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Relationships Among Environmental Variables and Distribution of Tree Species at High Elevation in the Olympic Mountains

Abstract

Relationships among environmental variables and occurrence of tree species were investigated at Hurricane Ridge in Olympic National Park, Washington, USA. A transect consisting of three plots was established down one north- and one south-facing slope in stands representing the typical elevational sequence of tree species. Tree species included subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), mountain hemlock (*Tsuga mertensiana*), and Pacific silver fir (*Abies amabilis*). Air and soil temperature, precipitation, and soil moisture were measured during three growing seasons. Snowmelt patterns, soil carbon and moisture release curves were also determined. The plots represented a wide range in soil water potential, a major determinant of tree species distribution (range of minimum values = -1.1 to -8.0 MPa for Pacific silver fir and Douglas-fir plots, respectively). Precipitation intercepted at plots depended on topographic location, storm direction and storm type. Differences in soil moisture among plots was related to soil properties, while annual differences at each plot were most often related to early season precipitation. Changes in climate due to a doubling of atmospheric CO_2 will likely shift tree species distributions within, but not among aspects. Change will be buffered by innate tolerance of adult trees and the inertia of soil properties.

Introduction

Mountainous areas have steep gradients of moisture and temperature (Whittaker, 1975), and provide the opportunity to study biologically significant differences in environment over short distances. These gradients are caused by orographically induced precipitation patterns, adiabatically and topographically induced changes in temperature, and hydrologic processes that redistribute water in steep terrain (Barry, 1992; Ambroise, 1995). The resulting vegetation pattern is typified by closely spaced ecotones, and because of the overwhelming influence of environmental factors, may be especially sensitive to climate change.

Landscape-level effects of global climate change (GCC) on vegetation will manifest at the scale of species distributions of physiognomically dominant organisms. Describing environmental conditions controlling patterns at this scale is one approach to understanding effects of predicted changes in temperature and precipitation due to GCC. In addition to determining the magnitude of environmental difference driving vegetation pattern, relationships among variables predicted by general circulation models (e.g., temperature and precipitation) and other driving variables (e.g., soil moisture) can be evaluated.

This study describes environmental conditions that are associated with the occurrence of dominant tree species in the northeastern Olympic Mountains, Washington. The study was conducted in stands including subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amabilis*), and Douglas-fir (*Pseudotsuga mensiezii*). These stands were closely spaced, but they include species that are diagnostic of vegetation zones (sensu Henderson et al. 1989) which define vegetation pattern at a much larger scale. Critical variables affecting subalpine vegetation in temperate climates include snowmelt, length of growing season, soil and air temperatures, and midsummer soil drying (Tanquillini, 1979; Stevens and Fox, 1991). Measurements of these variables were conducted regularly during three growing seasons and complement studies of environmental-species relationships using less frequent measurements over a wider geographic area (e.g., Zobel et al., 1976; Henderson et al., 1989).

Site Description

Study plots were established on Hurricane Ridge (1550 m, 123° 30' N lat., 47° 58' E long.) near the northern border of Olympic National Park (Figure

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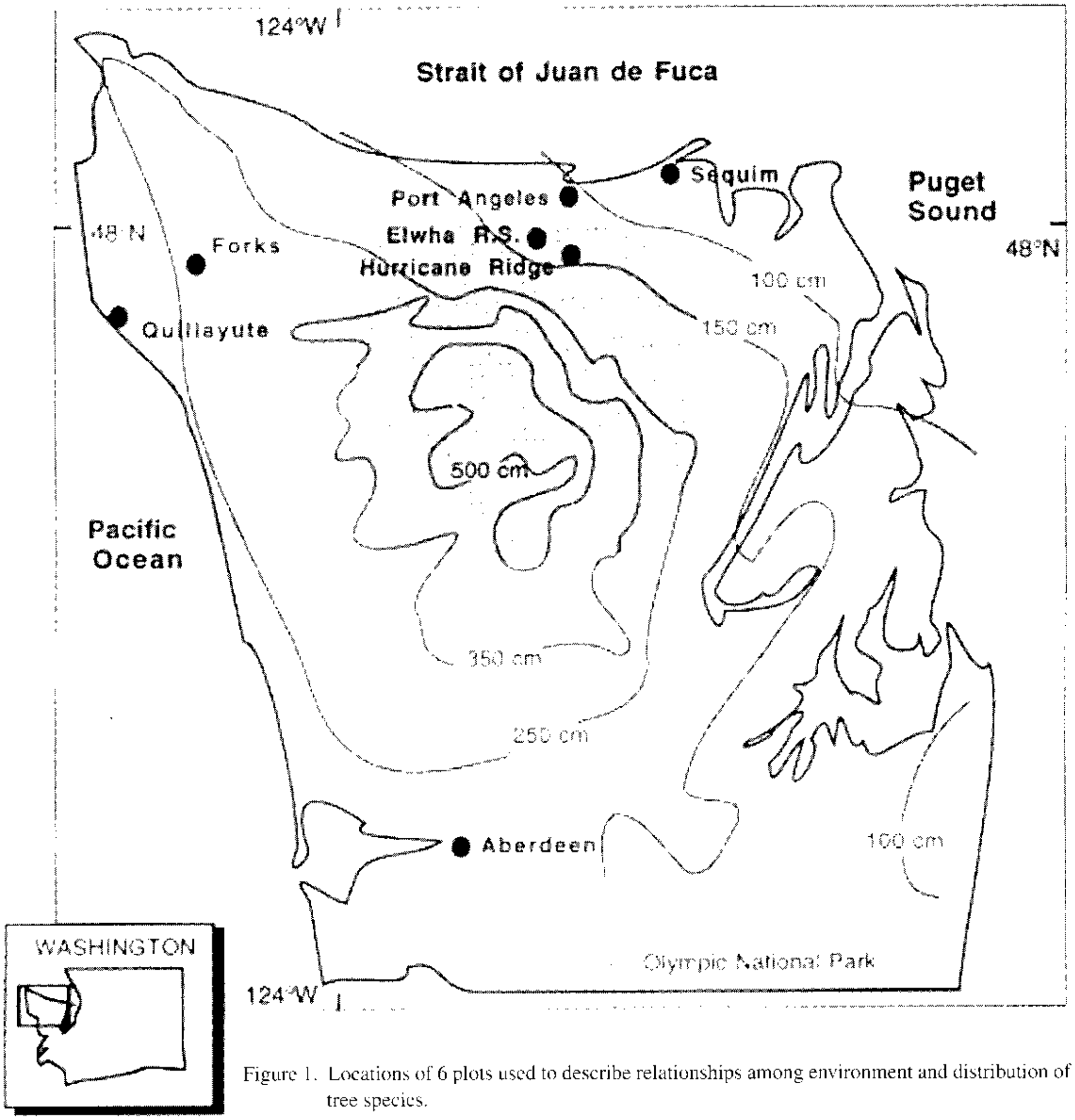

