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Influences of Environmental Gradients on the Patterns of Vegetation Structure and Tree Age Distribution in the East Side of Cascade Range, Washington, USA*

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워싱턴州 케스케이드山脈 東쪽 山林에서 環境勾配가 植生構造와 年齡分布에 미치는 影響*

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要　約

山林의 環境勾配에 따른 植生變化를 求明하기 위하여, 美國 워싱턴주 케스케이드 山脈 동쪽의 위나치 國有林에서 해발 975m, 1280m, 1700m에 있는 南斜面과 北斜面의 6개 天然林 지역을 對象으로 하여 線型法을 利用하여 植生調査를 實施하고, ordination법에 의하여 要因을 分析하였다. 美松(최고 수령 286년, DBH 110cm)은 海拔高와 斜面의 方位에 關係 없이 모든 6개 地域에서 優占種의 하나로 觀察되었으며, 폰데로사소나무(최고수령 312년, DBH 97cm)는 南斜面에서만 優占種이었다. 그란디스젓나무(최고수령 115년, DBH 51cm)는 1280m 北斜面에서, 그리고 라시오카파젓나무(최고 수령 127년, DBH 42cm)는 1700m 北斜面에서 優占種이었다.

斜面方向과 關係있는 水分은 특히 南斜面에서 植生構造를 決定하는 가장 重要한 要因 가운데 하나이었다. 南斜面에 비해서, 北斜面은 水分이 制限要因이 아니었고, 樹冠이 더 크게 자랐으며, 高度 혹은 相互樹種간 競爭이 더 重要한 要因이었다. 種의 多樣性은 環境要因이 惡化됨에 따라 減少하는 傾向을 보였는데, 특히 南斜面은 北斜面보다 水分不足과 심한 溫度差로 因하여 種多樣性이 減少하였다.

上層植生의 年齡構造는 北斜面과 南斜面이 서로 다른데, 光量, 水分, 그리고 氣候가 양쪽斜面에서 다르게 作用하기 때문이며, 큰 規模의 攪亂(山火 혹은 害蟲의 被害) 이 年齡構造를 바꾸는 要因이었다. DBH와 年齡과의 相關關係는 成熟木보다 어린樹木에서 높았고, 南斜面에서 陽樹의 DBH값은 北斜面에서 보다 큰 값을 보였는데, 이는 斜面의 方向이 年齡과 크기를 決定짓는 가장 重要한 要因 가운데 하나라는 것을 보여 주는 것이다.

ABSTRACT

To understand vegetation changes along environmental gradients in the natural forests in the east side of the Cascade Range in Washington state, USA, line transects were used to sample six different forest environments in the Wenatchee National Forest in the north-facing and south-facing sites at 975, 1280 and 1700m elevation. Data were analyzed using ordination by detranded correspondence

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analysis.

Pseudotsuga menziesii was found as one of the dominant species on all the six sites regardless of elevation or aspect, while *Pinus ponderosa* was dominant on south slopes only. *Abies grandis* and *A. lasiocarpa* were dominant species on north slopes at elevations of 1280 and 1700m, respectively.

Moisture, as it related to aspect, was identified as one of the most important environmental gradients for explaining the variation of vegetation types. On north-facing slopes, compared to south-facing slopes, where moisture was not as limiting and canopies could grow denser, probably, elevation or competitive interaction was more important. Species diversity tended to decrease with increasing environmental severity, with south slopes having less diversity than north slopes due to extended water stress and harsher temperature extremes on south slopes.

The age structure on north-facing and southfacing slopes was different. Light intensity, moisture and climate were different between these two slopes. Large scale disturbances(e.g., big fire or insects) were major causes in changing age structure.

Younger trees showed a closer relationship between size and age than adult trees. DBH values of shade intolerant species in south-facing slope were bigger than those of north-facing slope, which suggested that aspect of stands be the most important factor for age and size.

Key words : Natural forests, disturbance, environmental gradients, vegetation structure, age distribution, aspect, elevation, Washington, North America.

INTRODUCTION

Competition and large scale disturbances influence plant structure, vegetation type and species composition, and affect the form of a plant community at a particular period(Oliver, 1981). Competition and disturbances, which are deeply related to environmental gradients, have sometimes been used to explain plant communities in the Pacific Northwest(Daubenmire, 1965).

The distribution of individual plant species and plant community types in the Cascades Range of Oregon and Washington is determined by environmental gradients, such as moisture and temperature(Zobel et al., 1976 ; Agee and Kertis, 1986). Plant community is directly related to environmental gradients(Franklin and Dyrness, 1988). Two environmental gradients, moisture and temperature, give immense influence to patterns of vegetation in the Cascade Mountains of the Pacific Northwest(Franklin and Dyrness, 1988). However, less is known about which environmental gradients are most important, in the east of the Cascade Range although aspect and elevation have often been used to describe vegetational zones in eastern Washington(Daubenmire, 1965 ; del Moral and Watson, 1978 ; Franklin and Dyrness, 1988).

The objectives of this study were (1)to understand how species composition and age structure are determined across environmental gradients on the east side of the Cascades Range, and (2)to determine the relationships between diameter at breast height(DBH) and age distribution, which can provide information about stand history and dynamics.

