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Quercus garryana Communities in the Puget Trough, Washington

Abstract

Among the legacies of the Vashon Glaciation are Oregon white oak (*Quercus garryana*), prairie, wetland, and Douglas-fir (*Pseudotsuga menziesii*) communities arrayed in a mosaic in the Puget Sound Area (PSA). Much of this mosaic has been destroyed. The largest remaining portion is on Fort Lewis Military Reservation. We examined oak communities on Fort Lewis to assess encroachment by exotic plants and by Douglas-fir, to determine amounts of regeneration of oak and other tree species, and to compare oak community diversity with that of nearby Douglas-fir forests and glacial till prairies. For the 22 largest communities, we determined densities of trees, distributions of tree diameters and heights, amounts of regeneration for each tree species, evidence of exogenous disturbances, and covers of vascular understory species. For study sites, we calculated basal areas of tree species, richness and diversity of vascular plants, and percentages of species that were exotic. We constructed species accumulation curves for oak communities, Douglas-fir forests, and prairies. We performed Bray-Curtis and weighted averaging ordinations for 176 sampling plots from the 22 sites. Oak communities were typically more diverse than either Douglas-fir forests or prairies and were transitional in species composition between them. However, oak communities contained numerous exotics, particularly Scot's broom (*Cytisus scoparius*) and colonial bentgrass (*Agrostis capillaris*). Most oak communities contained large-diameter Douglas-firs and other tree species and appeared to be transforming to conifer or conifer/mixed hardwood forests. With succession, exotic species become less prevalent, but the extent and abundance of oaks is diminished. Maintenance of oak communities, and the PSA natural mosaic, may require tree-density management in oak stands, removal of Douglas-fir, development of replacement oak sites, prescribed burning, and mechanical suppression of exotics before burning.

Introduction

The Puget Sound Area (PSA) of Washington contains much of the human population of the state as well as land forms and plant associations not found in adjacent forested regions (Franklin and Dymess 1973, Kruckeberg 1991). The near sea-level elevation of the Puget Trough, Puget Sound itself, and the surrounding mountain ranges provide PSA with a warm and relatively dry climate. The Vashon Glaciation shaped the soils and physiography of PSA. Kettle lakes and ponds, moraines, gravelly outwash plains and terraces, and well-drained soils ranging from cobbles to sandy loams, along with rivers originating in the mountains, provided a diversity of habitats within the landscape (Leighton 1918, Kruckeberg 1991).

The PSA has long been inhabited by people. Indigenous people shaped vegetation by setting fires to maintain grasslands dominated by Idaho fescue (*Fstuca idahoensis*) and containing useful food plants, including small camas (*Camassia quamash*) (Norton 1979, Agee 1996; Tveten and Fonda [1999] provide a recent review). Fire, mild climate, and diverse physiography led to diverse plant associations including kettle wetland communities, riparian hardwood forests, Douglas-fir (*Pseudotsuga menziesia*)-*western* hemlock (*Tsuga heterophylla*)-*western* redcedar (*Thuja plicata*) old-growth forests, Douglas-fir fire-climax forests, Idaho fescue prairies, ponderosa pine (*Pinus ponderosa*) savannas and forests, Oregon white oak (*Quercus garryana*) savannas, woodlands, forests, and ecotones, including wetland-oak-grassland, wetland-oak-fir, riparian hardwood-oak-grassland, and grassland-oak-fir. These biotic communities and their ecotones comprised the PSA lowland ecosystem—a dynamic, shifting mosaic of diverse plant communities maintained by indigenous people.

