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Source: *Journal of Biogeography*, Vol. 4, No. 2 (Jun., 1977), pp. 181-192

Published by: [Wiley](#)

Stable URL: <http://www.jstor.org/stable/3038162>

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Ecosystem dynamics in the coniferous forest of the Willamette Valley, Oregon, U.S.A.

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SUMMARY. Forested communities in the proposed Fox Hollow Research Natural Area in the foothills of the Willamette Valley, Oregon were sampled to determine how the distribution of tree species has varied with time and topographic position. Prior to 1850, a forest almost exclusively dominated by *Pseudotsuga menziesii* occupied the north-facing slopes of this area, while south-facing slopes were occupied by an open forest of mixed *Pseudotsuga menziesii* and more xeric species such as *Pinus ponderosa* and *Quercus garryana*. Since 1850, the density of this forest has increased spectacularly, apparently because of the cessation of annual Indian burning practices. Associated with this increase in density are successional trends, which vary with topographic position. Most of the current reproduction on north-facing slopes and lower south-facing slopes is of *Abies grandis*. *Pseudotsuga menziesii* is reproducing well only on ridge crests and on upper south-facing slopes, in situations where *Abies grandis* is only just beginning to invade. All the other more xeric tree species appear to be unable to reproduce well in this forest. Thus a forest dominated by *Pseudotsuga menziesii*, and attuned to former Indian burning practices is being replaced by one dominated by *Abies grandis*, which is spreading widely as a result of protection from fire. Both human influences, burning and fire protection, result in unnatural frequencies of disturbance to this ecosystem, and the consequences of both appear to be the gradual impoverishment of the tree flora therein.

Introduction

The vegetation of the Willamette Valley, Oregon, is today largely a reflection of the changing human patterns of modification of the environment. Prior to white settlement, which occurred during the middle of the nineteenth century, annual Indian burning practices significantly altered the composition of the vegetation; and its subsequent modification has resulted from a wide variety of human activities, including logging, farming and the development of urban areas. In view of the extent of these disturbances, data on successional relationships and community types of vegetation within the Willamette Valley are scarce.

An unlogged stand in foothills at the southern end of the Willamette Valley provided an opportunity to study recent successional trends in the coniferous forest of the region, under conditions of minimal human disturbance. The east-west orientation of the landforms in these foothills further results in the juxtaposition of strongly contrasting topographic positions, so allowing the study of a wide range of community sub-types within a relatively small area.

This report analyses temporal and spatial variations in the distribution of tree species within this area of old-growth forest. Temporal variations refer largely to the recent period of fire suppression, which is currently eliminating the formerly significant influence on the

vegetation of both human- and lightning-initiated fires. Spatial variations are related to differences in the microclimates which occur in contrasting topographic positions. In addition, the effects of logging on species composition are discussed through a comparison of adjacent logged and unlogged sites.

The site

The study site is part of the proposed Fox Hollow Research Natural Area, which is located about 16 km southwest of Eugene, Oregon (Fig. 1). The investigation was confined to the northernmost of three east-west ridges, although field reconnaissance confirmed the presence of similar conditions on the other ridges. Elevations range from approximately 215 m.a.s.l. at the valley bottom to 305 m.a.s.l. at the ridge crest.

The area has a wet Mediterranean climate, with less than 10% of its mean annual precipitation of about 1150 mm falling in the summer months. The dry summers are relatively hot, with mean July maximum temperatures of about 27° C. The wet winters, however, are mild, with mean January minimum temperatures of about 0° C (U.S. Weather Bureau, 1965).

The parent material of the soil is part of the Fisher formation, being comprised of

sedimentary rocks of continental origin that are composed primarily of andesitic lapilli tuffs and breccias (Vokes *et al.*, 1951; Baldwin, 1964). In some places, solid rock outcrops at the surface, but in most places soils high in clay have developed. In these areas the surface is highly unstable and mass movement is evident.

Methods

Six series of ten sample plots were established, one each along the crest of the ridge, the valley bottom, and along contour lines 75 and 175 m below the crest on both north- and south-facing slopes. These will be referred to hereafter as the crest, bottom, upper north-facing, lower north-facing, upper south-facing and lower south-facing slope segments respectively (Fig. 2). Individual plots measured 10 × 20 m, with the long dimension parallel to the contour, and were spaced at 30 m intervals.

For each plot, species name and diameter at breast height of all trees were recorded. Species nomenclature followed that of Hitchcock & Cronquist (1973). The period of establishment of each tree was determined; trees were then placed in age classes of those less than 25 years old, those between 25 and 125 years old, and those greater than 125 years old. Ages of the younger trees were estimated