Figure 1. Locations of 6 plots used to describe relationships among environment and distribution of tree species.

1). The Ridge is oriented east-west and is at or below treeline for most of its length. It is composed of Eocene basalts and slightly younger marine sediments including sandstones, shales, and conglomerates (Tabor, 1987). Soils are classified as Typic Cryumbrepts. Subalpine fir (*Abies lasiocarpa*) is the most abundant species on north and south aspects near the ridgeline. Mountain hemlock (*Tsuga mertensiana*) occurs with subalpine fir down north-facing slopes, grades into stands of Pacific silver fir (*Abies amabilis*)and eventually into stands of Douglas-fir (*Pseudotsuga mensiezii*) and western hemlock (*Tsuga heterophylla*) at the base of the mountains. Subalpine fir grades into Douglas-fir at lower elevations on south-facing slopes (Henderson et al., 1989).

The Olympic Peninsula experiences a maritime climate. Most storms move across the peninsula from the southwest (Speer, 1986) and deposit over 600 cm of average annual precipitation on Mount Olympus (2430 m; Philips and Donaldson, 1972). The northeast Olympics are in a rainshadow and Hurricane Ridge averages approximately 100-150 cm precipitation annually, of which 80% falls during October-March and 5% falls July-August. Average January temperatures below 1000 m in the northeast Olympic Peninsula are ~0 °C; maximum August temperatures are ~21 °C (National Oceanic and Atmospheric Administration, 1978).

Two transects each consisting of three 20 x 20 m plots were established. One was on a north- and one was on a south-facing slope. Each transect described a gradient of tree dominance (Table 1). The top of the north transect (ALN) was at 1523 m in a stand of subalpine fir, and extended for 70 m of elevation going through a mixed stand of subalpine fir and mountain hemlock (ALTM), and ending in a Pacific silver fir stand with mountain hemlock in the understory (AA). The south transect spanned 116 m in elevation, starting in a subalpine fir stand (ALS), going through a mixed stand of subalpine fir and Douglas-fir (ALPM), and ending in a Douglas-fir stand (PM).

Methods

Air and soil temperatures, precipitation, soil moisture, and snowmelt were used to characterize growing season conditions during the study. Soil carbon, soil moisture release curves and potential incident solar radiation were used to describe relatively invariant features of the plots.

Temperatures

Air temperature was recorded weekly using max-min thermometers mounted at 1 m height in partial shade on stakes near the center of each plot. Measurements were made from 30 June until 27 November 1993, 10 April to 21 October 1994, and 13 May to 12 October 1995. Records for individual plots commenced when stakes were free of snow in 1994 and 1995. In addition, single-sensor data loggers (Model Hobo-Temp, Onset Computer Co., Inc., Pocasset MA) were installed on 27 November 1993 and recorded air temperature 5 times daily until 11 November 1994. The dataloggers were covered with plastic, put in small plastic containers having holes for ventilation, and hung in trees at approximately 2 m height. Monthly average air temperatures calculated from dataloggers and max-min thermometers when both

TABLE 1. Plot characteristics along north and south facing transects on Hurricane Ridge, Olympic Mountains. Plots are 20 x 20 m and are numbered from top to bottom of transects.

	Plot					
	ALN	ALTM	AA	ALS	ALPM	PM
<u>Location</u>						
Elevation(m)	1523	1503	1453	1520	1463	1404
Aspect (°)	35	38	35	213	190	228
Slope (°)	17	9	32	9	14	22
<u>Plant Community</u>						
Tree area/plot[1] (m^2)						
Abla	3.49	2.90	–	3.21	1.52	0.41
Tsme	0.07	0.33	0.24	–	–	–
Abam		–	3.84	–	–	–
Psme	–	–	–	0.09	0.94	2.19
Total	3.56	3.23	4.08	3.30	2.46	2.60
Understory[2] (trees < 2m tall)						
	Abla	Abam (Tsme) (Abam)	Abam (Tsme) (Abla)	Abla	Abla	(Abla)
<u>Soils</u>						
Texture[3]	L-SL	L-SL	SSiL	SL	SGL	SGL
Moisture at:						
Field Capacity (%)	40.3	41.4	43.6	37.8	33.4	27.3
Permanent Wilt (%)	16.3	17.4	20.6	15.5	14.0	8.2
Carbon (%)	5.6	6.4	8.5	7.0	4.0	3.6

[1] Area at breast height based on dbh measurements; abbreviations are for subalpine fir (Abla), mountain hemlock (Tsme), Pacific silver fir (Abam) and Douglas-fir (Psme).

[2] Species in parentheses had <5% cover; others had 6-25% cover.

[3] Loam (L), sandy (S), silt (Si), gravelly (G).

were available rarely differed more than 1 °C with max-min thermometers tending to give the higher values.

