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Gradient Analysis of Vegetation on the North Wall of the Columbia River Gorge, Washington

Abstract

The Columbia River Gorge represents an ecocline of shifting environmental factors, species populations, and vegetation associations. Combinations of wind, temperature, and precipitation create different environmental regimes from the west to the east. The north wall of the Gorge supported four physiognomic associations: western conifer forest, central mixed forest, central broadleaf forest, and eastern steppe. Each association comprised species distributed individually along the ecocline. Douglas-fir, western redcedar, bigleaf maple, dull Oregongrape, sword fern, bracken, vine maple, and red bilberry were centered in the western conifer forest. Garry oak, ponderosa pine, poison oak, and snowberry were centered in the central mixed forest. Cheatgrass, northern buckwheat, Wyeth's lupine, western serviceberry, mockorange, and Sandberg's bluegrass were centered in the eastern steppe. Although the center of distribution for each species was in one of the associations, few were confined to a specific association. The Columbia River Gorge is analogous to a mountain turned on its side, with the cool, moist summit to the west and the warm, dry base to the east. Plant species have migrated both eastward and westward along this ecocline during the lifetime of the Gorge, and each association has combinations of species derived from surrounding regions in Washington and Oregon.

Introduction

The Cascade Mountains are a major geographical barrier between distinctly different vegetation formations in Washington and Oregon. The cool, moist forests that lie west of the Cascades in both states, influenced by the prevailing maritime climate, contrast with the warmer, drier shrub-grass steppe, influenced by the prevailing continental climate, to the east of the mountains. The Columbia River cuts through the Cascade Mountains between Washington and Oregon (Figure 1) forming a gorge that has served as a migratory corridor between these two vegetation formations for millennia (Lawrence 1939, Detling 1958, Franklin and Dyrness 1988). The modern vegetation in the Columbia River Gorge (CRG) is a product of species from surrounding regions overlapping according to the varied habitats available in the Gorge (Detling 1958). Species distribution throughout the length of the CRG is regulated by climate (Lawrence 1939). The western CRG is cooler and wetter than the eastern CRG (Lawrence 1939, Lynott 1966, National Oceanic and Atmospheric Administration 2000). Wind is an important environmental factor in the CRG. Mean annual wind velocity is 12.8 km/hr (National Oceanic and Atmospheric Administration 2000). Gusts exceeding 190 km/hr were measured at Crown Point, Oregon, 8 km southeast of Washougal (Lynott 1966). Prevailing winds are from the west, but during winter, with a high pressure system in place over the Columbia Basin, exceptionally strong winds can blow from the east (Lawrence 1939, Lynott 1966, Sinton et al. 2000). For example, two winter storms in 1973 and 1983 created extreme northeast winds that caused windthrow in 8% of the forest in the Bull Run watershed, near the western end of the CRG in Oregon (Sinton et al. 2000). Because the walls on the north and south sides of the CRG face opposite directions, local climate differs markedly between Washington and Oregon locations. Compared to the south wall of the CRG, the growing season environment of the north wall is characterized by greater solar radiation, higher air and soil temperatures, and greater evapotranspiration. These factors typically combine to cause low vegetation cover (Cleary and Waring 1969, Barbour et al. 1999). Wind desiccation, combined with greater solar radiation, makes the north wall of the CRG considerably warmer and drier than the nearby upland forests of the Willamette Valley and the montane forests of the Cascade Mountains. On the north wall, local wind, temperature, and moisture differ according to slope aspect associated with individual habitats. Local differences

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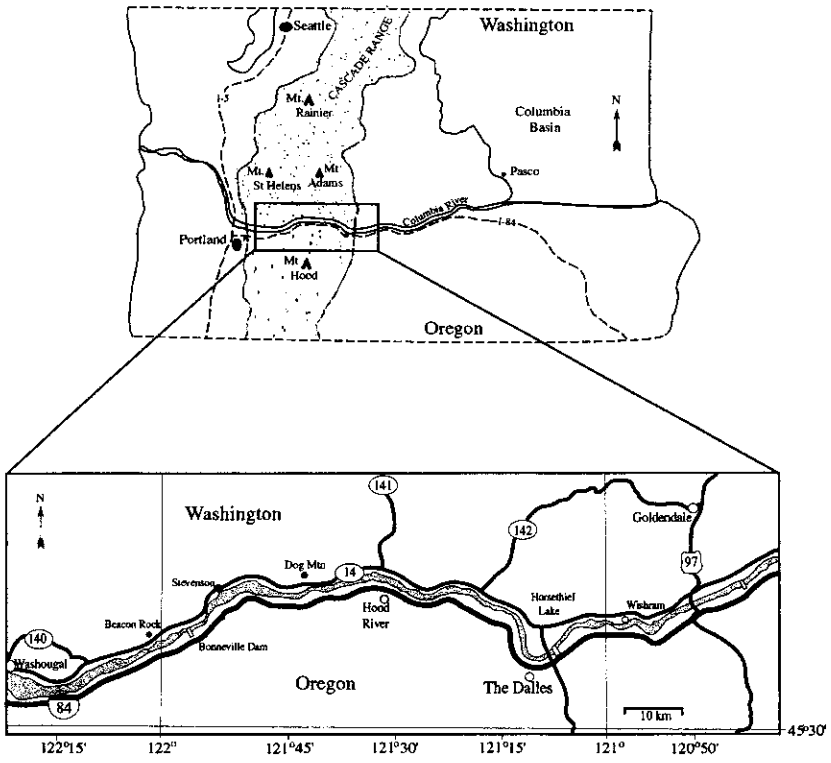

Figure 1. The study area, located on the Washington side of the Columbia River, extended from the western end of the Gorge at Washougal to the eastern end at Wishram.

among slope aspects and ravines clearly affect values of solar radiation, wind, temperature, and moisture (Barbour et al. 1999). During the growing season, southwest and south slopes are more exposed to higher wind, solar radiation, and temperature, making them drier than southeast slopes in the same location. Ravines are more protected from wind, are moister, and have lower ambient temperatures. Considering the entire ecocline in the CRG during the growing season, the eastern CRG is drier and hotter than the western CRG. On a microsite scale, southwest slopes are hotter and drier than southeast slopes. In sum, the CRG is an ecocline (Whittaker 1967) through which a mosaic of environmental factors and plant species vary in parallel.

The Columbia River is antecedent to both the Cascade and Coast Mountains of Washington and Oregon (Alt and Hyndman 1984). Three volcanic peaks are within 35 km of the CRG (Figure 1). Repeated basaltic floods during lower Miocene created the platform from which the Columbia Gorge was later carved (Baldwin 1966) from late Oligocene to middle Miocene as the high peaks of the Cascade and Coast Ranges rose and the river maintained its original flow (Alt and Hyndman 1984). The present soils in the CRG are formed in loess and fluvial deposits from the last advance of Pleistocene ice (Allen 1979). The CRG currently is a major thoroughfare through the Cascade Mountains, with railroads and state highways on both sides, and Interstate Highway 84 on the Oregon side (Figure 1). Within the CRG are state parks, the southern edge of the Gifford Pinchot National Forest (Washington), and some American Indian trust lands.