MATERIALS AND METHODS

Study area

The study sites, the Wenatchee National Forest, were located on the eastern side of the Cascade Range in Washington, USA(Latitude, 45° 11′ and Longitude, 120° 55′)(Fig. 1). Annual precipitation in the east Cascades varies with the topography and ranges from 530 to 990mm. The average January maximum temperature ranges from -4℃ to 2℃ and minimum from -8℃ to -26℃. The average July maximum temperature ranges from 21℃ to 29℃, and minimum from 7℃ to 10℃(U.S. Dept. Commerce, 1974). Six sites were selected to examine the responses of Eastern Washington forest communities to diffe-

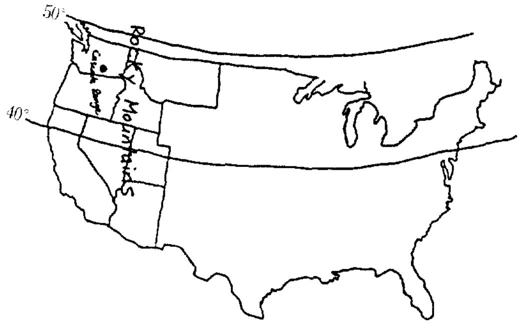

Fig. 1. Map of study area(Wenatchee National Forests), the Cascade Range, Rocky Mountains, and USA. Study area lies in between the Cascade Range and Rocky Mountains.

rent elevation and aspect regimes. Site A, at 975m, was located in the *Pinus ponderosa* vegetation zone. The climate of this site was characterized by severe periods of summer drought and short growing seasons(Franklin and Dyrness, 1988). Site B, at 1280m, was located in the *Abies grandis* vegetation zone. The climate of this site was very mild. This site was milder than any other east-side vegetation zone. Summer drought was still important, and winter snowfall was lower than in higher forest zones(Franklin and Dyrness, 1988). Site C, at 1700m, was located in the *A. lasiocarpa* zone. Climate in this zone was the coolest and most moist of the forested zones, and has cool summers and cold winters with deep snowpacks which shorten the germination and growing season(Franklin and Dyrness, 1988). Each pair includes a north(N) and a south aspect(S).

Line transects

Two transect locations along the contour of the slope within each site were randomly selected. Transects 30m long were established parallel to slope. Percent cover of each species encountered (at a frequency of 0.3m or greater) in both the overstory(taller than 1.8m) and understory(smaller than 1.8m) was recorded. Understory and overstory vegetation were sampled separately. If overlap occurred in the understory, only the tallest species were counted. If there were no understory herbs or shrubs under the transects, vegetation was classified to bare ground, rock, litter(smaller than 2cm diameter) or woody debris (greater than 2cm diameter).

Seedling plots, tree ages, DBH and sapling

Seedling density was sampled at each site by establishing 0.9m by 0.9m($0.8m^2$) plots at 7.5m, 15m and 22.5m marks on each 30m transect. The species and age were recorded for each seedling found. A plot(30m×30m) was established at each of the six sites. Species, DBH, and ring count were recorded for the trees within each plot. In the laboratory, age was estimated for trees in which increment cores do not intercept the pith. Age of saplings(<1.8m) were also recorded for each plot.

Data analysis

Cover data were summarized by transect and by site. The data were input to Detrended Correspondence Analysis(DCA), and the resulting axes of the ordination were interpreted as environmental gradients. DCA was chosen as the ordination method for the percent cover data and DECORANA(Hill, 1979) was used to analyze the data. DECORANA ordination was used because this method is useful in visualizing how the species and community types are distributed across environmental gradients.

Relationship between age and DBH.

Relationship between age and DBH at each site was determined by regression analysis. The computer program, MINITAB was used to equate a regression of DBH on age for the dominant tree species at each site.

RESULTS

Site description

Tree ages ranged from 2 to over 300 years, with distribution of age classes varying by site and species(Table 1). DBH also varied with larger trees distributed on the south sites. The lowest elevation of north-facing slope(AN) was characterized by *Pseudotsuga menziesii*, some *A. grandis* and *P. ponderosa*(Fig. 2). Charcoal on

Table 1. Age and DBH ranges of overstory tree species on six sites on the Wenatchee National Forest in Washington. Averages are shown in parentheses.

Species	AS*		AN		BS		BN		CS		CN	
	Age (yr.)	DBH (cm)	Age (yr.)	DBH (cm)	Age (yr.)	DBH (cm)	Age (yr.)	DBH (cm)	Age (yr.)	DBH (cm)	Age (yr.)	DBH (cm)
Abies			45-70	6-33	12-115		11-112	0.3-51				
grandis			(58)	(18)	(41)		(56)	(8)				
Abies											21-127	5-42
lasiocarpa											(65)	(16)
Larix							48-83	19-38				
occidentalis							(68)	(27)				
Picea												
engelmannii											(99)**	(47)
Pinus												
albicaulis											(76)	(22)
Pinus			31-86	5-25			72-95	11-15	120-140	10-55		19-22
contorta			(60)	(17)			(84)	(13)	(140)	(32)	(77)	(20)
Pinus	11-283	12-78	90-220	26-88	2-312	1-97			36-41	14-17		
ponderosa	(130)	(35)	(144)	(50)	(101)	(12)			(39)	(15)		
Pseudotsuga	15-147	6-72	13-163	5-70	8-268	0.6-80	45-114	8-35	15-236	7-110	51-74	7-46
menziesii	(94)	(37)	(63)	(22)	(61)	(7)	(76)	(21)	(79)	(38)	(67)	(26)