Soon after European settlement in the 1850s, grazing animals, especially sheep, were introduced to PSA prairies and, certainly, exotic plants were introduced and became naturalized (Meany 1918). Usurpation of most land by white settlers eliminated the indigenes' burning and wildfire, allowing

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Douglas-fir to encroach both on prairies and oak communities (Leighton 1918, Kruckeberg 1991, Ryan and Carey 1995*b*, Agee 1996). Development of transportation networks, agriculture, and settlements concentrated in the lowlands and continues to destroy prairies, wetlands, savannas, woodlands, and forests (McGinnis et al. 1997). Prairies were invaded by exotic grasses (e.g., colonial bentgrass, *Agrostis capillaris*) and Scot's broom (*Cytisus scoparius*). Scot's broom also invaded many oak-dominated sites. Wetlands were invaded by exotic species such as reed canarygrass (*Phalaris arundinacea*). Numerous exotic plants now compete with indigenous, especially rare, plants (Thomas and Carey 1996, Thysell and Carey 2000). Although Oregon white oak extends north to the islands of Puget Sound and southeastern Vancouver Island (Stein 1990), relatively intact oak communities exist primarily on areas protected from human development, particularly on the Fort Lewis Military Reservation. At risk of loss with the destruction of oaks, prairies, and lowland wetlands are the western gray squirrel (*Sciurus griseus*) listed by the State of Washington as Threatened and a Federal Species of Concern (Ryan and Carey 1995*a*, Bayrakci et al. 2001); the western pocket gopher (*Thomomys mazama*), a Federal Species of Concern (Ryan and Carey 1995b); and several species of birds, reptiles, amphibians, and butterflies including the Federal Candidate Species, mardon skipper (*Politer mardon*), and the Federal Species of Concern, valley silverspot (*Speyeria zerene bremneril*) (T. Thomas, U.S. Fish and Wildlife Service, personal communication), as well as several plant species, including Columbian whitetop aster (*Seriorcarpus rigidus* [*Aster* curtus]), longhair sedge (*Carex comosa*), greenfruit sedge (*Carex interrupta*), smallflower wakerobin (*Trillium parviflorum*) (Thomas and Carey 1996, Washington Natural Heritage Program 1997), Torrey's pea (*Lathyrus torreyi*), *a* Federal Species of Concern, and golden Indian paintbrush (*Castilleja levisecta*), a Federal Threatened Species (T. Thomas, U.S. Fish and Wildlife Service, personal communication). Thus, the citizens of Washington are in danger of losing a significant part of their natural heritage (Larson and Morgan 1998), the legacies of the Vashon Glaciation.

Our objectives in this paper are to assess the status, condition, and trend of the oak-dominated vegetation associations on Fort Lewis by: (1) determining total area and number of sites occupied by oak-dominated vegetation, (2) characterizing overstory and understory vascular vegetation, including extent of oak regeneration, degree of invasion by exotic plant species, and impacts of Douglas-fir encroachment, (3) comparing oak community diversity to that of prairies and Douglas-fir forests—two dominant types on the Fort Lewis landscape, (4) determining the landscape context of, or the nature of the two biotic communities adjacent to, the 20 or so largest oak communities, and (5) developing a conceptual model of the prevailing influences on oaks and associated vegetation in PSA. Finally, we discuss the implications of our findings for management and conservation.

Methods

Study Area

Fort Lewis Military Reservation is in Pierce and Thurston counties in the southern Puget Trough of Washington (Franklin and Dymess 1973). The area is near the southern limit of the Puget Lobe of the Vashon Stade of the continental glacier that retreated 13,000-15,000 years ago (Kruckeberg 1991). Relief is moderate to rolling, elevation ranges from 120 to 160 m, and annual precipitation is 800-900 mm with only 10-15% of annual precipitation falling during the peak growing months of June-September (Pringle 1990). Beneath oaks are deep, coarse-textured, well-drained soils of the Spanaway-Nisqually association derived from glacial till and glacial outwash deposited during the retreat of the continental glacier. Because of the influence of the Vashon Glaciation, Fort Lewis is characterized by a lack of sharp relief and by an absence of markedly divergent soil types (Zulauf 1979, Pringle 1990, Kruckeberg 1991).