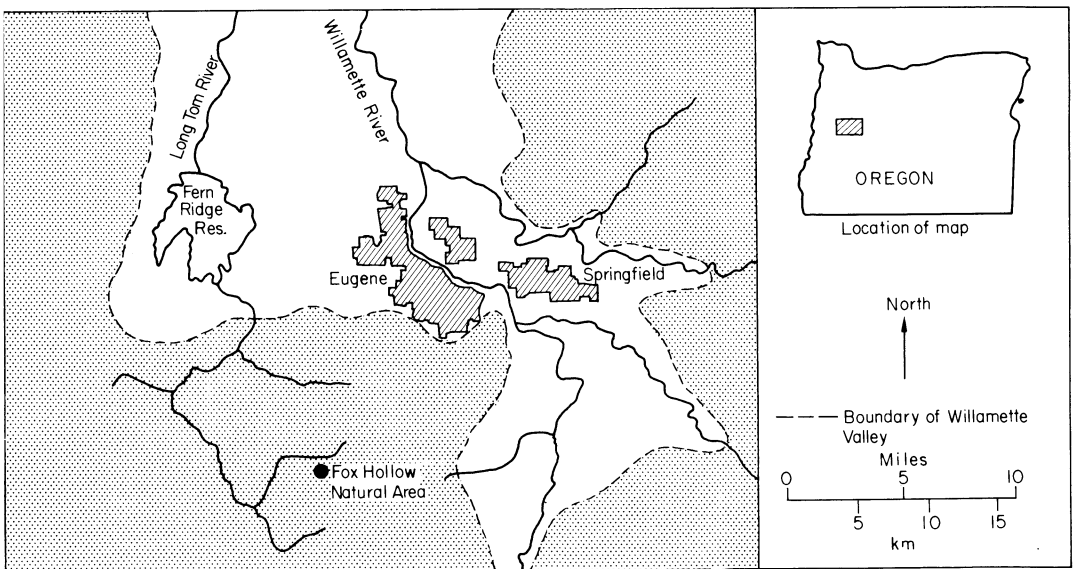


FIG. 1. Location of the Fox Hollow Natural Area.

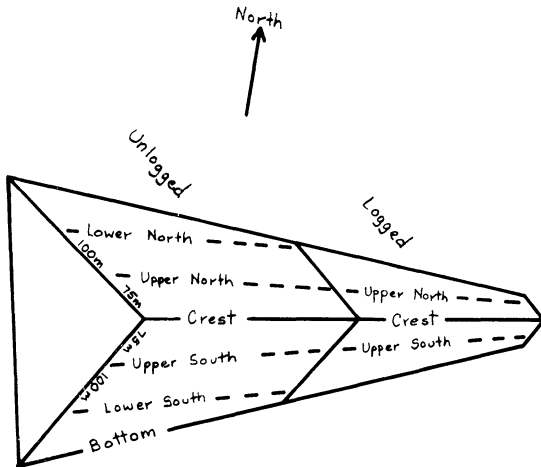


FIG. 2. Schematic view of topographic positions.

by counting whorls of branches, and those of older trees analysed from increment borings. Species such as *Acer circinatum*, which do not consistently exhibit a tree-like form, were not recorded.

The species composition of the pre-1850 forest can be inferred from the relative density of tree species in the age class of over 125 years. Any overstory tree alive at that time should still be evident in the present forest, either as a standing tree or as a tree decomposing on the forest floor. The presence of stumps left 100 years ago in neighbouring areas suggests that it takes more than this length of time for trees to decompose and, for this reason, fallen trees were included in the sample. However, abundance estimates of smaller trees, such as *Cornus nuttallii*, which would leave little trace once they had been removed, would be underestimated by this method, and this shortcoming should be kept in mind. The relative density of tree species in the 25–125 years old sample approximates the species composition of the forest which became established in the period between 1850 and 1950; and the relative density of tree species in age class of less than 25 years provides an indication of the forest of the future, which will result from present successional trends.

Starting at the eastern edge of the natural area, the adjacent logged area was sampled with three additional sets of ten plots, one along the crest, and the others 75 m below the

crest, on both north- and south-facing slopes. Slopes were judged to be too short in length to warrant additional sampling. There was very little variation in age or diameter at breast height on these plots, so species composition only was recorded therein.

Results

Variations in species composition with time.

Table 1 relates tree species composition to period of establishment. *Pseudotsuga menziesii* has dominated the overstory of this forest for a long time, accounting for 69% of all trees that have survived from the pre-1850 forest. Before 1850, its major associates were *Pinus ponderosa* and *Quercus garryana* on warm, dry sites and *Abies grandis* on cool, moist sites. In the period between 1850 and 1950, *Calocedrus decurrens* replaced *Pinus ponderosa* as a major associate on warm, dry sites and *Abies grandis* became the second most abundant tree species in the forest. Since 1950, *Abies grandis* has replaced *Pseudotsuga menziesii* as the most abundantly reproducing tree species in the forest (Fig. 3).

A significant increase in the density of the forest has coincided with these changes in species composition. There are presently 1068 trees in the 1.2 ha sampled, of which only ninety-three are over 125 years old. The density of this older forest must have been greater than this value indicates, in that many of the smaller trees of the former forest would not be evident in the present forest; however, the relatively even distribution of these older, obviously open-grown trees supports the contention that this forest was originally more open than it is today.