Two previous studies examined the distribution of plant species in the CRG. Lawrence (1939) provided a purely descriptive overview of the vegetation. He observed a wind gradient in the CRG, identified a general east-west environmental gradient, and noted that the vegetation of the north

TABLE 1. Mean maximum and minimum temperatures (°C) at four locations in the Columbia River Gorge, from west to east. Data are summarized from National Oceanic and Atmospheric Administration (2000).

	Mar-May		Jun-Aug		Sep-Nov		Dec-Feb	
	Max	Min	Max	Min	Max	Min	Max	Min
Washougal	19.2	2.0	25.7	9.1	22.6	2.9	8.3	-0.1
Bonneville Dam	19.1	3.2	25.9	11.3	23.2	4.4	8.4	0.3
Hood River	20.3	1.3	27.1	9.8	23.8	1.1	7.8	-2.5
The Dalles	22.9	2.0	30.7	12.4	26.7	1.8	8.9	-2.2

wall differed qualitatively from the corresponding south wall. Lawrence (1939) emphasized the severe winds and their impact on species distribution and plant morphology. Hydroelectric dams have since flooded many of the habitats Lawrence (1939) described. Later, Detling (1958) identified five distinct elements in the CRG flora, based on centers of distribution in surrounding regions. Of the 206 species described by Detling (1958), 34% were distributed widely in northwest North America, and another 26% were prominent in the Puget Trough area west of the Cascade Mountains. The Columbia Basin contributed 13% of the flora, and high elevations in the Cascades another 15%. Perhaps the most interesting element came from the Rogue River area in southwest Oregon, accounting for 8% of the flora. Seven species (3%) were endemic to the CRG. Detling (1958) did not analyze vegetation patterns and environmental relationships. The patterns created by vegetation associations and individual species on the north wall have not been studied.

Whittaker and Niering (1965) used gradient analysis to describe vegetation pattern in the Santa Catalina Mountains, Arizona. They showed that plant species were distributed individually, and that the vegetation pattern depended on environmental gradients created by elevation and slope aspect in the mountains. Gradient analysis has been used successfully to analyze and describe vegetation patterns of large and small areas (Whittaker 1960, 1961; Disraeli and Fonda 1979; Price et al. 1995; Lefstad and Fonda 1995; Sagers and Lyon 1997; Ohmann and Spies 1998).

We analyzed vegetation patterns on the north wall of the CRG by gradient analysis to describe the relationship between environmental factors and species distribution. Our objectives were to clarify how species are distributed in the CRG in relation to the regional climate through the CRG, and to microhabitats created by slope and ravine topography.

Methods

The study area was on the Washington (north) side of the 97 km Columbia River Gorge (Figure 1). The western end of the Gorge is located at Washougal, Washington (122° 15' longitude), and the eastern end is near Wishram, Washington (120° 50' longitude). Two cities, Hood River and The Dalles, Oregon, are located in the CRG, as are two hydroelectric dams at Bonneville and The Dalles (Figure 1). We limited our study area to sites ≤200 m above the Columbia River, because we wanted to ensure that the vegetation with which we worked was influenced only by the Gorge, not by the adjacent Cascade Mountains.

A general trend of increasing wind velocity (Lynott 1966), increasing summer temperatures (Table 1), decreasing winter temperatures (Table 1), and decreasing growing season precipitation (Table 2) defines the west-to-east environmental gradient in the CRG. Maximum temperatures are most consistent throughout the CRG during the December-May period, but they begin to diverge in June (Table 1). Differences of 4-5° between western and eastern stations last into September. Although minimum temperature differences exist among the stations, the range is less than among maximum temperatures. The lowest minima are in the east during September-February, but they are too variable to demonstrate a pattern during March-August (Table 1). Mean annual temperatures

TABLE 2. Mean average precipitation (cm) at four locations in the Columbia River Gorge, from west to east. Data are summarized from National Oceanic and Atmospheric Administration (2000).

Station	March–August	September–February	Annual total
Washougal	72.0	141.1	213.1
Bonneville Dam	57.1	138.8	195.9
Hood River	18.4	58.4	76.8
The Dalles	7.9	27.3	35.2

do not vary greatly between the western (10.5°C) and eastern ends (9.3°C) (National Oceanic and Atmospheric Administration 2000). The total amount of precipitation falling from March to August is an important component of the environmental gradient, because total growing season values are dramatically different between the ends of the CRG. March-August precipitation averages ~60-70 cm in the west but ~8-18 cm in the east (Table 2). Annual totals are similar between Washougal and Bonneville Dam, but The Dalles averages about half the total precipitation recorded at Hood River.

Data were gathered on species in the tree canopy, tall understory, and low understory layers using thirty-seven 20 x 50 m macroplots, at 18 locations at ~6' longitude intervals between Washougal and Wishram (Figure 1). Most locations were on public lands accessible along Washington State Route 14 (Figure 1). Obviously disturbed or managed locations, such as logged forests, abandoned fields, and grazed pastures, were avoided, although undoubtedly the entire study area no longer is pristine. Macroplots were situated on southwest (210-191°), south (190-170°), and southeast (169-150°) slope aspects, and in ravines at each sample location, when the location had such sites available. Macroplots on slopes were oriented with the central 50-m axis bearing 180°, and those in ravines were oriented with the long axis parallel to ravine bottoms. We located the macroplots using a random number table. For example, a macroplot on a south slope was located by first randomly choosing how far up the slope to proceed. Once that point was reached, a baseline was stretched parallel to the slope contour, then a random number was selected to represent the starting corner for the macroplot.

For trees >1 cm diameter at breast height, density was calculated as trees/ha for the entire macroplot. For tall and low understory species, cover was estimated to the nearest 1% for 1-10% cover, and nearest 5% for >10% cover, on twenty-five 20 x 50 cm microplots placed every 5 m along five 50-m lines in each macroplot. Cover and frequency were calculated from these data for each macroplot.

Prominence values were calculated for each species as PV=mean % cover * frequency$^{1/2}$ (Fonda and Bernardi 1976; Risvold and Fonda 2001). We entered density/ha for trees and PV for understory species into a detrended correspondence analysis (DCA) program in PC-ORD (McCune and Mefford 1995) to elucidate relationships among the 37 macroplots.

Botanical nomenclature follows Hitchcock and Cronquist (1973). Voucher specimens are deposited in the Biology Department herbarium (WWB) at Western Washington University.