Of 34,400 ha within Fort Lewis, 1,200-1,400 ha (3-4%) in 573 sites are defined as Oregon white oak woodlands (see Ryan and Carey 1995*a*:206 for a map). Some sites are inaccessible (in artillery impact areas) and some mapped sites no longer have oaks. Visits to 333 accessible sites revealed that 85 sites had <5 oak trees on areas <0.1 ha or were within developed areas (Ryan and Carey 1995*a*). The remaining sites were 0.2-44 ha and usually contained mixtures of tree species—oak, Douglas-fir; Oregon ash (*Fraxinus latifolia*), bigleaf

TABLE 1. Characteristics (0± SE, *n* = 8 plots) of 22 Oregon white oak (*Quercus garryana*) communities, Fort Lewis, Washington, 1999.

Site No.	Slope (%)	Modal aspect	Basal area[a] QGA (m²/ha)	PSME (m²/ha)	QUGA no./ha)	QUGA dbh (cm)[b]	Major (minor) overstory Species[c]	Understory[d] No. species	Exotics (%)	Adjoining features[e]
22	0-2	SW	21 ± 5	12 ± 6	395 ± 75	40 ± 2	Q, P, (Frla, Prav)	14 ± 1	8 ± 3	WL, DF/RD
28	0-10	SE	24 ± 5	13 ± 4	320 ± 67	41 ± 2	Q, P, (Frla)	12 ± 1	12 ± 2	PR, DF/MF)
34	0-15	varied	23 ± 7	8 ± 2	355 ± 113	37 ± 4	Q, P	11 ± 1	13 ± 5	RD/SH, DF/MF
81	0-3	flat	8 ± 2	13 ± 4	110 ± 24	32 ± 4	P, Q	18 ± 1	31 ± 5	WL, DF/SH
92	0-42	NW	13 ± 3	1 ± 1	260 ± 49	31 ± 2	Q, (Psme)	17 ± 2	7 ± 4	RD/SH, RT/SH
174	0- 8	flat	12 ± 2	12 ± 6	150 ± 38	32 ± 4	P, Q	18 ± 2	42 ± 6	PR/SH, DF
183	0-14	E	17 ± 4	0 ± 0	225 ± 69	40 ± 3	Q, (Psme, Frla)	14 ± 2	55 ± 5	WL, SV
215	0-3	flat	7 ± 1	0	250 ± 41	22 ± 2	Q	15 ± 1	49 ± 4	DF, DF/MX)
243	0-10	varied	9 ± 3	9 ± 3	235 ± 112	32 ± 1	P, Q	23 ± 3	19 ± 4	WL, SH
265	0-10	flat	16 ± 3	5 ± 4	335 ± 33	31 ± 2	Q, P	22 ± 2	32 ± 5	DF, MX
293	0-22	S	14 ± 4	8 ± 2	270 ± 84	31 ± 4	Q, P, (Acma)	16 ± 1	14 ± 4	PR/RD, DF
314	8-20	SE	12 ± 2	9 ± 3	155 ± 21	35 ± 2	Q, P, Frla, (Acma, Prav)	19 ± 1	4 ± 1	PR, WL
335	0-13	varied	21 ± 2	3 ± 3	230 ± 38	42 ± 3	Q, (Psme, Acma, Frla)	14 ± 2	16 ± 6	PR/SH, WL
343	0-12	varied	10 ± 4	4 ± 3	185 ± 89	35 ± 6	Q, P, Prav, (Frla)	19 ± 2	29 ± 7	PR, DF/MX
348	3-12	S	15 ± 3	14 ± 5	425 ± 117	30 ± 2	Q, P	16 ± 1	19 ± 5	PR, DF/MF
367	0-22	SE	16 ± 5	16 ± 5	180 ± 49	40 ± 4	Q, P, (Acma, Frla, Prav)	15 ± 1	8 ± 3	PR, WL
399	0	flat	6 ± 2	3 ± 2	140 ± 45	26 ± 3	Q, P	18 ± 1	26 ± 4	DF, DF
525	0-10	flat	13 ± 3	5 ± 2	200 ± 48	33 ± 4	Q, P	27 ± 2	21 ± 3	PR, DF
528	0-40	varied	17 ± 3	9 ± 3	310 ± 42	32 ± 2	Q, P	17 ± 1	26 ± 7	PR, DF/MF
530	0	flat	4 ± 1	10 ± 3	105 ± 37	16 ± 1	P, Q	22 ± 2	22 ± 4	PR, DF
541	0-5	flat	13 ± 2	5 ± 3	295 ± 58	29 ± 3	Q, P	19 ± 1	23 ± 7	PR, DF/MF
550	0	flat	17 ± 2	2 ± 1	450 ± 65	31 ± 3	Q, (Psme)	14 ± 1	36 ± 5	PR, DF