Soil temperatures were recorded from buried copper-constantan or chromel-alumel thermocouples using a hand-held electronic thermometer. Thermocouples were buried in pairs at 6 cm and 35 cm below the soil surface, with 4 pairs per plot. Pairs were located randomly in each quadrant of the plot by throwing an object over the shoulder. Readings were made at mid-day, bi-weekly from 27 July to 3 November 1993 and 10 April 1994 to 20 May 1994, and weekly from 3 June to 21 October 1994 and 8 June to 12 October 1995.

Precipitation

Throughfall precipitation was measured weekly using cylindrical, funnel-topped rain gauges mounted on the same stakes as the max-min thermometers from 30 June to 3 November 1993, 10 April to 21 October 1994, and 25 May to 12 October 1995. The gauges were partially under canopy, but not under canopy driplines. It was impossible to locate rain-gauges on the ground away from the influence of trees in these plots.

Long-term average of maximum snow depth was estimated from height of lichens growing on tree trunks (Long, 1982). The plots were visited bi-weekly beginning 10 April 1994 and weekly beginning 13 May 1995 to estimate when plots were completely bare of snow.

Soil Moisture

Soil moisture was estimated bi-weekly from four samples taken at 15 cm depth and randomly located in each quadrant of the plot by throwing an object over the shoulder. Samples were collected into heavy plastic bags, labeled and taken to the lab. Two approximately 10 g subsamples were taken from each bag and gravel >2-4 mm in diameter was removed as quickly as possible. These samples were weighed, dried at least 12 hrs at 105 °C, and reweighed to determine gravimetric water content. Some samples (n = 48) were also dried for 24 hours and demonstrated that no significant additional drying occurs between 12 and 24 hours.

Soil moisture release curves were developed so soil moisture percentages could be expressed as soil water potential (Richards, 1949). Composites of 6 samples from each site were subsampled and gravel > 2-4 mm was removed so they were similar to samples used for soil moisture determinations. Two sets of 4 subsamples were used to represent each site. One set was used to determine moisture content at pressure values of .033, 0.1, 0.3, and 0.5 MPa. The other set was used for 0.1, 0.2, 0.5 and 1.5 MPa. Two sets were used because the samples no longer produced results describing a smooth curve after several cycles of wetting and drying. The two sets gave consistent values for 0.1 and 0.5 MPa of pressure.

Soil Carbon

Subsamples of the composite soil samples used for moisture release curves were sieved to < 2 mm and finely ground with a mortar and pestle for each site. They were analyzed for carbon content using a total CHN analyzer (Perkin-Elmer CHN Analyzer Model 2400; Page et al. 1982).

Potential Incident Solar Radiation

Plot locations were determined using a portable global positioning system (GPS) and entered into a geographic information system (GIS). Values for potential incident solar radiation (PISR) were calculated for the entire 22nd day of each month using the Solarflux model (Hetrick et al. 1993) for each plot. The model uses solar angle, slope, aspect and local topographic shading derived from USGS 7.5 minute digital elevation models with 30 x 30 m resolution to approximate radiation for a given point. The model does not account for shading due to vegetation or cloud cover.

Weather Data

Individual storms were described using daily weather maps (National Oceanic and Atmospheric Administration, 1993-1995b), and radiosonde soundings taken on the coast at Quillayute (National Climatic Data Center 1993-1995; Figure 1). The 700 millibar (mb) sounding used here corresponds to approximately 3050 m elevation, or slightly higher than the highest point in the Olympic Mountains.

Stand Age

Two cores were taken in November 1995 at 1.4 m height from 8 trees of each dominant or co-dominant species at plots ALTM, AA, ALPM, and PM as part of another study. Tree age was determined by counting annual rings of cores and adding 10 years to compensate for core height. If the core did not include the pith, missing rings where estimated based on extrapolating pith location from the curvature of rings included in the core. Not all cores could be aged.

Statistical Methods

Summary statistics for environmental variables were calculated for each plot. Weekly air and soil temperatures from each plot were averaged across the maximum number of available weeks during the growing season (weeks 26-40), and expressed as heat sums (degree-days) above 0 °C from snowmelt in the spring to snowfall in the fall for 1994. Precipitation was summed for the entire growing season (weeks 26-40) and the early growing season (weeks 26-31). Soil moisture was summarized as a cumulative water potential value (MPa-days).

Precipitation measured at the plots was compared for storms > 25 mm at ALN. Storms were categorized based on average wind direction measured by the Quillayute radiosonde at 700 mb: south to southwesterly (compass degrees 175-217), westerly (compass degrees 250-262), and northwesterly (compass degrees 286-334). Storms were also classified by type based on daily weather maps (National Oceanographic and Atmospheic Administration 1993-1995b) Precipitation coinciding with passage of a front was considered a frontal storm; precipitation occurring in association with a stationary or slowly moving low, in the absence of a front, was considered a convective storm (Philips and Donaldson 1972). Differences in precipitation at plots due to storm type were evaluated using a general linear models procedure (SAS Institute, 1988). Least-squares means were used to compensate for unequal group sizes. Spearman rank correlations were used to compare precipitation distribution among plots due to storm type. Ranks were used to reduce variance due to storm size.

Stepwise regression (SAS Institute 1988) was used to describe the relative importance of variables determining soil moisture. Data from all plots were combined to evaluate the importance of average maximum and minimum air temperatures and heatsums, average soil temperature, total growing season precipitation, early (weeks 26-31) and late (weeks 32-40) growing season precipitation, PISR, soil carbon, snowmelt timing, field capacity, permanent wilting point, aspect, and slope. Regressions were also run by plot to evaluate listed variables that vary annually (air and soil temperatures and precipitation). Because of the small number of years ($n = 3$) variables significant at $p < 0.15$ were reported for plots.