* A : site A(elevation 975m), B : site B(elevation 1280m), C : site C(elevation 1700m)
S : south aspect, N : north aspect

** The absence of range indicates a single tree on the site

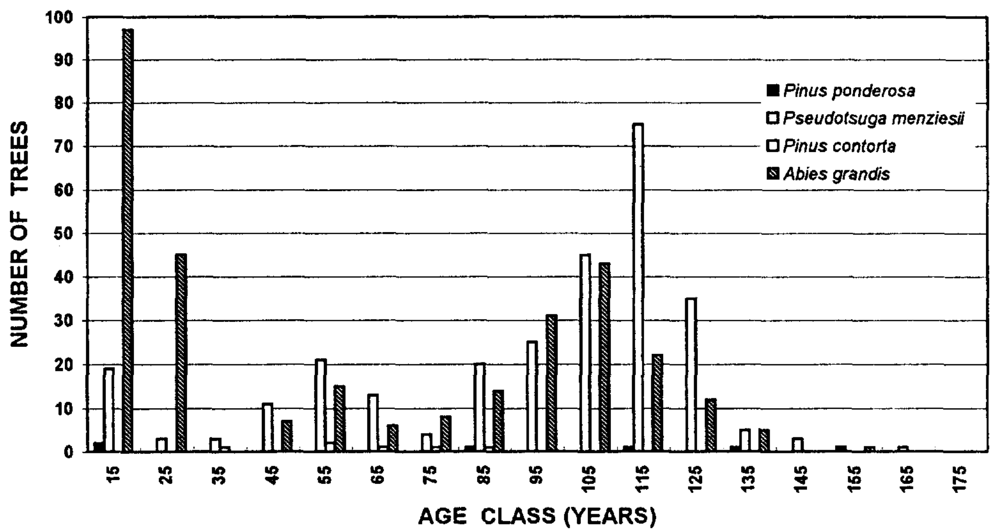

Fig. 2. Relationship between age class(years) and number of trees(per 900 square meter) in site AN (elevation 975m, North facing slope)

the ground and some fire scars on the trunks of many trees suggested that ground fires were somewhat common in this site. The lowest elevation south-facing site(AS) was characterized by *P. ponderosa* and *P. menziesii*(Fig. 3). This site was very open and dry, therefore, seedlings and saplings of *P. ponderosa* which were dry tolerant species scattered on the ground(Table 2,

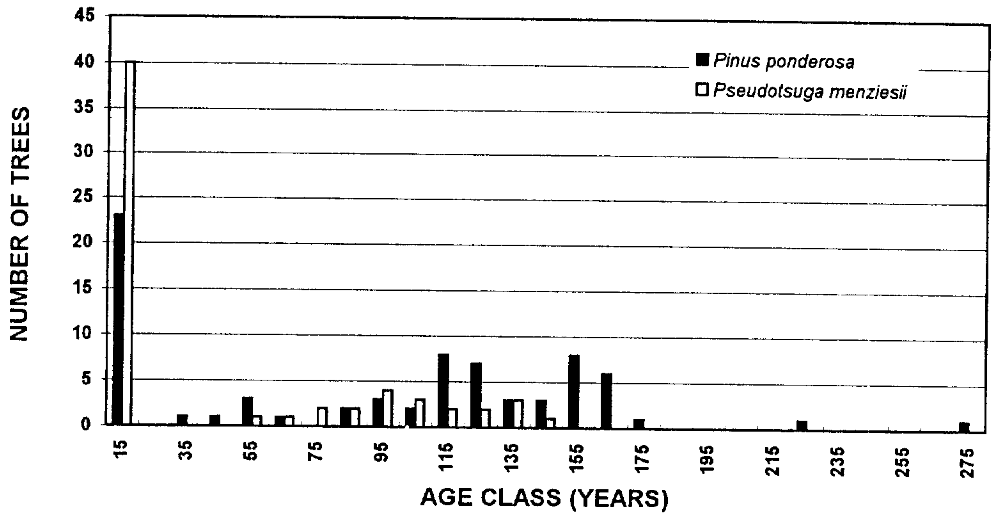

Fig. 3. Relationship between age class(years) and number of trees(per 900 square meter) in site AS (elevation 975m, South facing slope)

Table 2. Number of seedlings per 2.4m^2 on each site in the Wenatchee National Forests, Washington, USA.(A : 975m, B : 1280m, C : 1700m, N : north slope, S : south slope)

	AS	AN	BS	BN	CS	CN	Total
Pseudotsuga menziesii	38	35	9	134	5	3	224
Pinus ponderosa	20		4				24
Abies grandis		64		53			117
Pinus contorta		2		23			25
Larix occidentalis				5			5
Abies lasiocarpa						24	24
Total	58	101	13	215	5	27	419

Table 3. Number of saplings per 900m^2 on each site in the Wenatchee National Forests, Washington, USA.(A : 975m, B : 1280m, C : 1700m, N : north slope, S : south slope)

	AS	AN	BS	BN	CS	CN	Total
Pseudotsuga menziesii	5	15	31	5	4	4	64
Pinus ponderosa	9	1	24				34
Abies grandis		23	1	44			68
Pinus contorta		3	1	23			27
Larix occidentalis				1			1
Abies lasiocarpa						23	23
Picea engelmannii				1			1
Total	14	42	57	74	4	27	218

3). Number of seedlings appeared to be strongly related to number of saplings pattern(Table 2, 3). *P. ponderosa* seedlings and saplings did not appear in north-facing sites.