[a]Includes only *Q. garryana* (QUGA) and *Pseudotsuga menziesii* (PSME) >10 cm dbh.
[b]Based on the 2 largest diameter oak trees per plot, 8 plots per site.
[c]In order of dominance; tree species codes: major species, Q = *Q. garryana,* P = *P. menziesii*; minor species, Acma = *Acer macrophyllum*, Fria = *Fraxinus latifolia,* Prav = *Prunus avium,* Psme = *P menziesii.*
[d]Vascular plant species richness/plot, 8 plots per site; exotic species as a percentage of total vascular plant species richness.
[e]Adjoining landscape features: DF = Douglas-fir forest; PR = prairie; MF = mixed oak and Douglas-fir forest; RD = road; RT = ridge top; WL = wetland; SH = shrubland; MX = mixed; SV = oak or mixed savanna.

maple (*Acer macrophyllum*), and others (Tables 1 and 2). Other plants frequently found with Oregon white oaks include common snowberry (*Symphoricarpos albus*), Indian plum (*Oemleria cerasiformis*), Pacific poison oak (*Toxicodendron diversilobum*), yampah (*Perideridia gairdneri*), sanicles (*Sanicula* spp.), and snowqueen (*Synthyris reneformis*) (Stein 1990, Ryan and Carey 1995*b*, this study). Oaks were commonly ecotonal—where forests, prairies, or wetlands transition to another community type—and often found at breaks in the terrain, such as the bottom or tops of hills (Table 1, Ryan and Carey 1995*a*,*b*). The former extent of oaks on Fort Lewis is unknown, but our observations of dead oaks under Douglas-fir and distant from remaining living oaks, suggest oaks were more widespread in the past. Analysis of land survey notes from 1853 suggests a marked decline in area covered by oaks since then (Tveten and Fonda 1999).

Field Sampling

Based on previous visits to 333 sites with oaks (Ryan and Carey 1995*a*), we identified sites that were either large enough to be considered oak communities (i.e., >8.0 ha, dominated or co-dominated by oaks), as opposed to prairie or conifer communities with a few happenstance oaks, or >4.8 ha and that had functioned historically as

TABLE 2. Density and prevalence of seedlings and saplings of major tree species and of stems >10 cm dbh of minor species found in 22 oak communities on Fort Lewis, Washington, 1999.

Variable	Density (no./ha)[a]		Prevalence (%)	
	Mean ± S.E.	Range	Sites[b]	Plots[c]
Quercus garryana				
Seedlings/suckers	961 ± 226	0-4450	96	42
Saplings	205 ± 56	5-1025	100	49
Pseudotsuga menziesii				
Seedlings	116 ± 69	0-1300	18	5
Saplings	34 ± 15	0-315	55	23
Fraxinus latifolia				
Trees > 10 cm dbh	10 ± 6	0-105	27	14
Seedlings	230 ± 192	0-4250	32	8
Saplings	26 ± 8	0-115	46	18
Acer macrophyllum				
Trees > 10 cm dbh	7 ± 4	0-55	18	10
Seedlings	11 ± 7	0-100	14	2
Saplings	5 ± 4	0-90	9	5
Prunus avium				
Trees > 10 cm dbh	4 ± 3	0-55	23	6
Seedlings	164 ± 75	0-1250	32	7
Saplings	9 ± 5	0-105	14	7