Results

DCA Ordination

The two-dimensional DCA ordination we constructed used all 37 macroplots. The eight ravine macroplots were embedded in the overall ordination matrix, but for clarity in understanding relationships through the CRG and among the three slope aspects, the ravine plots were omitted from Figure 2. The ordination confirmed that the distributional pattern of the macroplots was continuous through the CRG (Figure 2). The X-axis reflects floristic changes from west to east, whereas the Y-axis reflects relatively moister conditions low on the axis to relatively drier conditions higher on the axis. The ordination also shows the relative positioning of macroplots according to slope aspect. Most of the forested macroplots on southeast slopes (#1, 6, 10, 13, 20, 23) were clustered to the left of the ordination, at values <200 (Figure 2). In contrast, many of the forested macroplots on southwest slopes (#15, 21, 28) were arranged toward the center (values of 285-374). Plots 18, 19, and 20 represent a good example of this ordination alignment. All three were located on Dog Mountain (Figure 1). Plot 18, on the southwest slope, aligned to the right, in contrast to #20, a southeast slope that aligned to the left. Plot 19, on the south slope, aligned between #18 and #20. Plot 18 was a stand of Garry oak (*Quercus garryana*) with much cheatgrass (*Bromus tectorum*) and poison oak (*Rhus diversiloba*) in the understory, whereas #20 was a stand of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) with an understory of snowberry (*Symphoricarpos albus*), dull Oregon-grape (*Berberis nervosa*), and sword fern (*Polystichum munitum*). Plot 19 was a mixture of ponderosa pine, Douglas-fir, and Garry oak, with a complex understory of poison oak, dull Oregon-grape, cheatgrass, and snowberry.

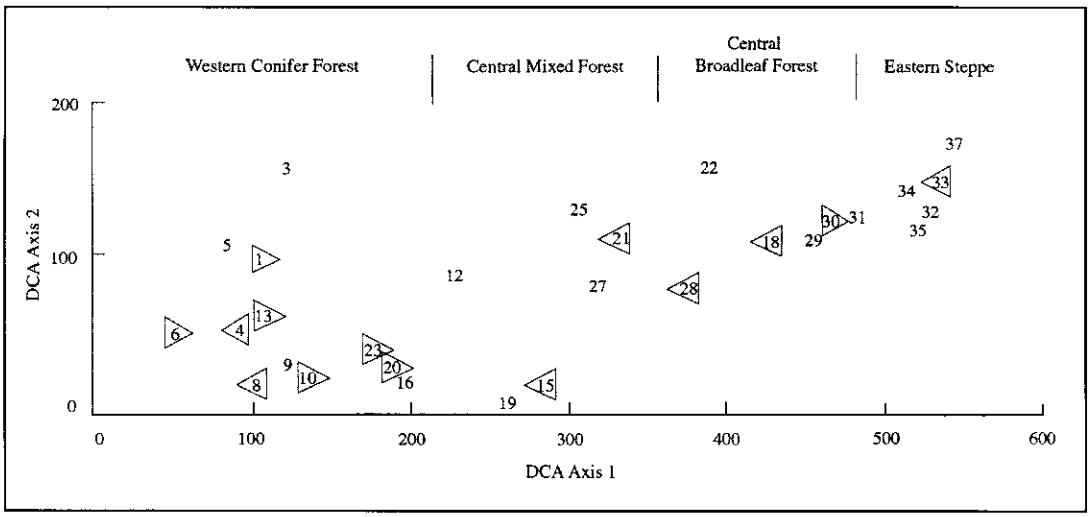

Figure 2. Two-dimensional DCA ordination of the 37 macroplots. Plot numbers inside ⩓ were on southwest slopes, those inside π were on southeast slopes, and those with no symbol were on south slopes. Plots in ravines were omitted from this figure.

Mosaic Diagram

After constructing the ordination, we inspected the data from each macroplot individually to identify patterns associated with tree density and mean cover of understory species. We combined these data and DCA patterns with forest physiognomy (either conifer dominance, mixed dominance, broadleaf dominance, or treeless) to create a mosaic diagram (Whittaker and Niering 1965) that identifies patterns associated with four physiognomic associations and the important plant species on the north wall (Figure 3). Plant species were distributed individually according to local and regional differences within the CRG, creating mixtures of dominant and subordinate species (Figure 3; Tables 3, 4). Within each association, ravines supported species combinations whose architecture differed from the surrounding slopes. In general, the total number of tree species and conifers declined eastward, whereas broadleaf trees increased eastward. In the understory, general indicators of moisture changed from west to east. For example, ferns were more prominent in the west, whereas graminoids were more prominent in the east. Of all the understory species, only cheatgrass averaged ≥50% cover on at least some locations in the study area. In each association, more than half the species present averaged <5% cover.

Western Conifer Forest Association

The western conifer forests extended from the western end of the CRG at 122° 15' to 121° 40' longitude (Figure 3). Coniferous trees in these forests were twice as dense as broadleaf trees. Macroplots in this association were dominated by Douglas-fir, which was uniformly dominant with high density and basal area over all slope aspects (Table 3), with 100% frequency. Eight other tree species were present in this association, of which bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) were the most prominent. Together these two subordinate species had about half the density of Douglas-fir, but much less basal area. Douglas-fir, bigleaf maple, and red alder were the only tree species on southwest slopes in the western conifer forests, whereas all tree species except Oregon ash (*Fraxinus latifolia*) and soft-leaved willow (*Salix sessilifolia*) grew on southeast slopes (Table 3). Western hemlock (*Tsuga heterophylla*) and grand fir (*Abies grandis*) were largely unimportant.

The understory of the western conifer forests was lush. No species accounted for >40% cover, frequency commonly was 30-60% for dominant species, and individual values for cover varied by slope aspect, yet the many species present in the forest contributed to the uniform structure of the understory. Sword fern, vine maple (*Acer*