Results

Air Temperatures

As expected, results from data loggers show that average air temperature was generally higher on the south transect than the north (Figure 2). South transect plots had fewer months with average temperature below 0 °C in the winter. Plot ALS was the coolest plot on the south transect; plot AA was the coolest northern plot from April through October, but the warmest during November through February.

The less extreme climate at AA compared with ALN and ALTM was also shown by the averages of maximum and minimum air temperatures during weeks 26-40 (Table 2). Plot AA had the lowest maximum temperatures on the north transect (difference from ALN and ALTM = 0.5-3.0 °C), but had the highest minimum air temperatures (difference from ALN and ALTM = 0.3-1.0 °C).

Growing season length varied with site. Based on number of weeks with freezing temperatures in 1993 and frost-free periods in 1994 and 1995 (Table 2), plots PM, ALPM, and AA had the longest growing seasons, plot ALN the shortest, and ALTM and ALS were intermediate. Higher heatsums from snowmelt to snowfall (PM, ALPM, AA) were associated with earlier snowmelt (Table 2).

Soil Temperatures

Early season soil temperature records are available for 1994 and 1995 and show soils warmed first at ALPM and PM, and last at ALN and ALTM (Figure 3 shows ALN and PM), reflecting order of snowmelt (Table 2). Snow melted at AA at the same time as at ALPM but colder air temperatures on the north transect prevented soil temperatures from warming as quickly as ALPM during both years.

Following snowmelt, average soil temperatures (average of 6 and 30 cm; Figure 3) generally

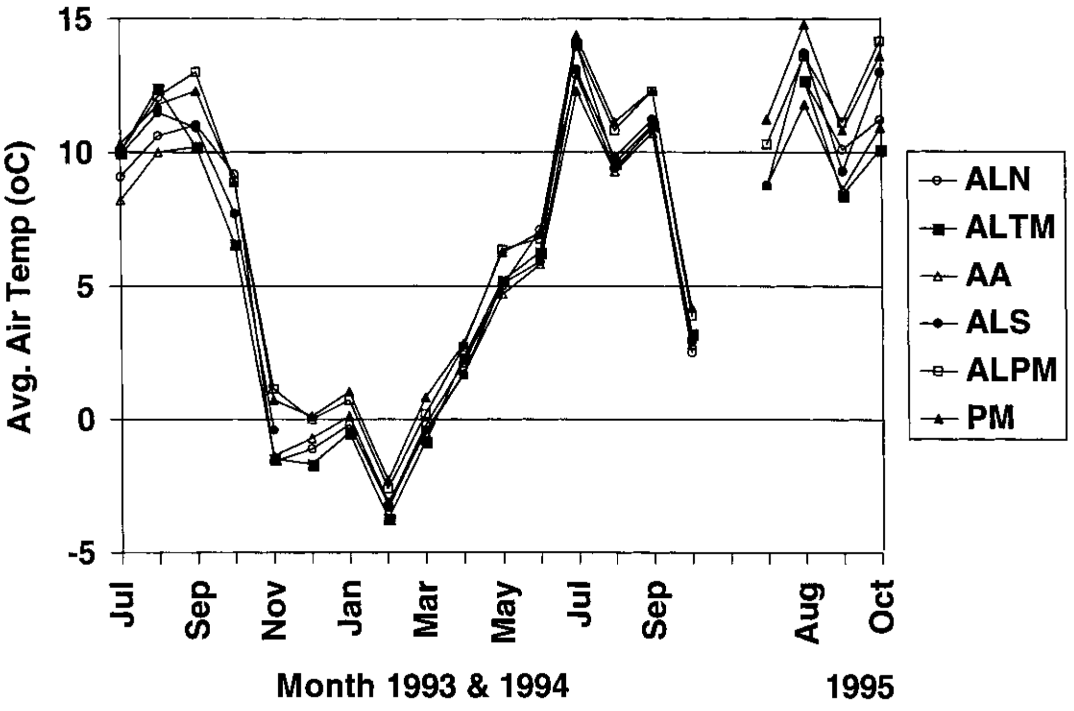

Figure 2. Monthly average of maximum and minimum air temperature at 6 plots from July 1993 to October 1994 and June to September 1995. Data from November 1993 to October 1994 are from dataloggers; others are from max-min thermometers.

followed patterns of average air temperature (Figure 2): peaks of both occurred in September 1993 (weeks 36-39), and July (weeks 27-30) and September (weeks 36-39) of 1994 and 1995. However, soil at 35 cm depth heated more slowly in the spring and cooled more slowly in the fall than soil at 6 cm. South-facing plots had higher average soil temperatures during the growing season (especially ALPM and PM) than the north, reflecting corresponding differences in air temperature and insolation (Table 2).

Soil temperature showed consistent patterns among plots when weekly plot means were compared using least significant difference tests. Plots ALPM and PM were significantly warmer than all other plots in 40 of the 44 weeks for which comparisons could be made. In 35 weeks, at least two other groups were distinguished. Plots AA and ALS usually fell in the intermediate group (counts in intermediate group = 63%, AA; 80%, ALS), and plots ALN and ALTM usually had the coldest soils (counts in lowest group = 54% ALN; 80%, ALTM).

Precipitation

Total precipitation during the growing season (July-September, weeks 27-39) was 81% of average at Elwha in 1993, 60% of average during 1994, and 136% of average in 1995 (National Oceanic and Atmospheric Administration, 1993-1995a, based on 30 yr average). The patterns of precipitation also differed among years 1993, 1994, and 1995, and from the pattern averaged over 20 years by week (Figure 4). The average pattern at Elwha shows that the driest summer period normally occurs at the end of July and early August (weeks 30-33). The precipitation record from ALN (Figure 4) shows drought later than normal in 1993 (weeks 35-39), three dry periods in 1994 (weeks 28-31, 33-35, 38-40) and two short dry periods in 1995 (weeks 26-27, 37-38).