The mid elevation site BN had young age distribution, and most trees were 115 years old or less(Fig. 4). This site initiated approximately 120 or 150 years ago. The site such as site AN, had charcoal and huge amount of scarred woody debris on the floor, suggesting that big fire killed

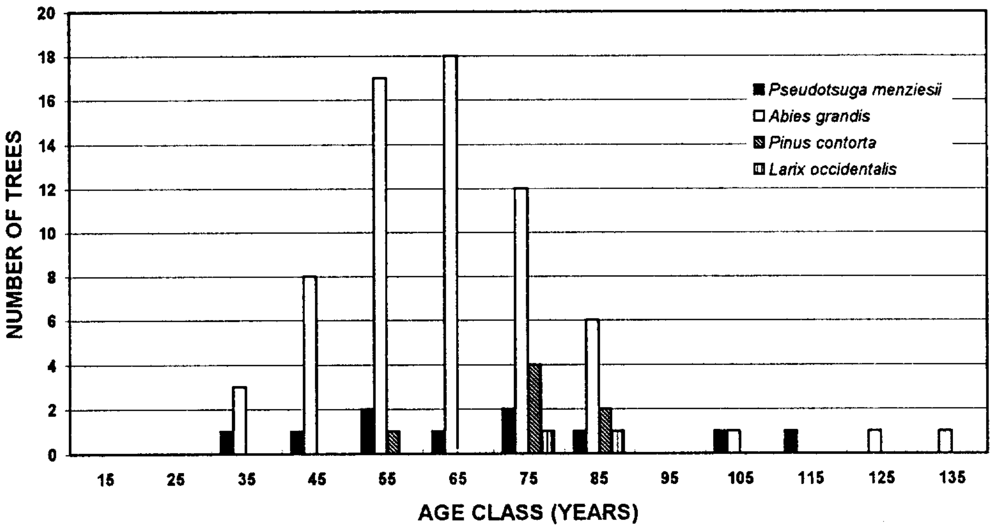

Fig. 4. Relationship between age class(years) and number of trees(per 900 square meter) in site BN (elevation 1280m, North facing slope)

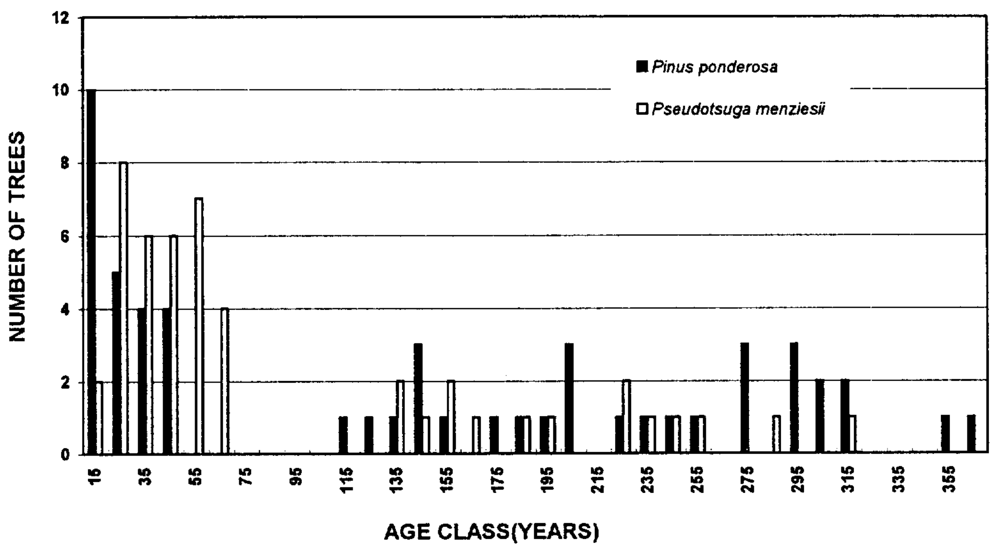

Fig. 5. Relationship between age class(years) and number of trees(per 900 square meter) in site BS (elevation 1280m, South facing slope)

overstory stands nearly 150 years ago. Huge amount of *A. grandis* seedlings and saplings (Table 2,3), on the contrary to site BS, implied that *A. grandis* was one of the shade tolerant species(Harlow et al. 1979). Site BS was very dry and steep slope with rocky ground, and had a broad age distribution(Fig. 5).