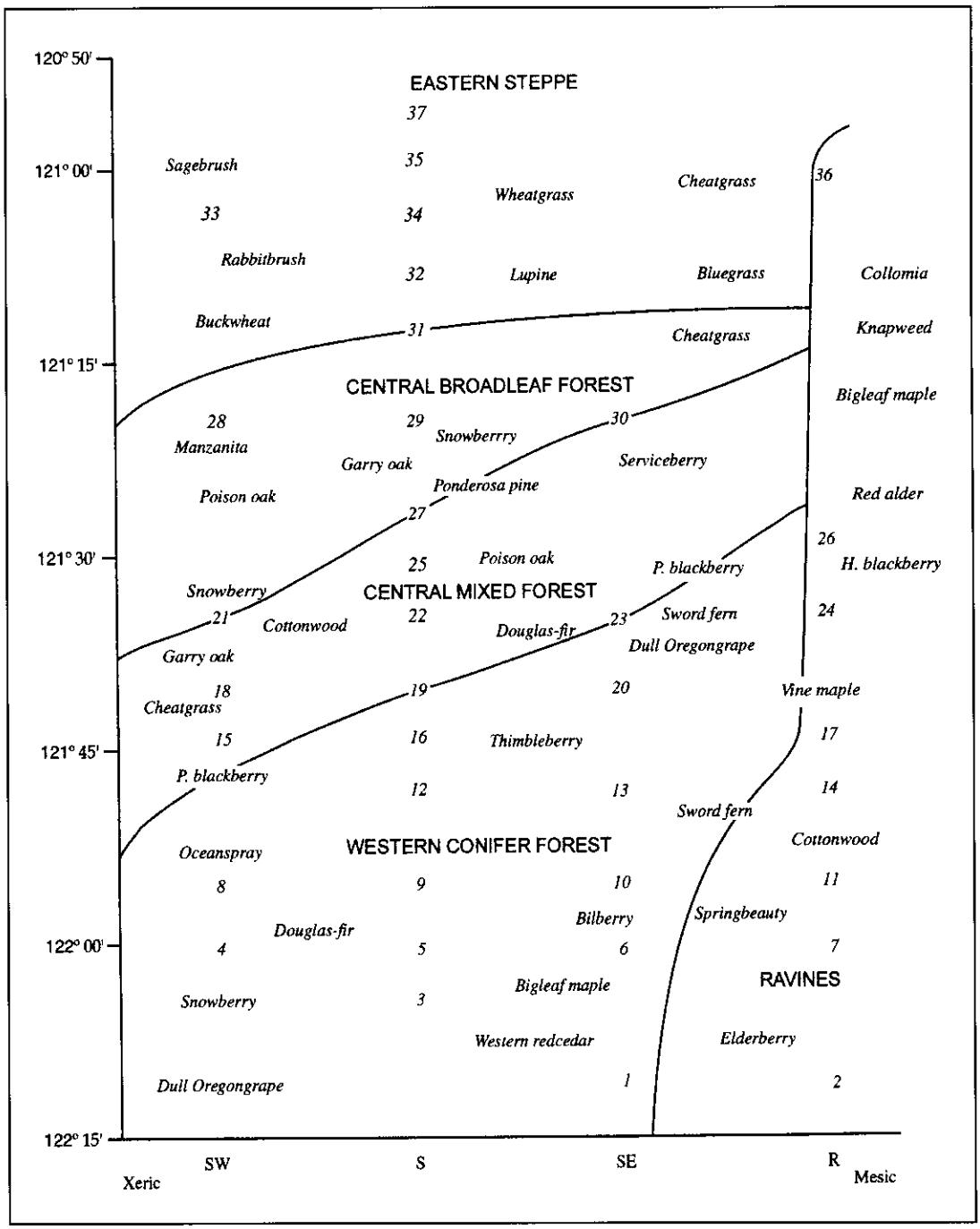

Figure 3. Mosaic diagram of environment, species, and associations on the north wall of the CRG. Major species are indicated by their centers of distribution and ranges on the north wall. Numbers 1-37 indicate the locations of the 37 macroplots.

TABLE 3. Mean density (D: trees/ha) and basal area (BA: m²/ha) for tree species in the four associations, by topographic position. Calculations to derive association means did not use ravine data.

	Association mean		Southwest slope		South slope		Southeast slope		Ravine	
	D	BA	D	BA	D	BA	D	BA	D	BA
Western conifer forest										
Douglas-fir	361	43.4	415	36.1	338	44.7	362	45.0	180	21.1
Bigleaf maple	112	3.4	115	4.1	118	3.5	104	2.9	114	5.7
Red alder	46	0.5	65	0.7	56	0.7	28	0.2	76	2.7
Western redcedar	33	4.1	-	-	18	0.3	60	9.5	34	4.6
Ponderosa pine	21	2.3	-	-	-	-	50	5.6	-	-
Grand fir	13	0.2	-	-	10	0.1	20	0.5	14	0.2
Garry oak	7	0.8	-	-	10	1.8	8	0.1	6	1.0
Western hemlock	11	0.4	-	-	-	-	26	1.1	28	0.8
Black cottonwood	10	0.1	-	-	22	0.2	2	<0.1	14	0.2
Oregon ash	-	-	-	-	-	-	-	-	14	0.1
Soft-leaved willow	-	-	-	-	-	-	-	-	4	<0.1
Central mixed forest										
Garry oak	260	10.1	420	6.9	205	15.1	-	-	-	-
Ponderosa pine	156	13.6	100	11.0	222	18.7	60	2.8	-	-
Douglas-fir	120	6.5	110	3.3	110	6.3	190	16.6	120	3.9
Bigleaf maple	38	0.4	7	<0.1	33	0.6	150	0.8	80	10.3
Red alder	38	0.3	20	0.1	53	0.6	30	0.1	180	0.2
Black cottonwood	28	0.2	30	0.1	33	0.4	-	-	30	0.1
Lodgepole pine	21	0.7	10	0.2	30	1.1	20	0.5	-	-
Grand fir	-	-	-	-	-	-	-	-	10	0.2
Soft-leaved willow	4	<0.1	10	<0.1	-	-	-	-	20	0.1
Oregon ash	-	-	-	-	-	-	-	-	60	0.4
Central broadleaf forest										
Garry oak	230	12.2	330	14.6	195	11.8	200	10.7	100	3.1
Ponderosa pine	55	3.2	160	11.5	30	0.7	-	-	30	2.4
Bigleaf maple	15	0.4	60	1.6	-	-	-	-	170	12.1
Soft-leaved willow	15	0.2	60	0.7	-	-	-	-	-	-
Black cottonwood	-	-	-	-	-	-	-	-	80	1.0
Eastern steppe										
Bigleaf maple	-	-	-	-	-	-	-	-	70	17.8
Garry oak	-	-	-	-	-	-	-	-	20	6.2
Black cottonwood	-	-	-	-	-	-	-	-	10	4.1

circinatum), red bilberry (*Vaccinium parvifolium*), and dull Oregongrape accounted for most of the cover (Table 4). All were contagiously distributed (Whittaker 1975), with ~40-70% frequency, and they had abundant cover on all slopes. The remaining species were minor. Cover for any of them was ≤13%, frequency generally was 10-30%, and individual values varied by topographic position. As with the trees, southwest slopes supported the fewest understory species, and southeast slopes supported the most (Table 4).

Central Mixed Forest Association

The central CRG (121° 40' to 121° 25' longitude; Figure 3) supported a mixed forest with approximately equal densities of conifer and broadleaf trees, but dramatically lower overall basal area compared to the western conifer forest (Table 3). Basal area for broadleaf trees was only 34% of the conifers. Mean densities for Douglas-fir and ponderosa pine were slightly higher than for Garry oak. Douglas-fir and ponderosa pine were more

TABLE 4. Mean percent cover and frequency for shrub, forb, and grass species, and total species, in the four associations, for species with ≥5% cover in the association under consideration. SW, S, SE, R = southwest, south, southeast, and ravine.