Amount of precipitation at plots did not vary significantly ($p < 0.05$) with storm direction, possibly due to the small number of observations and large variability among storms for size. However, distribution of precipitation among plots

TABLE 2. Environmental data for the 1993, 1994, and 1995 growing seasons.

	Plot					
	ALN	ALTM	AA	ALS	ALPM	PM
Air Temperature[1]						
Max. Temp. - Avg. (°C) and Heatsum (°C-days)						
1993(wks 26-40)	17.7	18.3	15.7	18.6	19.7	18.8
1994(wks 26-40)	17.6	19.3	16.3	18.5	20.3	19.3
1995(wks 26-40)	17.3	16.8	16.3	18.4	19.9	20.4
1994(melt-fall)[2]	1450	1687	1586	1656	2002	2191
Min. Temp. - Avg. (°C) and Heatsum (°C-days)						
1993(wks 26-40)	2.5	2.7	3.2	2.9	3.4	3.9
1994(wks 26-40)	3.6	4.1	4.6	4.6	4.9	5.4
1995(wks 26-40)	3.6	2.9	3.9	4.4	4.9	4.8
1994(melt-fall)[2]	846	767	996	938	1022	1207
Soil Temperature Avg. (°C) and Heatsum (°C-days)						
1993(wks 30-40)	7.1	7.6	7.3	6.3	9.5	9.7
1994(wks 30-40)	7.3	5.6	7.4	7.9	9.2	9.8
1995(wks 30-40)	6.7	6.4	6.8	7.0	8.0	8.8
1994(wks 26-40)	7.3	6.1	7.4	7.8	9.4	9.6
1995(wks 26-40)	6.9	6.2	6.9	7.2	8.3	9.1
1994(melt-fall)[2]	817	786	935	902	1179	1369
Precipitation (mm)						
1993(wks 26-40)	169	91	84	54	61	100
1994(wks 26-40)	148	99	58	54	65	49
1995(wks 26-40)	385	225	134	117	172	104
1993(wks 26-31)	109	50	58	32	41	74
1994(wks 26-31)	23	15	10	8	8	6
1995(wks 26-31)	83	40	30	29	29	20
Soil Moisture						
Water Potential Sum (MPa-days)						
1993(wks 26-40)	-11.13	-8.68	-4.20	-12.11	-16.59	-18.34
1994(wks 26-40)	-14.64	-14.63	-7.24	-21.18	-27.76	-43.96
1995(wks 25-39)	-11.41	-4.97	-5.95	-14.28	-26.60	-38.29
Snow						
Snowmelt (1994)(wk)	25	25	20	22	20	16
Snowmelt (1995)(wk)	26	27	21	22	20	<19
Max. Depth[3] (cm)	220	250	190	145	150	160
Frost-free Period						
1993						
Last Freeze (wk)	27	27	<26	26	26	26
First Freeze (wk)	41	42	42	42	43	43
Freeze during Season	31,34, 38	34.38	38.39	34,38	38	38
1994						
Last Freeze (wk)	27	25	25	25	24	24
First Freeze (wk)	40	40	41	40	41	41
1995						
Last Freeze (wk)	25	24	24	24	24	24
First Freeze (wk)	40	40	40	40	40	41
Freeze during season	—	35	—	33	—	—
Potential Incident Solar Radiation ($KJ/m^2/10^6$)						
Winter Solstice	1.2	1.2	0	1.3	1.0	1.3
Summer Solstice	40.0	40.5	40.4	39.3	42.9	41.8
Equinoxes	17.4	19.0	19.0	16.7	26.2	28.4

[1] Weeks 26-40 for both years are based on weekly readings of max-min thermometers; 1994 snowmelt to snowfall values are based on on daily records from dataloggers

[2] Snowmelt to snowfall

[3] Average of maximum snow depth based on lichen height (Long 1982)

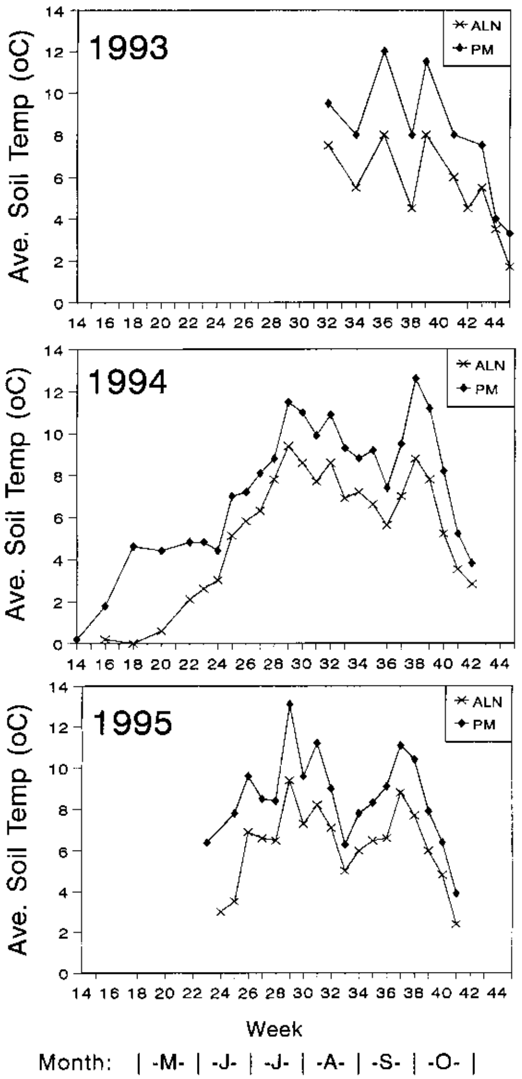

Figure 3. Weekly soil temperature averaged for depths of 6 and 35 cm during the growing seasons of 1993, 1994, and 1995 for the coldest (ALN) and warmest (PM) plots. Early season temperatures are not available for 1993.