The high elevation north-facing site(CN) was characterized by *A. lasiocarpa* which had very dense canopy. This site was another young stand like BN with most trees 140 years old or less(Fig. 6). Large fallen wood with root rot indicated that the stand was initiated after a windstorm or was breaking up now due to some disease. *A. lasiocarpa* seedlings and saplings occupied the most understory. The most common overstory species in site CS was *P. menziesii*, but *P. ponderosa* also appeared(Fig. 7). Even

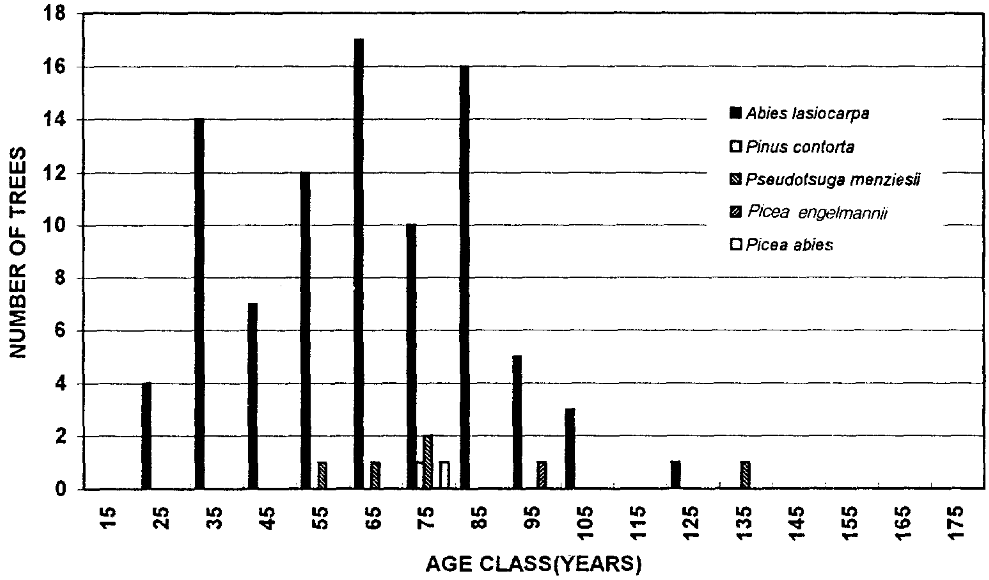

Fig. 6. Relationship between age class(years) and number of trees(per 900 square meter) in site CN (elevation 1700m, North facing slope)

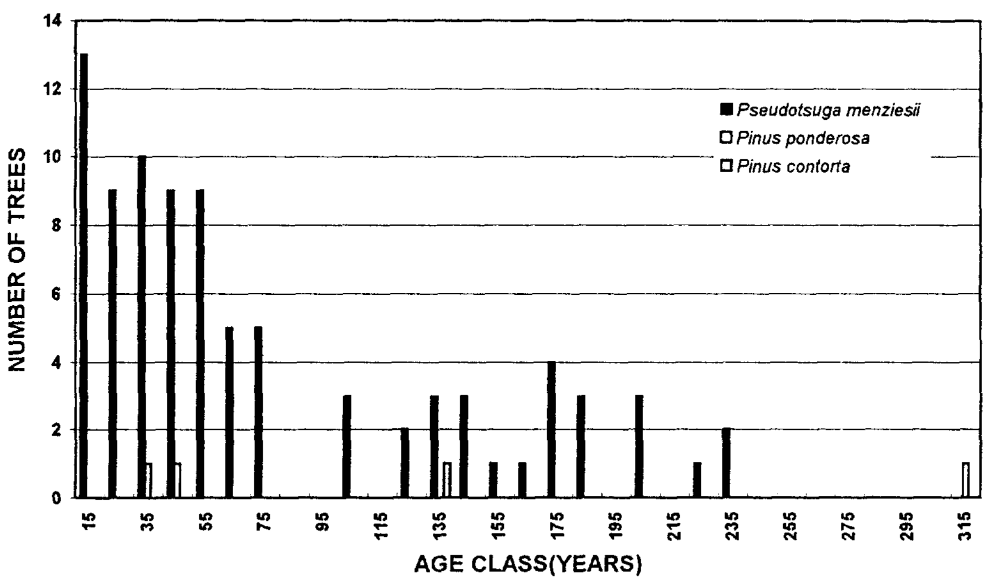

Fig. 7. Relationship between age class(years) and number of trees(per 900 square meter) in site CS (elevation 1700m, South facing slope)

though this site was on a south-facing slope, there were no *P. ponderosa* seedlings or saplings (Table 2,3).

Seedlings and saplings

Number of seedlings appeared to be strongly related to number of sapling pattern(Table 2,3). Number of living seedlings and saplings varied from site to site. Site BN and AN had more seedlings and saplings than other sites. Site BN had four different species of seedlings, site AN had three, site AS, BS and CN had two, and site CS had only one species. *P. menziesii* seedlings appeared on both north and south-facing sites. *P. ponderosa* seedlings and saplings appeared on south-slopes only, while *A. lasiocarpa*, *A. grandis*, and *P. contorta* seedlings and saplings only appeared on north-facing site.