	Cover				Frequency			
	SW	S	SE	R	SW	S	SE	R
Western conifer forest (42 species)								
Sword fern	36	16	30	26	62	28	55	46
Vine maple	36	21	19	19	56	32	33	33
Red bilberry	19	9	13	14	42	20	32	27
Dull Oregongrape	34	6	15	6	68	16	31	12
Pacific blackberry	8	8	11	4	32	27	44	11
Oceanspray	9	13	8	6	14	23	18	11
Himalayan blackberry	2	9	2	13	2	14	4	27
Thimbleberry	4	7	6	2	14	14	14	4
Snowberry	1	12	8	7	2	24	21	14
Poison oak	-	11	5	4	-	19	18	10
Bracken	8	4	2	2	28	14	13	9
Springbeauty	-	1	<1	5	-	4	2	15
Salal	-	1	5	-	-	1	12	-
Eastern red elderberry	-	-	-	8	-	-	-	17
Central mixed forest (38 species)								
Poison oak	27	27	10	2	52	57	16	12
Snowberry	12	20	23	-	21	34	48	-
Cheatgrass	38	28	-	-	73	68	-	-
Dull Oregongrape	8	8	16	-	17	24	28	-
Sword fern	-	2	24	17	-	2	40	32
Pacific blackberry	<1	7	7	7	1	24	28	28
Tall Oregongrape	7	4	-	-	16	9	-	-
Bluebunch wheatgrass	4	8	-	-	12	20	-	-
Wyeth's lupine	5	-	-	-	13	-	-	-
Maidenhair fern	-	-	-	9	-	-	-	16
Thimbleberry	-	-	-	8	-	-	-	12
Wall lettuce	-	-	-	6	-	-	-	32
Cow-parsnip	-	-	-	5	-	-	-	8
Central broadleaf forest (30 species)								
Cheatgrass	31	49	59	49	96	96	92	76
Poison oak	25	9	-	11	56	24	-	16
Western serviceberry	14	7	11	-	40	16	24	-
Sandberg's bluegrass	5	6	4	-	52	42	32	-
Squaw currant	2	6	7	-	8	14	16	-
Snowberry	5	-	-	4	12	-	-	4
Oceanspray	8	-	-	-	8	-	-	-
Arrowleaf balsamroot	4	9	-	-	20	28	-	-
Bristly manzanita	10	-	-	-	40	-	-	-
Wyeth's lupine	-	9	-	-	-	30	-	-
Mockorange	-	-	10	4	-	-	16	8
Spotted knapweed	-	-	5	12	-	-	40	52
Gray's lomatium	-	-	7	-	-	-	16	-
Eastern steppe (22 species)								
Cheatgrass	50	48	-	54	96	93	-	88
Northern buckwheat	14	7	-	-	40	23	-	-
Gray rabbitbrush	9	2	-	-	16	4	-	-
Big sagebrush	6	2	-	-	12	3	-	-
Mockorange	4	-	-	8	4	-	-	8
Wyeth's lupine	-	12	-	-	-	31	-	-
Sandberg's bluegrass	-	4	-	8	-	20	-	32
Bluebunch wheatgrass	-	5	-	-	-	19	-	-
Large-flowered collomia	-	-	-	28	-	-	-	52

important on southeast and south slopes, and this association supported the highest mean density of ponderosa pine. In contrast, Garry oak was more prominent on southwest slopes, often as dense stands of dwarfed trees, but was absent on southeast slopes (Table 3). The seven other tree species in this association were minor, except bigleaf maple on southeast slopes.

The sparse understory in the central mixed forest was dominated by poison oak. Except for cheatgrass on southwest slopes, however, no species reached 30% cover (Table 4). Poison oak and snowberry were distributed across all slope aspects, often contagiously with 30-50% frequency. Cheatgrass was prominent on southwest and south slopes, with ≥65% frequency, but absent from southeast slopes. Prominent species from the western conifer forest had dramatically different cover and frequency in the central mixed forest. For instance, in the central mixed forest, maximum mean cover for sword fern (24%) was lower than overall mean cover (36%) in the western forest. Dull Oregongrape mean cover was ~75% less on southwest slopes (Table 4). Vine maple and red bilberry were absent. Conversely, bluebunch wheatgrass (*Agropyron spicatum*) and Wyeth's lupine (*Lupinus wyethii*), abundant in the Columbia Basin, were sparse in central mixed forests. In general, the low frequencies indicate that understory species were distributed more irregularly in the central mixed forest than in the western conifer forest.

Central Broadleaf Forest Association

The central broadleaf forests extended from 121° 25' to 121° 10' longitude (Figure 3). These stands, strongly influenced by the drier climate in the eastern CRG (Table 2), supported low tree densities. Garry oak dominated, but all other species averaged well below 100 trees/ha on every slope aspect in this region (Table 3). Southeast slopes supported only Garry oak in the canopy. Ponderosa pine was the only prominent conifer, especially on southwest slopes that supported some sizeable trees (Table 4). The other three species were minor, and this region was beyond the tolerance range of Douglas-fir. The character of the forest was set more by broadleaf trees than by conifers.

The understory of the central broadleaf forest was a mixture of species from the central mixed forest and eastern shrub steppe, but total cover here was sparser than in the two forest associations to the west. Cheatgrass clearly dominated across all slope aspects, with mean cover >30% and high frequency (Table 4). Poison oak was an important associate on southwest and south slopes, and western serviceberry (*Amelanchier alnifolia*) was subordinate on all slope aspects (Table 4). Both species were clumped in the cheatgrass matrix. Sandberg's bluegrass (*Poa sandbergii*) had relatively high frequency, but this low-statured plant contributed little overall cover (Table 4). Otherwise no other species was consistently distributed throughout the region. Cover of these subordinate species was ≤10%, and frequency seldom exceeded 30%.

Eastern Steppe Association

This dry, treeless association extended east of Horsethief Lake at 121° 10' longitude (Figures 1, 3). Structurally, the stands in this region of the CRG were similar to the Columbia Basin shrub-grass steppe (Daubenmire 1970), characterized by broad expanses of grasslands through which contagiously grouped perennials were scattered. The eastern steppe is distinguished by hot summers and cold winters (Table 1), and it has the lowest precipitation of any association in the CRG (Table 2). No southeast slopes in this portion of the CRG met our sampling criteria. Southwest and south slopes were dominated by cheatgrass, with mixtures of other steppe species, none of which reached 15% cover (Table 4). Cheatgrass was uniformly distributed with high cover in the eastern steppe. Notable subordinates were northern buckwheat (*Eriogonum compositum*) on southwest slopes and Wyeth's lupine on south slopes. Gray rabbitbrush (*Chrysothamnus nauseosus*), big sagebrush (*Artemisia tridentata*), and mockorange (*Philadelphus lewisii*) provided sparse shrub cover (Table 4). None of these woody species exceeded 16% frequency.

Ravines

Species composition and community structure in the ravines in the western conifer forests were similar to the southeast slopes, but less similar to south and southwest slopes (Tables 3, 4). Bigleaf maple density in the ravines equaled or exceeded density on the slopes. Douglas-fir density and basal area were 40-50% compared to the slopes. Eight

other species on southeast slopes were present as subordinates in the ravines, although densities varied slightly. Oregon ash was present in the CRG only in ravines in the western and central forests (Table 3).

Ravines in the central mixed forest association had a strong broadleaf character. Compared to nearby slopes, red alder density increased dramatically; Garry oak, ponderosa pine, and lodgepole pine (*Pinus contorta*) were absent (Table 3). Bigleaf maple, Oregon ash, and soft-leaved willow were important subordinates. Black cottonwood (*Populus trichocarpa*) density was greater than in western ravines. Ravines in the central CRG supported fewer trees/ha than ravines in the western CRG. This trend toward broadleaf dominance continued eastward. Ponderosa pine was minor in ravines in the central broadleaf forests, and no conifers grew in the ravines in the eastern steppe (Table 3). Bigleaf maple was the dominant canopy species in the eastern ravines, with a few Garry oaks and black cottonwoods (Table 3).

