garryana* prior to settlement. Supporting the validity of these early descriptions are the large, old, savanna-form trees scattered at low density through the present high density stands of smaller, younger forest-form trees. This pattern is repeated throughout the valley. The mean age of 90 years (determined at breast height) for large forest-form *Quercus garryana* is further evidence of the relatively recent development of the forest. If an arbitrary 10 years is added to cover the growth period to breast height (1.4 m), the date of establishment of the

oak forests becomes 1862 A.D. This is approximately 20 years after the period of intensive migration and settlement (1842-45) in western Oregon.

The most probable cause for the conversion of oak savanna to oak forest is interruption of the repetitious ground fires that were an important environmental factor of the presettlement savanna. The climate of the Willamette Valley created an environment particularly conducive to fire. The cool, moist winter and spring allowed a dense herbaceous ground cover to develop. This cover was well dried by the normal semidrought conditions of summer and ready to burn in the fall. The anthropic origin of many of the presettlement fires was also reported by the early writers, but wildfires started by other causes were common throughout the Pacific Northwest prior to settlement (Morris 1934).

With settlement, fire became an economic as well as an ecologic factor, and fire control was needed to prevent destruction of property and crops. Clearly a rather sensitive ecological mechanism had operated to perpetuate the oak savanna in an environment suitable for oak forest. Early fire control was crude, but the effect of control in increasing the density of the oak was noticed as early as 1840, and by the late 1800's dense stands of scrubby oak forest were a prominent part of the landscape.

The above account of the development of oak forest from oak savanna in the Willamette Valley is remarkably similar to that given by Curtis (1959) for changes in the *Quercus macrocarpa* dominated "oak openings" of Wisconsin. The overstory of the Willamette Valley oak forests is also quite similar in general physiognomy to that of the Wisconsin oak forests. Both have savanna-form oak trees scattered through dense stands of forest-form trees. This appears to be an instance of like ecological processes operating in widely separated geographical areas, resulting in strikingly similar vegetation.

Nature of the plant communities

Amelioration of environmental extremes through the development of closed-canopy oak forest allowed plants unable to endure savanna conditions to spread and establish. The disseminule source would be along watercourses and around moist spots present in the savanna, or in the small areas of oak forest that did exist.

Throughout their existence the oak forest communities have been influenced by man's activities. Logging, livestock grazing, land clearance, etc., were important environmental factors and even if a stand were to escape actual disturbance, activity in adjacent stands would have an influence. Removal of disseminule sources or introduction of exotic species would directly or indirectly affect development. The present oak forest communities are, therefore, in a seral state, both because they are of relatively recent origin and because they have been disturbed by the activities of man throughout their existence.

A degree of floristic similarity is present among the four oak forest communities. Differences between communities are due mainly to shifts in the importance of a few shrub species, as this is indexed by their coverage and frequency, rather than distinct changes in species composition. Because of the floristic similarity it is possible the communities represent a sere and differences are caused by successional relationships. On the other hand, they may represent vegetational expression of different environments, albeit different positions or steps on an environmental gradient within the oak forest zone.

The relatively short time the oak forest appears to have been in existence makes the first possibility unlikely, and it is more realistic to suggest that the *Quercus/Corylus/Polystichum* community is present on the most mesic sites, the *Quercus/Rhus* community on the most xeric, and the *Quercus/Amelanchier/Symphoricarpos* community on sites intermediate between these extremes. Because *Prunus avium* is an introduced species, the *Quercus/Prunus/Symphoricarpos* community may have developed from one or more of the above communities.

The absence of autecological information on any of the species makes the classification only tentative. The *Quercus/Corylus/Polystichum* community has been called the most mesic community for a number of reasons. The primary reason is the presence and relative abundance of understory species which are also major components of the understory of coniferous forests in the higher precipitation zones of the Oregon Coast and Cascade Mountain Ranges. The most important of these is *Polystichum munitum* which has been recognized as a dominant or codominant in the understory stratum of *Pseudotsuga menziesii* forests by both Spilsbury and Smith (1947) and Corliss and Dyrness (1965). *Corylus cornuta* var. *californica* and *Holodiscus discolor,* also common in the higher precipitation zones, reach their greatest importance in this community, and a number of other common understory species of the *Pseudotsuga menziesii* forest are restricted to it. Among these are *Rubus parviflorus, Dryopteris arguta, Philadelphus lewisii, Athyrium felix-femina,* and *Ceanothus velutinus* var. *laevigatus.* The high density and greater basal area and maximum

height of large forest-form *Quercus garryana* as well as the greater density of *Pseudotsuga menziesii* and *Acer macrophyllum* and the presence of *Abies grandis* are also indicative of the mesic nature of the *Quercus/Corylus/Polystichum* community. Finally, the tendency for the community to occur on relatively steep north and east slopes also points to its mesic nature.

The *Quercus/Rhus* community has been called the most xeric community of the oak forest because of the decreased height and basal area of *Quercus garryana* and the lower density of large forest-form trees. The absence of a tall shrub stratum and the depauperate growth form of species that are tall shrubs in other communities indicate that growing conditions are less optimal. The presence of *Rhus diversiloba* in adjacent grasslands as well as in the oak forest shows it is adapted to relatively xeric environments and it reaches its greatest abundance in this community. The well-developed herbaceous layer composed of many grasses and forbs also present in the adjacent grasslands is further evidence of the generally xeric environment, as is the tendency for the *Quercus/Rhus* community to occur on exposed upper and middle slopes with southerly aspects.

The intermediate position of the *Quercus/Amelanchier/Symphoricarpos* community is less easy to justify. It is based both on the decline in importance of *Corylus cornuta* var. *californica, Polystichum munitum,* and other mesophyllic species and on the decline of *Rhus diversiloba* and other xerophyllic species, indicating that sites occupied by the *Quercus / Amelanchier / Symphoricarpos* community may be intermediate between the mesic and xeric extremes present in the oak forest. Basal area and the density of large forest-form and relict savanna-form *Quercus garryana* in the *Quercus/Amelanchier/Symphoricarpos* community are greater than in the *Quercus/Rhus* community, but less than in the *Quercus/Corylus/Polystichum* community which is also indicative of the intermediate position. The community has a tendency to occur on north- and east-facing ridges and slopes which are, in general, more exposed than sites occupied by the *Quercus/Corylus/Polystichum* community, but less exposed than the south slopes and ridges generally occupied by the *Quercus/Rhus* community.

The relatively high coverage and frequency of *Corylus cornuta* var. *californica* and *Polystichum munitum* in the understory and the abundance of *Pseudotsuga menziesii* and *Acer macrophyllum* in the overstory place the *Quercus/Prunus/Symphoricarpos* community floristically close to the *Quercus/Corylus/Polystichum* community, and possibly, with a seed source of *Prunus avium,* stands representative of the *Quercus/Corylus/Polystichum* community would develop into the *Quercus/Prunus/Symphoricarpos* community. However, the dominance of *Symphoricarpos albus* in the low shrub stratum and the relatively high coverage and frequency of *Amelanchier alnifolia* in the tall shrub stratum also indicate a relationship to the *Quercus/Amelanchier/Symphoricarpos* community. Possibly the *Quercus/Prunus/Symphoricarpos* community is developing on sites intermediate between the two indigenous communities.

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