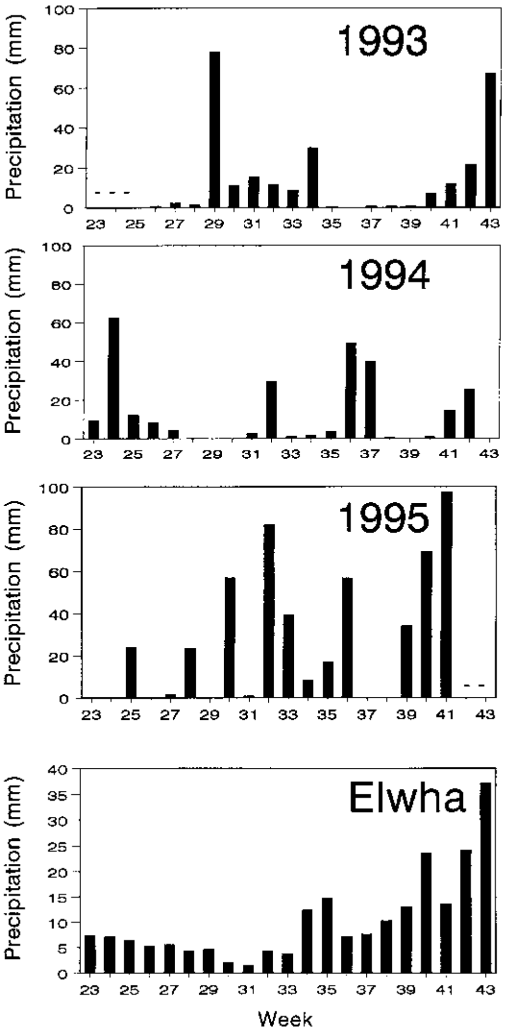

Figure 4. Weekly precipitation for plot ALN during growing seasons of 1993, 1994 and 1995, compared with 20-year average at Elwha Ranger Station.

showed three distinct patterns (Table 3): 1) all frontal storms and the one convective southwesterly storm were similar, 2) convective northwesterly, and 3) the one convective westerly storm each showed distinct patterns. Ignoring the pattern for which there was only one example, the two most frequent patterns were:

frontal W and SW: ALN > ALTM > ALPM > ALS > AA > PM
convective NW: ALN > AA > ALTM,PM > ALPM > ALS

Frontal westerly and southwesterly storms distributed precipitation on the at the top of the north and the middle of the south side of the ridge. Convective northwesterly storms distributed relatively more precipitation lower on slopes compared with the first pattern.

Soil Water Potential

Differences in soil texture and soil carbon resulted in plot specific differences in the relationship between soil moisture and soil water potential. Soil moisture at field capacity and permanent wilting increased down-slope on the north-facing

TABLE 3. Spearman rank correlations among ranks of precipitation falling at six plots due to storms categorized by direction (NW = northwesterly, W = westerly, SW = south to southwesterly) and type.

		Frontal			Convective		
		NW	W	SW	NW	W	SW
		(n=1)	(n=4)	(n=3)	(n=3)	(n=1)	(n=1)
Frontal	NW	--	0.987*	0.970*	0.329	0.647	0.986*
	W		--	0.969*	0.350	0.718	0.993*
	SW			--	0.538	0.668	0.972*
Convective	NW				--	0.462	0.343
	W					--	0.638
	SW						--

*$p < 0.02$

transect (ALN<ALTM<AA) but decreased downslope on the south-facing transect (ALS>ALPM>PM) (Table 1). These gradients corresponded to gradients of soil organic matter (estimated by soil carbon; Table 1). Plots ALN and ALS had similar values for soil moisture at field capacity and permanent wilting.

Soil water potential (Figure 5) was most variable among plots late in growing seasons when soils were relatively dry. Water potential reached -0.2 MPa at ALPM and PM by week 36 in 1993, by week 28 in 1994, and by week 23 at PM and week 29 at PM and ALPM in 1995 (Figure 5). Plot AA rarely measured below -0.1 MPa while ALTM measured as low as -3.0 MPa and ALN as low as -3.7 MPa during the study. On the south transect, ALS, ALPM, and PM had minimums of -4.1, -5.2, and -8.0 MPa, respectively. Decreases in soil water potential on the south transect sometimes lagged behind the north following storms (week 43, 1994; week 32, 1994; week 31, 1995).

Soil water potential was only partially related to annual precipitation. Most negative water potentials sums (Table 2) occurred during 1994, which had the lowest precipitation. However, most plots had more negative water potential sums in 1995 than 1993 despite higher precipitation in 1995.

Results from step-wise regression (Table 4) indicate that field capacity and minimum air temperature are the best predictors of soil moisture among plots. Annual variability of soil moisture at individual plots was predicted by early season precipitation (ALN, AA, ALS, PM), or minimum air temperature (ALPM). No variable was significant ($p < 0.15$) at ALTM.

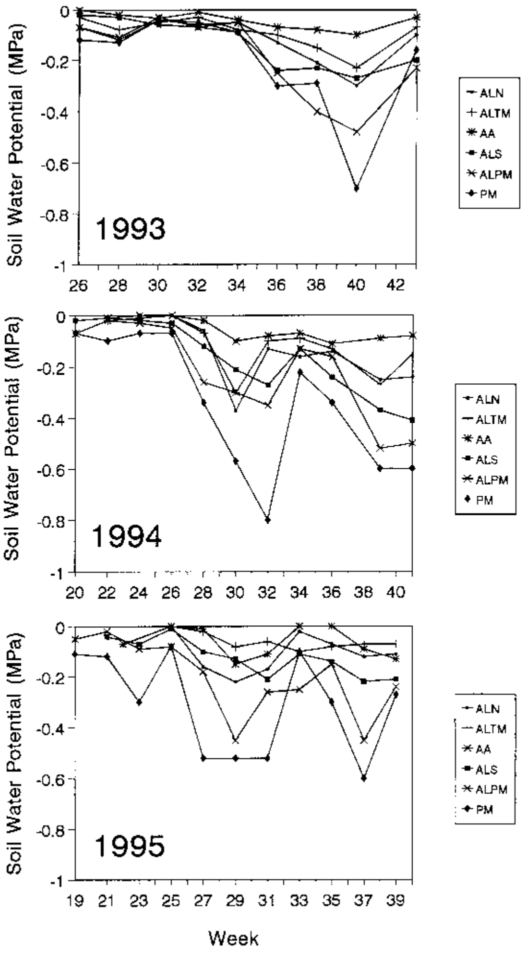

Figure 5. Soil water potential estimated from moisture release curves at 6 plots during the growing seasons of 1993, 1994 and 1995.