Compared to the canopy layer, understory differences in the ravines were less distinct than on the slopes. In the western conifer forests, sword fern, vine maple, and red bilberry clearly dominated ravine understories, as on the slopes (Table 4). The only species absent from the western ravines was salal (*Gaultheria shallon*). The alien Himalayan blackberry was abundant in the western conifer ravines, but minimal on the slopes, in contrast to the native Pacific blackberry (*Rubus ursinus*). In the central mixed forest, only six species had ≥5% mean cover, and no species had >35% frequency (Table 4). In the central broadleaf forests and eastern steppe, cheatgrass dominance on the slopes was maintained in the ravines. Few species grew in ravines in the eastern portions of the CRG, but the alien spotted knapweed (*Centaurea maculosa*) was favored by ravines in the central broadleaf forest association. Knapweed ranked second in cover, and frequency was >50% (Table 4). Few forbs were present in CRG ravines. The most important forbs were western springbeauty (*Montia sibirica*) in western ravines, wall lettuce (*Lactuca muralis*), cowparsnip (*Heracleum lanatum*), and Gray's lomatium (*Lomatium grayi*) in central ravines, and large-flowered collomia (*Collomia grandiflora*) in eastern steppe ravines.

Tree species

Douglas-fir was the dominant tree species in the western and central CRG, where maximum density exceeded 300 stems/ha (Figure 4). It was excluded from only the wettest sites in the western ravines. Douglas-fir was present in the eastern forests, but was limited to south aspects, where density was <50 trees/ha (Table 3, Figure 4).

Western redcedar (*Thuja plicata*) achieved maximum density in the western conifer forest on southeast slopes and in ravines (Figure 4). This species was narrowly confined to the most mesic sites in the CRG, and it did not grow east of 121° 55'.

Geographically, the most widely distributed tree species in the CRG was bigleaf maple, which extended from the western forests at 122° 15' to the ravines of the eastern steppe at 120° 55'. It reached maximum distribution in ravines of the western conifer forest, with density of ~200 trees/ha (Figure 4). In the eastern CRG, bigleaf maple grew on mesic sites, with density of ~100 trees/ha.

Black cottonwood was distributed almost as widely as bigleaf maple, but density was consistently lower (Table 3, Figure 4). The center of cottonwood distribution was in the central CRG, where it was found on southwest and south slopes, and in ravines. Maximum density, however, was in the ravines of the central mixed forest (Table 3).

The highest density of Garry oak (>475 trees/ha) occurred in the central mixed forest and central broadleaf forest (Figure 4). The high densities for Garry oak were observed in several isolated stands, either in a savanna structure or in dwarfed stands.

Ponderosa pine was concentrated in the central mixed forest and central broadleaf forest. It reached maximum density of >200 trees/ha on the southwest slopes of the central broadleaf forest (Figure 4). Southeast slopes in the western conifer forest were within the tolerance range of ponderosa pine, but it was absent from other sites (Table 3).

Understory species

Deciduous shrubs were indiscriminately distributed throughout the CRG, on almost all aspects in each of the forest associations (Figure 5). Maximum cover was reached in the ravines in the western conifer forest for vine maple, red bilberry,

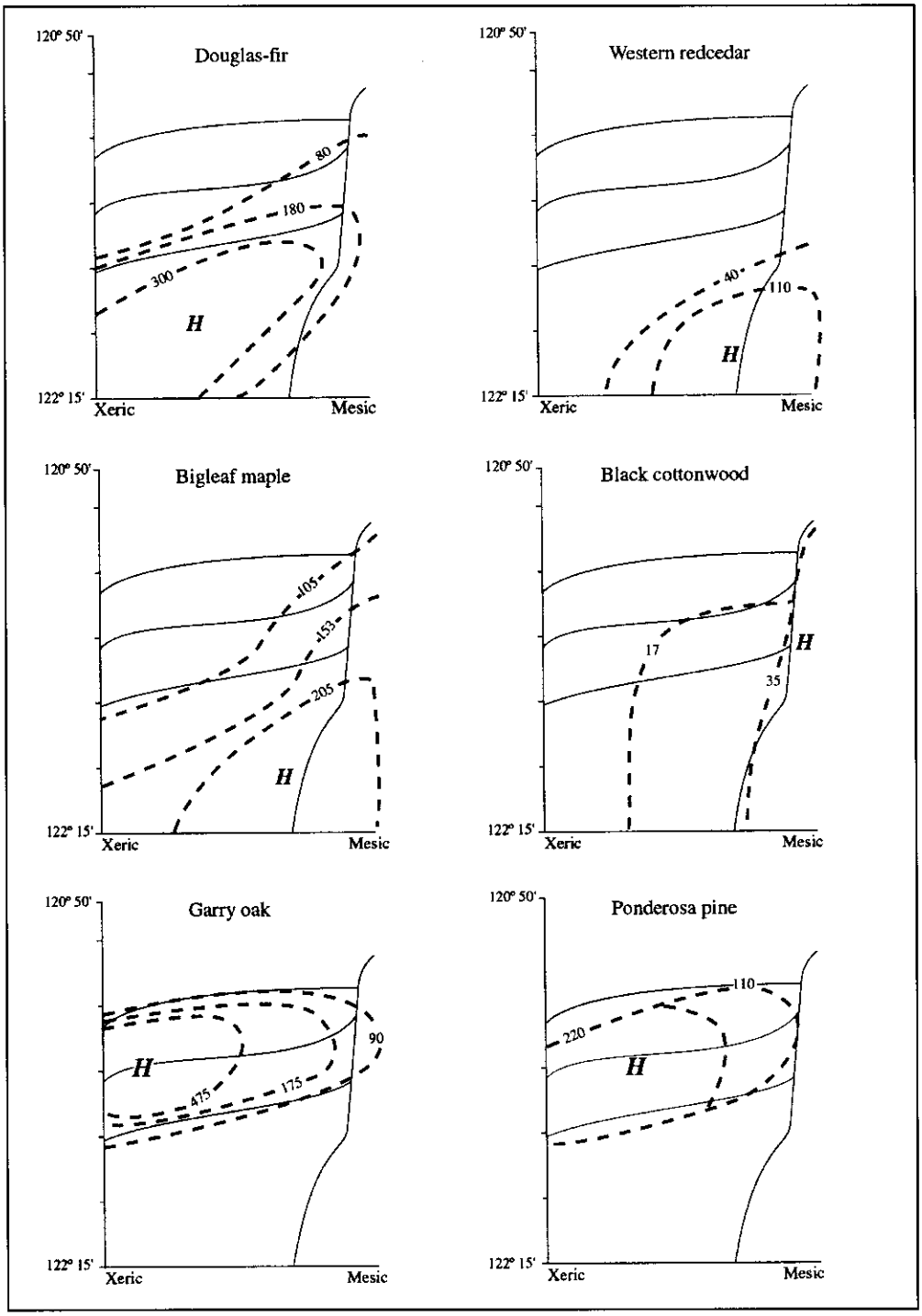

Figure 4. Distribution of important tree species on the north wall of the CRG. Values are trees/ha. H indicates maximum centers of distribution, according to actual density on the individual macroplots located on Figure 2. These diagrams are minimally connected to the mean data presented in Table 3, because they are based on measured values in specific macroplots.