Such observations indicate that rapid successional changes have occurred in this area since 1850. In this connection, Sprague & Hansen (1946) have reported that fires in the Willamette Valley were numerous before 1848. These fires were set annually by local Indians, and burned most of the valley and the neighbouring hills. Johannessen *et al.* (1971) have discussed the extent of this Indian burning, citing the writings of early explorers and settlers. Although the study site lies 11 km to the south of the Willamette Valley, fire must also have burned regularly over this area,

TABLE 1. Relative density (RD) and total number of stems (STS) of tree species as a function of the period of establishment

Species	Period of Establishment			
	Before	1850 to	After	All
	1850 RD:STS (%) (No)	1950 RD:STS (%) (No)	1950 RD:STS (%) (No)	periods RD:STS (%) (No)
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	69:64	50:319	36:119	47:502
<i>Calocedrus decurrens</i> (Torr.) Florin.	2:2	10:64	—	6:66
<i>Pinus ponderosa</i> Dougl.	9:8	+ :1	1:2	1:11
<i>Quercus garryana</i> Dougl.	7:6	10:65	6:19	8:90
<i>Quercus kelloggii</i> Newberry	—	2:13	—	1:13
<i>Castanopsis chrysophylla</i> (Dougl.) DC.	1:1	4:26	5:17	4:44
<i>Arbutus menziesii</i> Pursh.	—	1:4	—	+ :4
<i>Abies grandis</i> (Dougl.) Lindl.	4:4	15:99	47:156	24:259
<i>Acer macrophyllum</i> Pursh.	9:8	5:35	3:9	5:52
<i>Cornus nuttallii</i> Aud.	—	2:10	2:7	2:17
<i>Fraxinus latifolia</i> Benth.	—	+ :1	—	+ :1
<i>Taxus brevifolia</i> Nutt.	—	+ :1	—	+ :1
<i>Alnus rubra</i> Bong.	—	1:7	+ :1	1:8
Density (trees/ha)	77.5	537.5	275.0	890.0

Relative density (%) = number of stems of the indicated species ÷ total number of stems of all species. + indicates relative density less than 0.5%.

creating and maintaining the open character of the forest.

The pre-1850 forest appears to have been adapted to this frequent burning. The wide spacing and open growth habit of the trees suggest that fire was acting not as a catastrophic agent, but as a regular environmental input, to which both tree density and species composition were in adjustment. The forest dominants (*Pseudotsuga menziesii* in association with *Pinus ponderosa* and *Quercus garryana*, as previously indicated) are relatively fire-resistant and can germinate in open conditions, and other locally-abundant species such as *Acer macrophyllum* and *Abies grandis* were present mainly along the valley bottoms, where it was cool and moist enough for them to survive both the summer drought and the periodic fires.

With the cessation of burning following the arrival of white settlers in the mid-1800's, forest density increased rapidly. In general, numerous *Pseudotsuga menziesii*, *Calocedrus decurrens* and *Quercus garryana* established themselves among the scattered older trees. In terms of relative density, this was the only favourable period for *Calocedrus decurrens*, much as the pre-1850 period was the only favourable period for *Pinus ponderosa*. Less

numerically-important species in the forest community that responded well to the absence of fire and a relatively open, litter-free stand were *Quercus kelloggii*, *Castanopsis chrysophylla*, *Arbutus menziesii*, *Acer macrophyllum* and *Alnus rubra*. Only *Pinus ponderosa* reacted adversely to this change in conditions.

The initial responses to the removal of periodic fire from the ecosystem thus included an increase in tree density, an increase in the variety of species, and a decrease in the overall dominance of *Pseudotsuga menziesii*. These changes in the structure of the forest undoubtedly caused readjustments in most of the other components of the ecosystem. Presumably soil and air temperatures, wind speed, surface evaporation, and runoff decreased, while organic matter, depth of litter, and field capacity increased. Other factors, such as increased transpiration, might have counteracted to some extent these trends toward more mesic conditions, but for the most part the moisture stress during late summer must have been moderated. At the same time, the reduction in surface temperatures and light intensity which are inferred must have limited the reproductive capacity of certain species.

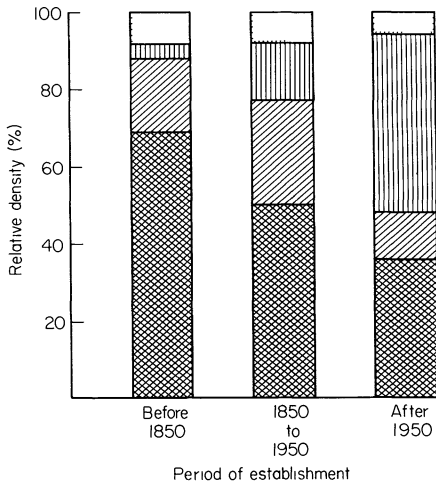


FIG. 3. Relationships between the relative density of tree species and their period of establishment. Stippled area, mesic associates (*Acer macrophyllum*, *Cornus nuttallii*, *Fraxinus latifolia*, *Taxus brevifolia* and *Alnus rubra*; vertical hatch area, *Abies grandis*; slant hatch, xeric associates (*Calocedrus decurrens*, *Pinus ponderosa*, *Quercus garryana*, *Quercus kelloggii*, *Arbutus menziesii* and *Castanopsis chrysophylla*); crossed hatch area, *Pseudotsuga menziesii*.