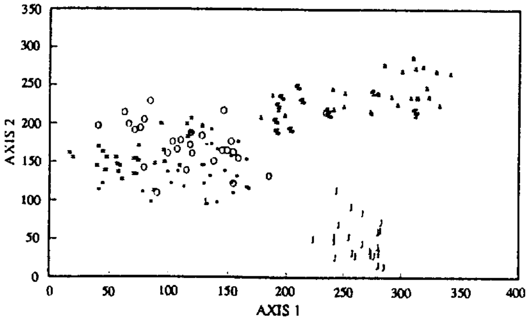

Fig. 8. Results of detranded correspondence analysis by transects from east side of Cascade Range in Washington State, USA.
- A : site A(elevation 975m), B : site B (elevation 1280m), C : site C(elevation 1700m)
- S : south aspect, N : north aspect
- Symbols : * : AS, % : AN, o : BS, a : BN, = : CS, J : CN

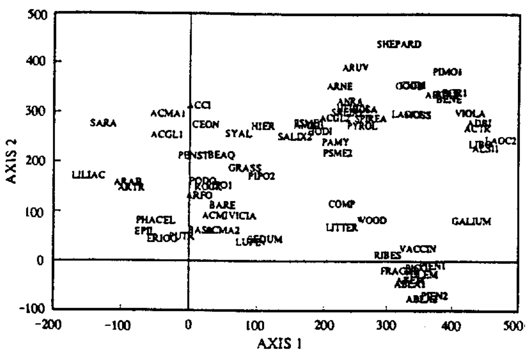

Fig. 9. Results of detranded correspondence analysis by species from east side of Cascade Range in Washington State, USA. Only the code of major species was listed (ABGR=*Abies grandis*, ABLA=*Abies lasiocarpa*, ACGL=*Acer glabrum*, ACMA =*Acer macrophyllum*, LAOC=*Larix occidentalis*, PIAB=*Picea abies*, PIEN=*Picea engelmannii*, PICO=*Pinus concorta*, PIMO=*Pinus monticola*, PIPO= *Pinus ponderosa*, PSME=*Pseudotsuga menziesii*). Refer other species in the text.

Ordination

Results of ordination by transect showed all three south-facing sites to aggregate in the lower left side, with small variation from one another on axes 1 and 2 of the ordination although BS is slightly higher than AS and CS(Fig. 8). The north-facing sites ordinated with high axis 1 values. The AN and BN sites were clumped near the top with BN being slightly higher. CN site, which had a low axis 2 value and high axis 1 value, was well differentiated in the lower right-hand corner. Transect data showed that north and south-facing sites were segregated from right to left side on ordination(Fig. 8).

A. grandis appeared in the top right corner where AN and BN were located(Fig. 9). *P. menziesii* was in the center of the ordination close to AN, BN and all the south-facing sites. *P. ponderosa* was on the left side of the ordination where the south-facing sites were located. *A. lasiocarpa*, *P. contorta* and *Picea englmannii* appeared in the low right corner of the ordination associated with CN which had high axis 1 values and negative axis 2 values(Fig. 9).

Species on the top right side of sites AN and BN were *Adenocaulon bicolor*, *Arctostaphylos nevadendis*, *Arctostaphylos uva-ursi*, *Berberis nervosa*, *Viola sp.*, and *Pyrola sp.* Species on the left side of the ordination space were *Arenaria fomosa*, *Artemisia tridentata*, *Ceonothus sp.*, and *Purshia tridentata*. *Galium sp.*, *Ribes sp.*, and *Vaccinium sp.* were on the lower right corner in the ordination(Fig. 9).

Age and size structure

Big differences existed between age structures of south-facing sites and north-facing sites. South-facing sites had considerably more large trees than do sites located on north-facing sites (Fig. 2-7). The north-facing sites generally showed normal-distribution curves. However, south-facing sites showed pretty irregular shapes. Age structure in the south-facing sites were older with maximum ages of 300 years, compared to the age structure in north-facing sites with maximum ages of 160 years.

P. menziesii and *A. grandis* were generally widespread trees in AN site. Recruitment of *P. menziesii* started approximately 150 years ago. Recruitment of *A. grandis* started nearly at the same time. For the recent 30 years, recruitment of *A. grandis* had increased(Fig. 2). The diameter distribution of this site showed that a majority of the remaining trees was small size of *A. grandis*. Recruitment of *P. menziesii* started nearly 150 years ago in AS site. There were fewer *P. menziesii* trees than on site AN. Some *P. ponderosa* trees were older than 180 years. Recruitment of both species had increased in the past 20 years(Fig. 3). Site BN had the youngest age structure among every sites. Trees of all species were younger than 135 years. Recruitment started increasing 100 years ago, peaked 50-60 years ago, and declined 30 years ago when recruitment appears to be ceased(Fig. 4).

Site BS had low numbers of *P. ponderosa* and *P. menziesii* stems between 100 and 360 years. Recruitment of these two species began increasing 65 years ago(Fig. 5). The most common species in CN site was *A. lasiocarpa*. This stand originated approximately 100 years ago. Small numbers of *P. contorta*, *P. engelmannii*, and *P. menziesii* established between 50-135 years ago(Fig. 6). Establishment of *P. menziesii* in site CS increased during the past 70 years. Nearly even numbers of *P. menziesii* appeared between 90 and 240 years(Fig. 7).

Regression analysis between age and DBH

All regression equations of DBH on age for the dominant tree species at each site were statistically significant at the 5% significance level. R^2 values ranged from 0.420 to 0.947(Table 4).

DISCUSSION

Regeneration ; seedlings and saplings

North facing sites had more seedlings and saplings than those in the south facing sites, especially BN and AN sites. Water contents in the soil and temperature were the most important factors for seedling mortality(Cui and Smith, 1991). North-facing sites had more moisture due to lack of soil evaporation from the ground. A deep snowpack in winters on north aspects may also contributed to keeping more moisture during the growing season. Competition with grass might reinforce seedling mortality, because grass and adult trees used water resources which were needed for seedling survival. Root competition between seedlings and other plants increase water stress for seedlings(Coates et al., 1991).