TABLE 4. Predictor variables for soil moisture sum. Early precipitation describes weeks 26- 31.

Site	n	Variable	Partial r^2	p
All Sites	18	Field Capacity	0.7418	0.0001
		Min. Air Temp.	0.1114	0.0042
		Soil Carbon	0.0228	0.1309
ALN	3	Early Precip.	0.9492	0.1447
ALTM	3	nothing with $p < 0.15$		
AA	3	Early Precip.	0.9999	0.0056
ALS	3	Early Precip.	0.9866	0.0740
ALPM	3	Min. Air Temp.	0.9911	0.0602
PM	3	Early Precip.	0.9997	0.0102

Potential Incident Solar Radiation

Potential incident solar radiation was highest at ALPM and PM throughout the year (Table 2). Values among plots were similar at summer solstice. Plot ALS was more similar to north transect plots than southern plots during the winter solstice and the equinoxes. Plot AA received the highest PISR among north transect plots at the equinoxes and no PISR at the winter solstice due to the low sun angle and its shaded topographic location.

Stand Ages

Dominant trees on the south transect were all of similar age. Douglas-fir at both ALPM (n = 4) and PM (n = 4) averaged 105 yr (ALPM range = 98-114; PM range = 102-110). Subalpine fir at ALPM (n = 4) averaged 103 (range = 95-110). Dominant trees on the north transect showed two age classes. Subalpine fir at ALTM was older than 150 yr (n = 3) or averaged 126 yr (n = 3, range = 124-129 yr). Mountain hemlock at ALTM were older than 150 yr (n = 2) or averaged 107 yr (n = 4, range = 94-113 yr). Most Pacific silver fir at AA were older than 150 yr (n = 5, range 154-222 yr) but one established more recently (age = 128). Although cores were not collected at ALS and ALN, neither site appeared to have the larger, older cohort, and dominant trees seemed to be similar in size to the younger cohort on ALPM and ALTM.

Discussion

Suitability of Trees as Indicators of Environment

The environmental conditions described in this study are thought to be biologically significant because they describe sites differing in dominant tree species. However, the validity of using tree species distributions to define significant contemporary gradients is questionable because tree distributions are largely determined by conditions at the time of establishment (Lassoie et al., 1985). In this study, at least one cohort of dominant trees in each stand except AA was relatively young (~100 years). The relatively uniform age of the young cohorts, the presence of charcoal in all soils, and burned branch stubs and burned snags at plot AA, suggest that the entire area experienced the same fire, though less intensely at AA. Fires were widespread in the Olympic between ca. 1870 and 1900 (Henderson et al., 1989), including the Morse Creek drainage, just east of Hurricane Ridge (Wetzel, 1995). Typically there is a 30-50 yr lag between between subalpine fires and tree reestablishment (Agee and Smith, 1984; Little and Peterson, 1994), suggesting that the study stands most likely burned in the fire of 1870. Conditions at the time of establishment were similar to the present conditions based on Washington Division 4 summary data meant to represent the central Olympic Peninsula (average annual temperature: 1895-1905 = 9.9 °C, 1985-1995 = 10.4 °C; average annual precipitation 1895-1905 = 160 cm, 1985-1995 = 154 cm). Therefore, I would expect the same species to become established in these plots if a new disturbance occurred today.

Moisture and temperature are thought to largely determine distributions of conifer species in the Pacific Northwest (Franklin and Dyrness, 1988), especially at the seed establishment and seedling stage (Lassoie et al., 1985). Douglas-fir occurred on the driest plots with highest soil and air temperatures, Pacific silver fir and mountain hemlock occurred on wet sites with intermediate temperatures, and subalpine fir occurred on the coldest sites with intermediate moisture. This distribution generally matches the relative ranks given to them for moisture optimum and tolerance to excess moisture, drought, frost and cold soils based on regional distributions (Minore 1979). This further supports the assumption that these plots describe environmental differences that distinguish among these species.

Factors Creating and Maintaining Moisture Gradients

Soil moisture, which is crucial for determining tree distribution in the Pacific Northwest, is determined by the interception and redistribution of precipitation, soil moisture holding capacity, and evapotranspiration (Band et al. 1993). All of these factors are functions of temperature and precipitation, but each at different time scales and in combination with other factors. Hence it is difficult to specify the biological consequences of changes in temperature and precipitation due to GCC predicted by general circulation models.

Regional interception of precipitation is known to depend on topographic location and storm direction (Speer, 1986). This study shows that storm type and direction are also important in determining the distribution of precipitation at the local scale. Two major patterns of distribution occurred during the study. Frontal storms from the southwest, west, and northwest all produced a nearly typical orographic pattern expected of southwesterly storms (Barry, 1992; Sinclair, 1994): heaviest precipitation at the top of the leeward slope (ALN and ALTM, in this case) and large amounts on the windward slope (ALPM). This pattern would have been more typical if ALS had received more precipitation than ALPM. The second most common pattern resulted from northwesterly storms accompanied by lighter winds, and occurring during synoptic conditions conducive to convective activity (Philips and Donaldson, 1972; Pickford et al., 1980). Convective storms are caused by mountain-valley temperature gradients, and may be the main source of summer precipitation in the Olympics (Barros and Lettenmaier, 1993). Northwesterly convective storms distributed more precipitation on northerly aspects and lower on slopes than frontal storms. The dependence of rainfall pattern on storm type and direction may partially explain the weak statistical relationships seen between local topography and precipitation alone (Taylor, 1996).