The recent abundance of *Abies grandis* seedlings in this forest and the decline in the reproductive capability of all other species, excepting *Cornus nuttallii* and *Castanopsis chrysophylla*, are related to the inception of further environmental changes which result from the extended protection of the area from all fire, including natural fire. In the past, lightning fires were an important feature in the forests of western Oregon (Morris, 1934), but in recent years they have been effectively controlled in most areas. In consequence, *Pinus ponderosa*, *Calocedrus decurrens*, *Quercus kelloggii*, and *Arbutus menziesii* appear unable to reproduce satisfactorily under present forest conditions. Seed germination of these species is discouraged by the low light intensities under the closed canopy, and those seedlings which are occasionally found in gaps created by windthrow are usually either dead or stunted. Moreover, *Pseudotsuga menziesii*, although still dominating the overstory of the whole forest, is only reproducing well on the driest, most exposed sites within it. On other sites, *Abies grandis* seedlings are most common.

One may argue that although *Pseudotsuga menziesii* will remain a major associate in this forest, it will in future probably be relegated to a 'gap phase' reproduction role on the most xeric sites (Fig. 3).

Of the other component species, *Quercus garryana* is still reproducing abundantly on the crest and upper south slopes, although much of the regeneration is stunted and under insect attack. Sprague & Hansen (1946), working in foothills 64 km to the north of the study site, found no *Quercus garryana* reproduction in a similar forest of *Pseudotsuga menziesii*, and numerous relict *Quercus garryana* snags, and further studies by Habeck (1961) and Johannessen *et al.* (1971) strongly suggest that this species is now in decline in these forests. *Castanopsis chrysophylla* and *Cornus nuttallii*, however, appear to be quite capable of reproducing in the present forest, although they are largely confined to certain topographic positions. This is somewhat surprising in the case of *Castanopsis chrysophylla*, which has often been considered to be intolerant of shade in that it favours exposed, upper slope positions. In contrast, *Acer macrophyllum*, which is considered to be shade tolerant and has been categorized as a climax associate in these forests (Franklin & Dyrness, 1973), is represented by only nine seedlings in the entire sample population. Fowells (1965) states that *Acer macrophyllum* often invades following disturbance, but is often shaded out by conifers at a later stage, a tendency which has also been reported by Dyrness, Franklin & Moir (1974), who found that at low elevations in the Cascades, *Acer macrophyllum* is usually a seral species, dependent on open stand conditions. *Acer macrophyllum* apparently will continue to be present in this forest, although limited both in numbers and spatial distribution.

In summary, the cessation of Indian burning resulted in an increase in species diversity in this forest because shade-tolerant, fire-susceptible species were no longer excluded from it. In recent years, however, the elimination of natural fires has allowed the development of a closed canopy, the result being a gradual impoverishment of the tree flora therein.

Variations in species composition with topographic segment. Variations in species

composition also result from the microclimatic differences of the several topographic segments (Tables 2 and 3). These differences in microclimate are related primarily to distance from the crest, aspect, and slope angle. Conditions become more mesic with increasing distance from the crest, as soil depth and soil moisture increase, and as wind speed and evaporative stress decrease. Variations in aspect and slope angle are also important, in that these control the amount of solar insolation received. Variations in the amount of received precipitation with aspect are insignificant on features of this scale, and those of wind speed had to be ignored due to lack of data.

The two dominant aspects of the ridge are N 30° E (the north-facing slope) and S 30° W (the south-facing slope). On both slopes the average slope angle is about 20°, until one reaches the crest and bottom plots, in which case it approximates zero. Figure 4 indicates the average direct-beam solar radiation, on a clear day, as a function of the slope angle (from 0–30°), the aspect (S 30° W and N 30° E), the time of day (from 08.00–16.00 hours), and the time of year (21 Dec., 21 March, 21 June, and 21 Sept.), as computed from:

$$Q'_i = Q'_n (\cos Z \cos i + \sin Z \sin i \cos(a - a'))$$

where Q'_i is the instantaneous flux of direct-beam solar radiation on the sloping surface, Q'_n is the intensity of direct-beam solar radiation on a surface normal to the sun's rays, Z is the solar zenith angle, i is the angle between the sloping surface and a horizontal surface, a is the azimuth angle of the sun from the south, and a' is the azimuth angle of the normal to the vertical surface from south (Sellers, 1965). This formula provides a good approximation of the relative amounts of solar radiation received in all topographic positions, other than the valley floor, where shade from adjacent slopes reduces solar radiation income, particularly in winter. Figure 4 confirms that at all times of the year the average south-facing slope (20°) receives more direct-beam solar radiation than either the crest or the average north-facing slope (20°). Differences in the solar radiation income of these slopes are most extreme in winter, when the average north-facing slopes

receive direct-beam solar radiation for only about 3 h each day. The amounts then received at noon on the average north-facing slope are only 0.10 langly/min, as opposed to 0.44 ly/min on the crest and 0.74 ly/min on the south slope. At noon, on the summer solstice, the average north-facing slope, crest, and south-facing slope receive 1.2 ly/min, 1.4 ly/min, and 1.5 ly/min, respectively. But by the end of the summer, when moisture stress is greatest, the south-facing slope again receives about twice the amount of radiation as the north slope. These differences in solar radiation income are of great importance in any explanation of the variations in species composition which occur with topographic position (Fig. 5).