P. ponderosa seedlings and saplings were only found on south slopes, because north-facing sites generally had little strong light in the understory due to closing overstory. North slope sites were

Table 4. Regression equations of DBH on age and R^2 for the dominant tree species at each site. All R^2 are statistically significant($P<0.05$)

Site	Species	Equation	R^2
AN	*Pseudotsuga menziesii*	DBH=−0.32+0.14*age	0.625
AN	*Pinus ponderosa*	DBH= 0.02+0.12*age	0.947
AS	*Pinus ponderosa*	DBH= 3.01+0.08*age	0.538
AS	*Pseudotsuga menziesii*	DBH=−0.07+0.17*age	0.931
BN	*Abies grandis*	DBH=−4.57+0.17*age	0.451
BN	*Pseudotsuga menziesii*	DBH= 0.33+0.09*age	0.827
BN	*Pinus contorta*	DBH= 0.02+0.13*age	0.946
BS	*Pinus ponderosa*	DBH= 2.46+0.08*age	0.781
BS	*Pseudotsuga menziesii*	DBH= 3.18+0.06*age	0.729
CN	*Abies lasiocarpa*	DBH= 0.03+0.10*age	0.420
CS	*Pseudotsuga menziesii*	DBH= 3.63+0.15*age	0.661

more shaded by overstory trees and taller brush. *P. ponderosa* was somewhat drought tolerant and shade intolerant. These facts made *P. ponderosa* difficult to establish on north–facing slopes. However, seedlings and saplings of *A. lasiocarpa*, *A. grandis*, and *P. contorta* appeared in north-facing sites because *A. lasiocarpa* and *A. grandis* were shade tolerant species(Harlow et al., 1979).

Even though site CS was on a south-facing slope, there were no *P. ponderosa* seedlings or saplings(Table 2,3). The elevation was too high to establish seedlings because there were stronger wind, more burrowing mammals and more shrubs on the ground than the other two south-facing slope sites preventing seedling establishment in this site. These facts suggested that habitat for seedlings generally varied with individual species.

Ordination

Environmental gradients of temperature and moisture have been used to describe forest distribution for the region(Zobel et al., 1976 ; Agee and Kertis, 1986 ; Franklin and Dyrness, 1988). del Moral and Watson(1978) identified temperature and moisture gradients as primary gradients for forest vegetation in Washington Cascade. The species in the right side of the ordination space were *A. grandis*, *A. lasiocarpa*, *P. contorta*, *Adenocaulon bicolor*, *Arctostaphylos nevadendis*, *Arctostaphylos uva-ursi*, *Berberis nervosa*, *Viola sp.*, *Pyrola sp.*, *Galium sp.*, *Ribes sp.*, and *Vaccinium sp.* These species were drought intolerant(Harlow et al., 1979). The species on the left side of the ordination space were *P. ponderosa*, *Arenaria fomosa*, *Artemisia tridentata*, *Ceonothus sp.*, and *Purshia tridentata*. These species were drought tolerant. *P. menziesii* was located in the central portion of the ordination space. It suggested that *P. menziesii* was moderate shade intolerant species(Harlow et al., 1979).

Axis 1 of the ordination might be related to temperature and solar radiation which were strongly related to aspect. All of the north facing sites were on the right side of axis 1, while south facing sites were classified to the left on axis 1. Solar radiation provided strong light intensity into south facing sites. South-facing sites had very high drought stress(Fig. 8). The amount of evaporation on south-facing slopes was probably greater than on north-facing slopes. The rate of decomposition on south slopes was probably faster than that of north facing sites due to different temperatures and light intensities. The organic matter and litter layer on north facing sites were denser than those of south facing sites. Therefore, solar radiation and temperature were the main elements for determining axis 1. Axis 2 of the ordination might be related to drought stress and temperature. Though sites CS and CN differ in many ways, both sites had very high drought stress(Fig. 8). These two sites were located at high elevation. *A. lasiocarpa*, the dominant species on the sites C, had high tolerance to snow and frost, and low to moderate tolerance to drought reflecting the cold, dry conditions on those sites. Sites AN and BN experienced less drought stress than site CN. Sites C had the coldest temperatures because this site was located on the highest elevation. These facts suggested that temperature and drought as related to elevation were elements for determining axis 2. However, it was hard to define which gradients were most efficient to explain the ordination axis. More environmental factors such as length of growing season, role of snowpack, solar radiation, temperature, summer moisture stress, soil pH, amount of humus, and nitrogen contents also had to be considered.

Age structure and stand history

Age and size frequency distribution were useful for determining the past disturbance and history of the stand. This was because competition, disturbance and environmental interaction generally influence age distribution and stand dynamics. Among many kinds of disturbances, fire was the most important stand initiating event in the Pacific Northwest, even in the Coast Range (Hemstorm and Franklin, 1982). Age structures on south and north-facing sites were very different, even though they were distributed or initiated at similar times.