Early in the growing season, and especially during and immediately after snowmelt, soil moisture can be redistributed by subsurface flow or runoff in steep topography (Band et al. 1993, Ambroise, 1995). Subsurface flow may contribute, along with other factors, to the highest level of soil moisture at AA despite receiving the least precipitation of plots on the north transect.

Soil properties are fundamentally determined by parent material, but climate plays a significant role in determining the rate and results of soil formation (Brady and Weil, 1996). In fact, differences in climate alone can explain the finer texture, higher carbon, and consequently higher water holding capacity in plot AA compared with plots ALPM and PM. Greater precipitation on the north aspects affects soil texture by causing greater transport of fine material and minerals through the soil profile by illuviation, and sediments across the landscape due to mass transport, especially by snow, compared with drier southerly sites. Higher soil carbon at plot AA compared with ALPM and PM can be explained by higher litter input due to higher site productivity (see tree areas, Table 1), limited decomposition due to cold soils, and lower quality litter due to species composition of vegetation. Specifically, litter from Pacific silver fir and mountain hemlock at plot AA decomposes more slowly than Douglas-fir litter at plots ALPM and PM (Topik, 1982). Periodic removal of litter by fire may also be less complete at plot AA if fire intensity is reduced by wetter conditions. This is supported by the observation that the 1870 fire seems to have resulted in stand replacement on the southerly plots but some trees survived on the northerly plots.

Differences in evapotranspiration among plots were not directly addressed in this study. However, the 4 °C difference between the average maximum temperature of the warmest plot (ALPM or PM) and the coldest plot (AA) each year suggests an important difference in evaporative demand. Differences in evapotranspiration, however, may be less than suggested by temperature differences alone if drought stress at dry sites results in stomatal closure.

Climate Change

General circulation models predict 2 to 4 °C increase in annual temperature in the Olympics with a doubling of CO_2 (Gates et al. 1992). The change may be the same in winter and summer, or may be higher in summer. Models also predict a 0 to 1 mm per day decrease in June-July-August precipitation (Gates et al. 1992). Predicting how changes of these magnitudes might impact the distribution of tree species depends on understanding the relative importance of factors affecting current distributions.

Differences in soil moisture among plots, represented by mean values (Figure 6), primarily reflect differences in soil properties, a relatively static feature of plots and not immediately responsive to GCC. Differences among years at each plot, represented by plot ranges (Figure 6), was most often driven by early season precipitation, a variable which will be affected by GCC. Global climate change cannot be expected to alter the distribution of tree speices unless annual variability, which is driven by precipitation, results in overlap of the soil moisture conditions among plots. During 1993-1995, an average 1 mm/day variation in early season precipitation resulted in soil moisture sums at plot PM nearly including the range of values at plot ALPM, values at plot ALS nearly included the range of plot ALN, and plot ALTM included the range of plot ALN and most of plot AA (Figure 6). This range of precipitation is similar to the change predicted due to GCC and indicates that changes in soil moisture could shift the distribution of species within aspect, but not from north to south.

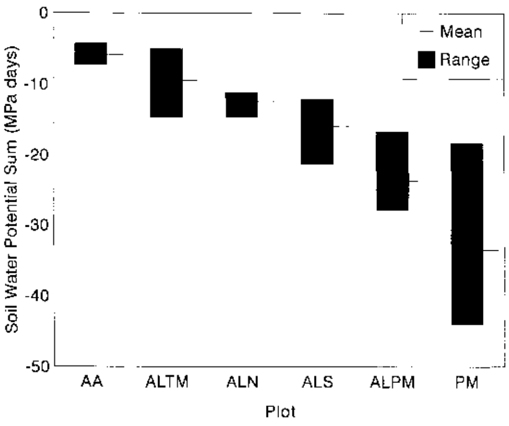

Figure 6. Soil water potential sum (Mpa-days) for 6 plots showing mean and range for three growing seasons.

Air temperature was also important in determining soil moisture differences among plots and among years at plot ALPM, as well as affecting plant physiological response. Predicted changes in temperature of 2-4 °C compare with an average maximum air temperature difference of 4 °C, and an average minimum air temperature difference of 2 °C between the coldest and warmest plots across years. Therefore, these differences can be expected to influence the distribution of tree species.

This study identifies several areas where weather models could increase our ability to predict biotic responses to GCC. First, although weather models often ignore weather patterns during the summer (Speer, 1986; Barros and Lettenmaier, 1993), conditions during the growing season have important consequences for soil moisture. Timing as well as amount of precipitation are important, as severity of summer drought appeared to be reduced by early growing season precipitation. In this study, a year with above-average precipitation (136%, 1995) distributed late in the season had similar soil moisture sums as a year with lower than average precipitation (60%, 1994) for plots ALPM and PM. An early season dry spell (1994 and 1995) may create hydrophobic soils which cannot effectively absorb rainfall later in the season (DeByle 1973), especially at the dry sites. Finally, convective and frontal storms result from different synoptic weather patterns (Lilly, 1983), and their relative frequency could alter distribution of precipitation among sites.

Changes in climate will not likely result in immediate changes in forest composition. The response of adult trees to climate is buffered by the adaptive tolerance to climate change needed by organisms surviving several centuries. In addition, climate change will not immediately impact soil properties, which have an important role in determining growing conditions. Changes may not be observed until these stands experience castrophic events, such as fire, or mortality due to old-age or disease. Instead, changes may be noticed sooner in the establishment of seedlings in subalpine meadows (Woodward et al., 1995).

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