Prior to 1850, the moist valley floor was dominated by *Pseudotsuga menziesii* (53% of the trees) and *Acer macrophyllum* (29%); *Abies grandis* is, however, the most conspicuous tree species in the present seedling layer (54%). Before 1850, this slope segment had a relatively dense cover as compared to others (85 trees/ha), but a lack of reproductive capacity in recent years has now resulted in it having the lowest tree density of all segments (405 trees/ha). Low light intensities, the tangled shrub layer of *Acer circinatum*, and the high frequency of swampy conditions now makes this an unfavourable site for germination. The magnificent old *Pseudotsuga menziesii* cannot reproduce in sufficient quantities to avoid replacement by *Abies grandis*, which germinates more frequently under these conditions.

The environmentally similar lower north-facing slope (although it is better drained) was almost completely dominated by *Pseudotsuga menziesii* in the pre-1850 forest (92%); now this is essentially absent from the seedling layer, which is almost exclusively comprised of *Abies grandis* (70%). The major difference between this slope segment and the valley floor is the reduced importance of *Acer macrophyllum*, and the increased abundance of *Abies grandis* reproduction, the almost pure former *Pseudotsuga menziesii* stand of old trees being replaced by an equally pure stand of *Abies grandis*. Only *Acer macrophyllum* and *Cornus nuttallii* appear as minor associates of the latter.

On the upper north-facing segment, light

TABLE 2. Relative density (RD) and total number of stems (STS) of tree species as a function of topographic position and period of establishment

Species	Bottom				Lower north				Upper north			
	Before	1850 to	After	All	Before	1850 to	After	All	Before	1850 to	After	All
	1850 RD:STS (%) (No)	1950 RD:STS (%) (No)	1950 RD:STS (%) (No)	periods RD:STS (%) (No)	1850 RD:STS (%) (No)	1950 RD:STS (%) (No)	1950 RD:STS (%) (No)	periods RD:STS (%) (No)	1850 RD:STS (%) (No)	1950 RD:STS (%) (No)	1950 RD:STS (%) (No)	periods RD:STS (%) (No)
<i>Pseudotsuga menziesii</i>	53:9	4:2	15:2	16:13	92:11	14:6	4:2	19:19	91:19	55:45	27:12	51:76
<i>Calocedrus decurrens</i>	—	—	—	—	—	—	—	—	5:1	—	—	1:1
<i>Pinus ponderosa</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Quercus garryana</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Quercus kelloggii</i>	—	2:1	—	1:1	—	—	—	—	—	4:3	—	2:3
<i>Castanopsis chrysophylla</i>	—	—	—	—	—	2:1	6:3	4:4	—	20:16	16:7	15:23
<i>Arbutus menziesii</i>	—	—	—	—	—	—	—	—	—	1:1	—	1:1
<i>Abies grandis</i>	18:3	33:17	54:7	33:27	—	67:29	70:33	61:62	5:1	20:16	55:25	28:42
<i>Acer macrophyllum</i>	29:5	39:20	15:2	33:27	8:1	5:2	6:3	5:6	—	1:1	2:1	1:2
<i>Cornus nuttallii</i>	—	6:3	8:1	5:4	—	12:5	13:6	11:11	—	—	—	—
<i>Taxus brevifolia</i>	—	2:1	—	1:1	—	—	—	—	—	—	—	—
<i>Alnus rubra</i>	—	14:7	8:1	10:8	—	—	—	—	—	—	—	—
Density (trees/ha)	85	255	65	405	60	215	235	510	105	390	225	720

Relative density (%) = number of stems of the indicated species ÷ total number of stems of all species.

TABLE 3. Relative density (RD) and total number of stems (STS) of tree species as a function of topographic position and period of establishment

Species	Crest						Upper south						Lower south					
	Before	1850 to	After	All	Before	1850 to	After	All	Before	1850 to	After	All	Before	1850 to	After	All	Before	1850 to
	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)	RD:STS (%) (No)
<i>Pseudotsuga menziesii</i>	43:6	66:163	77:74	68:243	54:7	56:55	47:18	54:80	75:12	39:48	12:11	31:71	75:12	39:48	12:11	31:71	75:12	39:48
<i>Calocedrus decurrens</i>	—	14:35	—	10:35	8:1	20:20	—	14:21	—	7:9	—	4:9	—	7:9	—	4:9	—	7:9
<i>Pinus ponderosa</i>	29:4	—	1:2	2:6	23:3	—	—	2:3	6:1	1:1	—	1:2	6:1	1:1	—	1:2	6:1	1:1
<i>Quercus garryana</i>	29:4	13:33	5:12	14:49	8:1	19:19	13:5	17:25	6:1	10:13	2:2	7:16	6:1	10:13	2:2	7:16	6:1	10:13
<i>Quercus kelloggii</i>	—	3:7	—	2:7	—	1:1	—	1:1	—	1:1	—	—	—	1:1	—	—	—	1:1
<i>Castanopsis chrysophylla</i>	—	1:2	1:2	1:4	8:1	1:1	13:5	5:7	—	5:6	—	—	—	5:6	—	—	—	5:6
<i>Arbutus menziesii</i>	—	1:2	—	1:2	—	1:1	—	1:1	—	—	—	—	—	—	—	—	—	—
<i>Abies grandis</i>	—	2:5	2:5	3:10	—	—	26:10	7:10	—	26:32	84:76	47:108	—	26:32	84:76	47:108	—	26:32
<i>Acer macrophyllum</i>	—	—	1:1	4:1	—	1:1	—	1:1	13:2	9:11	2:2	7:15	13:2	9:11	2:2	7:15	13:2	9:11
<i>Cornus nuttallii</i>	—	—	—	—	—	—	—	—	—	2:2	—	—	—	2:2	—	—	—	2:2
<i>Fraxinus latifolia</i>	—	—	—	—	—	—	—	—	—	1:1	—	—	—	1:1	—	—	—	1:1
Density (trees/ha)	70	1235	480	1779	65	490	190	745	80	620	455	1154	80	620	455	1154	80	620

Relative density (%) = number of stems of the indicated species ÷ total number of stems of all species. + indicates relative density less than 0.5%.