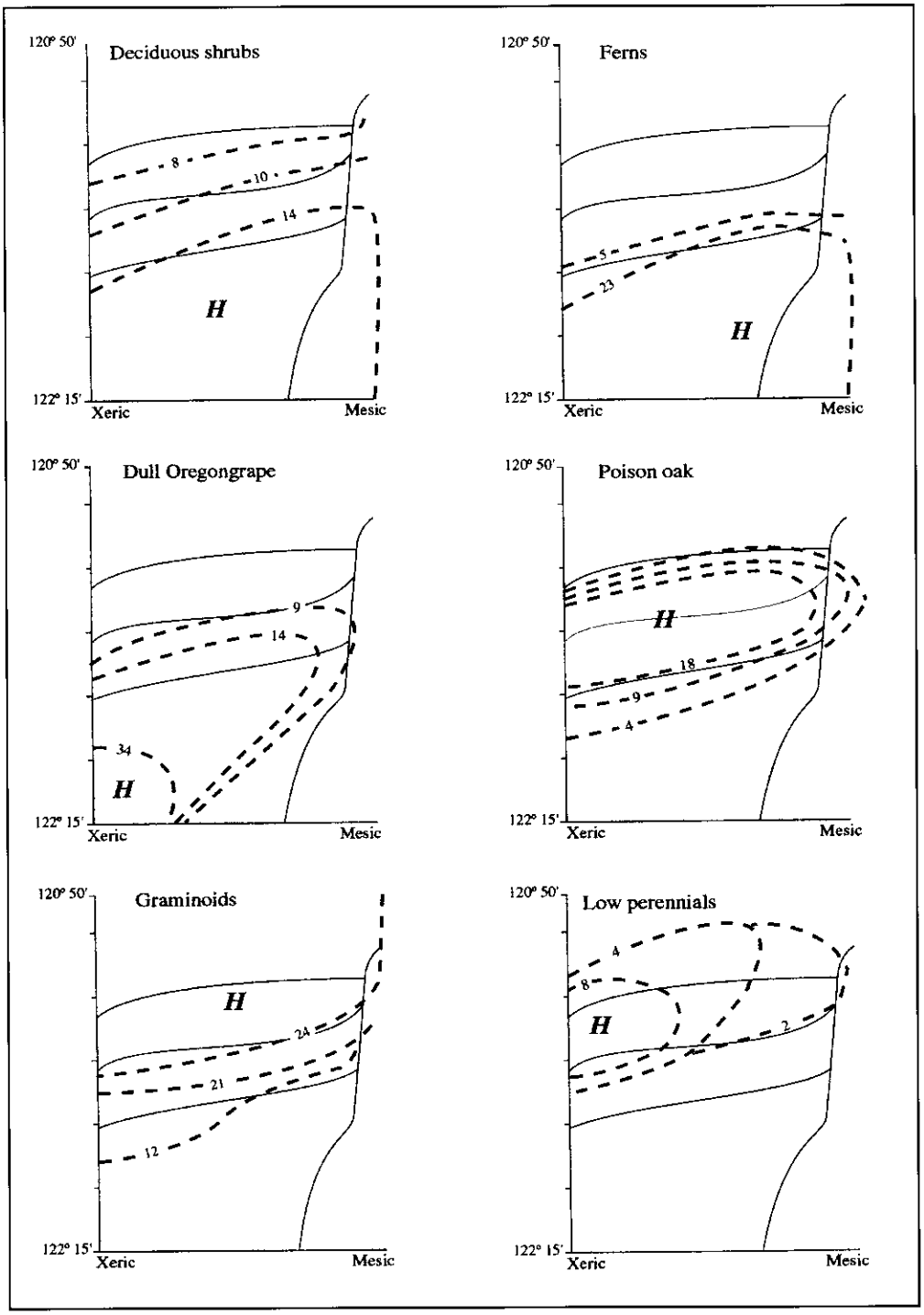

Figure 5. Distribution of important understory growth forms and species in the CRG. Values are percent cover. H indicates maximum centers of distribution, according to actual cover values on the individual macroplots located on Figure 2. These diagrams are minimally connected to the mean data presented in Table 4, because they are based on measured values in specific macroplots.

oceanspray (*Holodiscus discolor*), thimbleberry (*Rubus parviflorus*), and eastern red elderberry (*Sambucus racemosa* ssp. *pubens*). Snowberry, western serviceberry, mockorange, and squaw currant (*Ribes cereum*) extended the distribution of the deciduous shrub growth form eastward as far as the ravines in the eastern steppe (Table 3, Figure 5).

Ferns, such as sword fern, bracken (*Pteridium aquilinum*), and maidenhair fern (*Adiantum pedatum*) reached highest cover in the western conifer forest and in ravines (Figure 5). They were indiscriminate species, and occurred at high frequencies on mesic sites. Ferns extended eastward in the CRG on southeast slopes and ravines of the central mixed forest.

The distribution of dull Oregongrape (Figure 5) generally encompasses the distribution of other evergreen shrubs in the forests, including salal, tall Oregongrape (*Berberis aquilifolium*), and bristly manzanita (*Arctostaphylos columbiana*). Dull Oregongrape was a dominant understory species in the western conifer forest, reaching maximum cover on southwest slopes (Table 4). It was a broadly tolerant species, found on all aspects except ravines, although its cover was low.

Poison oak was a prominent species in the central mixed forest and the central broadleaf forest (Figure 5). The tolerance range of this shrub extended onto south slopes of the western conifer forest, and into the ravines of all three forest associations (Table 3). Poison oak was most commonly encountered in the understory of stands dominated by Garry oak, but it was not restricted to these forests.

Graminoids were widely distributed throughout the CRG, extending onto southwest slopes from the western forests to the eastern steppe (Figure 5.) The highest cover for graminoids was encountered in the eastern steppe and central broadleaf forest, where they averaged ~45% cover. The vast majority of this cover was supplied by the alien cheatgrass (Table 4). Native species, such as bluebunch wheatgrass, Sandberg's bluegrass, and Idaho fescue (*Festuca idahoensis*) accounted for little cover.

Low perennials, such as arrowleaf balsamroot (*Balsamorhiza sagittata*), northern buckwheat, and Wyeth's lupine, were found primarily in the central broadleaf forest and eastern steppe (Figure 5, Table 4). Maximum cover was on south and southwest aspects, where they combined for 12-18% cover.