Approximately 170 years ago big fire probably occurred on both AN and AS sites. After the fire in AN site, *P. menziesii* began to occupy this site from an outside source because *P. menziesii* was a faster growing and less shade tolerant species than *A. grandis*. *P. menziesii* established in greater numbers than *A. grandis* for 100 years after the fire. For 50 or 60 years, *P. menziesii* had stem exclusion stage until the death of some trees made gaps allowing understory regeneration by *A. grandis*. Some *P. ponderosa* and *P. contorta* had established in the understory. This process was an example of the typical stand development in the Pacific Northwest(Oliver, 1981). Vegetation coverage of AN site was denser than those of AS site due to available moisture. Soil moisture content was one of the critical factors affecting survival of seedlings, saplings and overstory trees(DeLucia et al., 1988).

Site AS was so dry that dense stands could not establish. After disturbance(probably fire), *P. ponderosa* colonized in this site, and 30 or 40 years later the more shade tolerant *P. menziesii* began to establish(Agee, 1991). Seedlings in this site did not increase gradually, probably because of lack of moisture. In site AS extensive seedling establishment was prevented due to south-facing and drought. Site BN was dominated by *A. grandis* with a small number of *Larix occidentalis*, *P. contorta* and *P. menziesii*. This stand was young, with most trees 135 years old or less(Fig. 4). About 140 years ago, this stand was a *P. menziesii* stand, with *A. grandis* in the understory as regeneration. Then, disturbance removed the overstory allowing the release of *A. grandis*. The disturbance might have been insect attack, because this site shows thick-trunked trees with evidence of mountain pine beetle(*Dendroctonus ponderosae*) damage(Amman and Baker, 1972). This stand had higher density of undeveloped younger trees in the understory compare with AN site. This suggested that BN was growing into the stem exclusion phase of stand development, as *A. grandis* was a shade intolerant species(Oliver, 1981).

Site BS had sparse canopy coverage due to drought and periodic fire. Periodic absence of overstory tree species(Fig. 5) suggested that a large fire occurred about 350 years ago, and medium sized ground fires happened periodically after that. The lack of older trees in this site suggested that the disturbance was not a crown fire but a ground fire. The age structure of site CN was similar to site BN but site CN was dominated by *A. lasiocarpa*. About 140 years ago, this stand might have had *P. menziesii* or *P. engelmannii* in the understory as advanced regeneration, when a disturbance came through the stands, and removed the overstory trees. Then, *A. lasiocarpa* occupied this stand. This was high elevation site, which was characterized by cool and moist conditions. These conditions might be optimum forest zone for *A. lasiocarpa* at many locations in Washington and Oregon (Franklin and Dyrness, 1988). *A. lasiocarpa* forest zone was the coolest and most moist of the forested zones. Cool summers, cold winters and development of deep winter snowpacks were important factors for *A. lasiocarpa* growth (Daubenmire, 1965 ; Franklin and Dyrness, 1988).

Site CS closely resembles AS and BS in age structure. A major disturbance, probably fire, occurred about 240 years ago with another periodic disturbance allowing tree establishment. The establishment of *P. menziesii* during the past 80 years suggested that the stand was in the understory reinitiation stage. After the major disturbance, *P. menziesii* occupied this site due to its fast growth and shade intolerance(Harlow et al., 1979). After the stem exclusion stage ended, large numbers of seedlings established in this site. In short, the age structure, species composition, and stand structure on north and south-facing stands were different. This was a result of differences in light intensity, moisture, and climate between north and south-facing sites.

Relationship between age and DBH

All regression equations of DBH on age for the dominant tree species at each site were statistically significant at 5% level(Table 4). Generally, later recruits(younger trees in some sites) showed a close relationship between size and age. Uniformly similar light levels in the lower canopy were one of the causes of the better correlation between age and DBH among younger individuals. On the other hand, older trees experience the effects of site disturbances, genetic variance and temporal and spatial variation in stand composition which might disrupt the correlation between DBH and age(Harcombe, 1986). Older stems vary more in size than younger stems after a disturbance. Early age classes have less variation than older age classes because they had not yet reached the stem exclusion stage where growth might be suppressed by competition(Oliver, 1981). According to the regression equations, DBH values of *P. ponderosa* and *P. menziesii* in south facing sites were bigger than those of the same species on north facing sites at the same age. This fact suggested that these two trees were shade intolerant species even though *P. menziesii* was known as moderate shade intolerant species(Harlow et al., 1979).

The most important factor which influences age and size could be aspect. The intercept and slopes of the *P. ponderosa* regressions on south facing sites(AS and BS) were very similar. However, the intercept of the regression equations for *P. ponderosa* on south facing sites(AS and BS) and north facing(AN) were different (Table 4). This suggested that the same direction of aspect provided similar growth conditions such as water stress, light intensity, and growing space. Most of the DBH and age scatterplots appeared to have a linear relationship. However, a few *P. menziesii* in south-facing slopes were clearly non-linear. Old *P. menziesii* trees had relatively smaller DBH than those of young trees implying that *P. menziesii* invading first might lose their vigor if they were subjected to harsher site conditions. Once weakened, *P. menziesii* might not regain the vigor. Agee(1987) reported that *P. menziesii* first invading a xeric, windy meadow did not grow as rapidly as those invading in later years in the same place. Old *A. grandis* and *A. lasiocarpa* had relatively bigger DBH than those of young trees because diameter growth was slow when the trees were young and too small to accumulate energy for rapid volume growth. As the tree size and foliage increased, more energy was available for diameter growth, causing a rapid increase in diameter until it reaches its highest growth rate(Oliver and Larson, 1990).

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