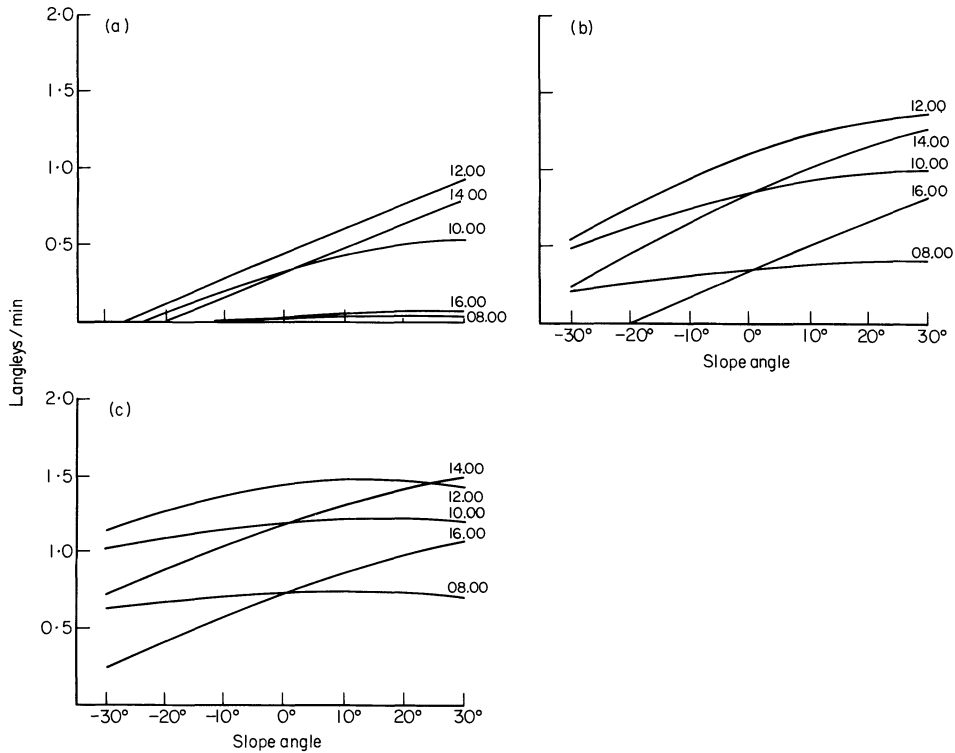


FIG. 4. Direct-beam solar radiation (langleys/min) as a function of slope angle, aspect (negative slope angles are for aspect = N 30° E, positive slope angles are for aspect = S 30° W), time of day (24 hour clock), and time of year. (a) 21 Dec.; (b) 21 March or 21 Sept.; (c) 21 June.

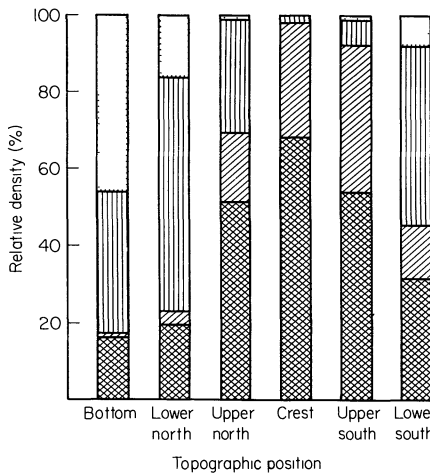


FIG. 5. Relationships between the relative density of three species and topographic position. Key as for Fig. 3.

intensities are higher and soil depth and moisture are reduced. As in the case of the lower, north-facing slopes, prior to 1850 the forest was almost completely dominated by *Pseudotsuga menziesii* (91%), while today *Abies grandis* is the most abundant seedling (56%); the shift to *Abies grandis* is not as extreme as on the lower north-facing slopes, however, in that *Pseudotsuga menziesii* is still reproducing in places. The increased importance of *Castanopsis chrysophylla*, which is more abundant on this segment than on any other, and the occasional occurrences of *Calocedrus decurrens*, *Quercus kelloggii* and *Arbutus menziesii* give this segment a greater variety of tree species than either those of the valley floor or the lower north-facing slope.

Although receiving less direct-beam solar radiation than the south-facing slope, the crest is the most exposed and probably the most xeric position. *Pseudotsuga menziesii* was not as dominant in the pre-1850 forest as it was in other slope segments (43%), but it

now almost completely dominates the seedling layer (74%). In many places, the young thicket of *Pseudotsuga menziesii* seedlings is so dense that their growth is stunted. *Abies grandis* seedlings are also present, but not abundant. *Pinus ponderosa* and *Quercus garryana* were major associates in this segment before 1850, but only *Quercus garryana* is still reproducing. *Calocedrus decurrens* formerly germinated abundantly following the cessation of burning, but can no longer reproduce under the dense thicket of seedlings. Although the crest supported a relatively open forest before 1850 (70 trees/ha), it currently has the highest tree density of all positions (1779 trees/ha), because of the recent abundant reproduction.