Discussion

The ecocline on the north wall of the Columbia River Gorge reflects the interaction among precipitation, wind, temperature, soil moisture, and the individual tolerance ranges of plant species. Each association in the CRG supported species distributed individually along the ecocline (Figures 3, 4, 5). The centers of distribution were in the western CRG for a number of species, including Douglas-fir, western redcedar, bigleaf maple, dull Oregongrape, sword fern, bracken, vine maple, and red bilberry (Figures 4, 5). The centers of distribution for Garry oak, ponderosa pine, poison oak, and snowberry were in the central CRG (Figures 4, 5). The centers of distribution for cheatgrass, northern buckwheat, Wyeth's lupine, western serviceberry, mockorange, and Sandberg's bluegrass were in the eastern CRG (Figures 4, 5).

Although each species reached maximum distribution in one region of the CRG, few were confined to a specific geographic location or vegetation association. Douglas-fir grew eastward to 121° 20', whereas cheatgrass was present westward to 122° 05'. Garry oak grew on all aspects from 121° 45' to 121° 15', and poison oak occurred from 121° 55' to 121° 15'. Bigleaf maple was the only species with high density throughout the CRG, and cheatgrass and Wyeth's lupine also were present in all four associations. The prominent plant species in the CRG ranged well beyond their centers of distribution.

The ecocline in the CRG is a product of changes in environmental factor complexes, species distribution, and physiognomic associatons. This ecocline is similar to the Santa Catalina Mountains, Arizona, where slope aspect was superimposed on the variable mountain environment (Whittaker and Niering 1965). The CRG is analogous to a mountain turned on its side, with the cool, moist summit to the west and the warm, dry base to the east. The cooler, moister conditions in the western CRG promote the dense western conifer forest. The western conifer forests in the CRG are extensions of the regional upland forests in southwest Washington and northwest Oregon. The potential natural vegetation of this region constitutes forests dominated by Douglas-fir

in association with western hemlock, western redcedar, and bigleaf maple, with sword fern, vine maple, and dull Oregongrape prominent in the understory (Troll 1955, Habeck 1961, Franklin 1965, Detling 1958, Johannessen et al. 1971, Franklin and Dyrness 1988, Schoonmaker and McKee 1988, Brockway 1998, Bailey et al. 1998, Barbour and Billings 2000). The gradation from western conifer to central mixed forest coincided with the loss of several species adapted to mesic conditions, such as western redcedar and western hemlock, and the reduction of sword fern (Figures 4, 5).

The central mixed forest and central broadleaf forest marked the transition to a warmer and drier growing season. These drier forests were dominated by Garry oak, with mixtures of ponderosa pine (Table 3). Floristic patterns in the central broadleaf forests resembled the central mixed forests, except for the lack of conifers eastward. A similar environmental change involving pines and oaks was observed in the Klamath Mountains eastward from the Pacific Ocean (Whittaker 1961). The central mixed forest is unique in the Pacific Northwest. The nearest similar combination of species occurs in the Siskiyou Mountains of southern Oregon, where lower elevation forests on xeric slopes are dominated by mixed combinations of sugar pine (*Pinus lambertiana*), Douglas-fir, canyon live oak (*Quercus chrysolepis*), and California black oak (*Q. kelloggii*), with poison oak and dull Oregongrape prominent in the understory (Whittaker 1960). Detling (1958) previously noted the strong floristic connection between the Rogue River area and the Columbia River Gorge.

The hot, arid, windy environmental regime in the eastern CRG severely limits plant growth and diversity, and it excludes trees in favor of grasses. The vegetation of the eastern steppe is similar to the Columbia Basin, where cheatgrass, northern buckwheat, lupines, big sagebrush, and rabbitbrush are prominent (Daubenmire 1970, 1975; Cline et al. 1977; Sauer and Rickard 1979; Franklin and Dyrness 1988). The potential natural vegetation of the eastern CRG falls within the bluebunch wheatgrass-Sandberg's bluegrass zone (Daubenmire 1970), however, it is unlikely that this pattern will ever return to the CRG given the current prominence of the alien cheatgrass in the eastern CRG.

The CRG is the only near sea level corridor through the Cascade Range from California to British Columbia, and plant species have migrated between the Columbia Basin and the Willamette Valley via the Gorge for millennia (Lawrence 1939, Franklin and Dyrness 1988). Movement historically has been primarily from east to west, with aridly adapted species invading new habitats, sometimes as far west as Cape Horn (Detling 1958), 12 km east of Washougal in the western conifer forest. The warmer and drier soils caused by greater insolation on the north wall have allowed steppe species, such as northern buckwheat, and Wyeth's lupine, to migrate from the Columbia Basin westward along the Columbia River (Lawrence 1939, Detling 1958). Two species important to this study, bigleaf maple and Garry oak, have migrated from west to east in the CRG (Lawrence 1939). They have been particularly successful in ravines (bigleaf maple) and xeric slopes (Garry oak) of the CRG.

In recent decades alien species have begun to migrate into and through this corridor. The most widespread alien species in the CRG, cheatgrass, has extended from the Columbia Basin to plot 1, at Cape Horn in the westernmost part of our study area (Figure 3). Cheatgrass occurred on 21 plots, and dominated the low layer of many of the plots in the eastern CRG. Cheatgrass PV on plot 18 (576), on the southwest slope of Dog Mountain, was exceeded only by plot 35 (942) in the eastern steppe association.

Himalayan blackberry occurred on 13 plots, mainly in the western CRG, and extended east as far as plot 27. Maximum PV for Himalayan blackberry came on plot 17 (202) and plot 3 (179).

The other alien species in the CRG were more narrowly distributed, and were less prominent. Wall lettuce grew on four plots (#1, 8, 12, 24) in the western conifer forest, and spotted knapweed grew on two plots (#26, 30) in the central portion of the CRG. Scot's broom (*Cytisus scoparius*) never achieved sufficient cover to be included in Table 3, but it occurred on three plots (#12, 26, 27) in the central portion of the CRG. We recorded 10 other alien species, all with low cover and frequency: hairy vetch (*Vicia villosa*), Tangier peavine (*Lathyrus tingitanus*), herb Robert (*Geranium robertianum*), filaree (*Erodium cicutarium*), dogtail (*Cynosurus echinatus*), Viper's bugloss (*Echium vulgare*), Jim Hill mustard (*Sisymbrium altissimum*), St. John's

wort (*Hypericum perforatum*), and orchard-grass (*Dactylis glomerata*).

The distribution of Garry oak and ponderosa pine in the CRG illustrates the important environmental differences between the north and south walls of the Gorge. Ponderosa pine dominates extensive forests on the east slope of the Cascade Mountains, and it is a dominant species on the Oregon side of the central and eastern CRG (Lawrence 1939). Although present in the three forest associations on the north wall of the CRG, ponderosa pine at best was a strong subordinate in the central mixed forest. The highest pine densities were on south slopes in the central mixed forest, and on southwest slopes in the central broadleaf forest, yet either Douglas-fir or Garry oak dominated the stands (Table 3). No pure oak stands exist on the Oregon side of the CRG (Lawrence 1939), yet on the Washington side Garry oak accounted for a larger percentage of total tree density, dominated many slope aspects, occurred with much greater frequency, and extended much farther west than isolated oaks on the south wall. Oaks in the north wall forests typically were smaller than those on the south wall, which grow farther east beyond the limits of the CRG (Lawrence 1939).

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