Upper south-facing slopes are similar to the crest environmentally, but probably do not suffer as much evaporative stress during late summer. In comparison with the crest, *Pseudotsuga menziesii* was more important in the pre-1850 forest (54%) and is less important in the present seedling layer (47%) in this segment. *Calocedrus decurrens* and *Quercus garryana* germinated abundantly in the period immediately following the cessation of burning, but no longer do so. *Abies grandis* is reproducing, but not as abundantly as *Pseudotsuga menziesii*. The crest and the upper south-facing slope are the segments in which *Pseudotsuga menziesii* was least dominant prior to 1850, and is currently most abundant.

On lower south-facing slopes, relatively high insolation, in combination with abundant moisture, results in a high degree of environmental diversity. The pre-1850 forest was dominated by *Pseudotsuga menziesii* (75%), but associates ranged from *Pinus ponderosa* to *Acer macrophyllum*. With the cessation of burning, almost all of the available tree species found suitable habitats, and the number of species is correspondingly greatest today on this segment of the slope. Presently, *Pseudotsuga menziesii* seedlings can be found under the closed canopy, but *Abies grandis* is by far the most abundant seedling (84%).

The forest communities on all of these slope segments are unique. Differences in structure and composition are a response to contrasting microclimatic conditions. In

addition each community has adapted differently to the radical change associated with the cessation of Indian burning and subsequent fire suppression. On the more mesic sites, almost pure forests of *Pseudotsuga menziesii* are being replaced by *Abies grandis*, along with associates such as *Acer macrophyllum* and *Cornus nuttallii*. The more xeric sites supported a more open forest of numerous *Calocedrus decurrens*, *Pinus ponderosa* and *Quercus garryana* associated with *Pseudotsuga menziesii*. These sites are now covered with dense stands of *Pseudotsuga menziesii* seedlings, to the exclusion of most other tree species. *Abies grandis* appears to be invading these sites, however, and may eventually dominate here as well. *Pseudotsuga menziesii*, *Castanopsis chrysophylla*, and possibly *Quercus garryana* will remain as associates.

Changes in species composition associated with logging

The public relation campaigns of logging corporations often suggest that clearcut logging takes the ecological place of fire in maintaining the *Pseudotsuga menziesii* forest. Table 4, which compares the species composition of adjacent logged and unlogged stands, shows that logging does indeed increase the relative density of *Pseudotsuga menziesii*, and that there is also a significant subsequent increase in the abundance of *Acer macrophyllum* on north-facing slopes and of *Arbutus menziesii* on south-facing slopes of the logged area. However, *Pinus ponderosa* and *Quercus garryana*, which were important in the fire-adapted forest, do not reproduce abundantly after logging, and the vigorous reproduction by *Pseudotsuga menziesii* evidently makes it very difficult for these species to find a suitable germination site. Logging, then, results in the increased importance of *Pseudotsuga menziesii*, but the resulting forest lacks the more xeric, fire-adapted species found in the pre-1850 forest. It also lacks the shade-tolerant species, such as *Abies grandis* and *Cornus nuttallii*, which are found in the unlogged and unburned forest. The result, again, is an impoverishment of the tree flora.

TABLE 4. Relative density (RD) and total number of stems (STS) of tree species in logged and unlogged stands

Species	Logged	Unlogged
	RD:STS (%) (No)	RD:STS (%) (No)
<i>Pseudotsuga menziesii</i>	86:948	58:399
<i>Calocedrus decurrens</i>	1:6	8:57
<i>Pinus ponderosa</i>	1:10	1:9
<i>Quercus garryana</i>	3:38	10:74
<i>Quercus kelloggii</i>	1:7	2:11
<i>Castanopsis chrysophylla</i>	2:23	7:34
<i>Arbutus menziesii</i>	1:13	1:4
<i>Abies grandis</i>	1:6	13:62
<i>Acer macrophyllum</i>	5:53	1:4
<i>Cornus nuttallii</i>	+ :3	—
Density (trees/ha)	1845	1090

Relative density (%) = number of the indicated species ÷ total number of stems of all species. + indicates relative density less than 0.5%.

Discussion and conclusions

The above observations seem to confirm the contention that *Abies grandis* forest is the climax vegetation of this area and probably of the whole Willamette Valley, under the present system of constant and effective fire suppression. It is evident, however, that this stand is not the product of undisturbed conditions and there is no reason to believe that this would be the type of forest found in the absence of all human disturbance.

Daubenmire (1968) has stated that 'as disturbance (fire) begins . . . floristic complexity increases because much the same group of invaders penetrates all the habitat types. As disturbance intensifies, most species that characterized the primary climaxes disappear and one or a few disclimaxes take over all the habitat types, with a resultant simplification in the flora as well as phytosociology.' This description fits the recent situation at Fox Hollow, with fire suppression rather than fire as the disturbing factor. Fire suppression is as much of an ecological disturbance as fire and results in a similar impoverishment of the flora.

Some of the implications of fire suppression have been discussed recently by Loucks (1970), who found a similar decrease in diversity in the forests of Wisconsin. Similar

changes due to fire suppression have been noted throughout the United States (Habeck, 1972; Cooper, 1960; Heinselman, 1970, and many more). Such studies suggest that 'stable' ecosystems incorporate random pulse-like disturbances, which periodically rejuvenate the system. Each ecosystem appears to have a characteristic frequency of disturbance which maintains the efficiency of that ecosystem and, without the proper frequency of disturbance, serious loss of diversity then results.

Annual Indian burning practices in the study area resulted in unnaturally frequent ecological disturbances, which kept out the shade-tolerant tree species. More recently, man has temporarily halted this process of rejuvenation by suppressing fire. In actuality man is merely decreasing the frequency of disturbance. Ultimately through catastrophic fire, insect attack or disease, the senescent forest will be recycled. The immediate result at Fox Hollow is a loss of environmental diversity, and as a consequence, the invasion of one species, *Abies grandis*, in most places. Pioneer species, which fix energy in the early stages of this rejuvenation process, are being lost.

The pre-1850 fire-adapted forest had a richer tree flora than the forest developing under conditions of no fire. Both lack the diversity of a forest developed under conditions of occasional disturbance, but the open conditions of the older forest resulted in higher diversity than occurs in the closed forest of recent years. Moral (1972), in a study of diversity patterns in Washington concludes that maximum diversity occurs under conditions of 'harshness' which prevent the development of a closed canopy, but which are mild enough to allow the establishment of some 'ecological specialists'. This would correspond to the condition immediately following 1850, when the forest canopy was just beginning to close.

Logging is one means of breaking up the forest, but it does not operate in the same way as fire. It gives selective advantage to fast-growing tree species, which often crowd out both the fire-resistant and the shade-tolerant species. The increasing extent of hand-planted monospecific forests even accelerates this loss of diversity.

Fire, as well as insect attack, windthrow,

mass movement, grazing, and other disturbances, keeps the ecosystem functioning efficiently. Man interferes with the frequencies of all of these disturbances, upsetting the equilibrium of the world's ecosystems. From the example of Fox Hollow it appears that fire suppression may be particularly harmful, resulting in the reduction of genetic resources and increasing the probability of catastrophic disturbances in the future.

Acknowledgments

I wish to thank C. Johannessen for his help throughout this research, C. Patton for help with the calculations of solar radiation, the biogeography students of the University of Oregon for help in collecting some of the field data, S. Cook, M. Donley, V. Mas, D. Fiedler, D. Chapin and P. Squier for advice and S. Allen for assistance with all aspects of this paper.

References

- Baldwin E.M. (1964) *Geology of Oregon*. University of Oregon Coop. Bookstore, Eugene.
- Cooper C.F. (1960) Changes in vegetation, structure and growth of southwestern pine forest since white settlement. *Ecol. Monogr.* 30, 129–164.
- Daubenmire R. (1968) *Plant Communities*. Harper & Row, New York.
- Dyrness C.T., Franklin J.F. & Moir W.H. (1974) A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. *Bull.* 4. *Coniferous Forest Biome*. University of Washington, Seattle.
- Fowells H.A. (1965) *Silvics of Forest Trees of the United States*. USDA Handbook 271.
- Franklin J.F. & Dyrness C.T. (1973) Natural vegetation of Oregon and Washington. *USDA Forest Service General Technical Report*, PNW-8.
- Habeck J.R. (1961) The original vegetation of the mid-Willamette Valley, Oregon. *NW Sci.* 35, 65–77.
- Habeck J.R. (1972) Fire ecology investigations in the Selway-Bitterroot Wilderness. *University of Montana, USDA Forest Service Publ.* R1-72-0001.
- Heinselman M.L. (1970) Restoring fire to the ecosystems of the Boundary Waters Canoe Area, Minnesota and to similar wilderness areas. In: *Tall Timbers Fire Ecology Conference*, 10, 9–24.
- Hitchcock C.L. & Cronquist A. (1973) *Flora of the Pacific Northwest*. University of Washington Press, Seattle.
- Johannessen C.L., Davenport W.A., Millet A. & McWilliams S. (1971) The vegetation of the Willamette Valley. *Ann. Ass. Am. Geogr.* 61, 286–302.
- Loucks O.L. (1970) Evolution of diversity, efficiency, and community stability. *Am. Zool.* 10, 17–25.
- Moral R. del (1972) Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. *Bull. Torrey Bot. Club*, 99, 57–65.
- Morris W.G. (1934) Forest fires in western Oregon and western Washington. *Ore. Hist. Quart.* 35, 313–339.
- Sellers W.D. (1965) *Physical Climatology*. University of Chicago Press, Chicago.
- Sprague F.L. & Hansen H.P. (1946) Forest succession in the McDonald Forest, Willamette Valley, Oregon. *NW Sci.* 20, 89–98.
- US Weather Bureau (1965) Climatic summary of the United States. Supplement for 1951 through 1960, Oregon. *Climatology of the United States*, No. 86–31. Washington, D.C.
- Vokes H.E. Snavely Jr., P.D. & Myers D.A. (1951) Geology of the southern and southwestern border area of the Willamette Valley, Oregon. *US Geological Survey*, ON 150.