[a] Mean and range of 22 site means of 8 plots/site.
[b] Percent of 22 sites containing any of this variable.
[c] Percent of 176 plots containing any of this variable.

oak habitat for western gray squirrels (Ryan and Carey 1995*a,b*). We visited 133 of these (Bayrakci et al. 2001) and found 22 that were large enough to be considered oak communities; most were ecotonal between Douglas-fir forest and prairies. For each site, we circumscribed a core area that included the living oaks. Visually drawing lines from one exterior crown point to another along the outermost oaks was the only objective procedure we could devise to identify the actual extent of the oak community.

We developed a sampling scheme for core areas based on reconnaissance of all 22 sites. We sampled core areas with eight nested plots. To place the plots, we established a 240-m transect with eight stations 40-m apart, ≥60 m from the delineated perimeter, and parallel to the long axis of the core. In large sites, we systematically placed consecutive transects along the long axis of the core, with one transect/8 ha, up to three transects/core. Where size or shape of the site precluded use of a single transect of eight stations, we established two parallel lines of four stations each with 80 m between lines. At each station, we randomly selected a bearing and a distance ≤30 m from the station, but always within the delineated core area, to locate each of eight centers for nested plots (at every, every other, or every third station in sites with one, two, or three transects, respectively). We chose 30 m because it (1) made available for sampling a large proportion of the points within delineated sites, and, thus, our samples would approximate random samples, (2) prevented sampling overlap among consecutive transects, and (3) provided, then, unbiased samples of core areas.

During June and July, 1999, we recorded the octave-scale percent cover of all vascular understory species and number and species of tree seedlings ≤°1 cm basal diameter on 2.8-m-radius plots (25-m^2) centered on sample points. We used the octave scale recommended by Gauch (1982) as appropriate for visual estimation of species cover—allowing precise estimates of the abundance of rare plants and avoiding estimation error due to poor visual discrimination between covers of high value in abundant plants (Bonham 1989, Carey et al. 1999*a*). Scale values are: 1 (0 < % cover < 0.5), 2 (0.5 ≤ % cover < 1), 3 (1≤ % cover < 2), 4 (2≤% cover<4%),..., 9 (64≤ % cover ≤100). We defined cover as the vertical projection of the vegetation onto a horizontal plane (i.e., the ground). For recording and analysis, we used the mid-point of each cover category. We did not distinguish between oak seedlings and oak suckers.

On 8.9-m radius (250-mz) plots, we recorded octave percent covers of vascular plant life forms: canopy trees, shrubs and understory trees ≥2 m tall but below the forest canopy, shrubs 0.5-2.0 m tall, trailing shrubs and vine species <0.5 m tall or scandent on other plants or snags, forbs, ferns, and graminoids. We also recorded (1) the number of tree saplings 1-5 cm basal diameter, (2) number of live and dead overstory trees by species and diameter-breast-height (dbh) category (5-10 cm, 11-20 cm, 21-30 cm, 31-40 cm, 41-50 cm, and > 50 cm) and whether oaks were single-stemmed or part of a cluster (≥ 2 stems), such as may develop from suckers around a stump or root collar, (3) bole and canopy dimensions for the two largest diameter oaks including dbh, tree height, and canopy diameter, and (4) evidence of fire, logging (species, number, and size of stumps, and percent cover of skid trails and roads), manual brush control, girdling of non-oak tree species, soil excavation, and past settlement (e.g., foundations, fences, fruit trees). From each plot, we estimated direction and distance to the two nearest primary adjoining landscape features (e.g., road, wetland, prairie, conifer forest).

Vascular plant nomenclature follows Kartesz (1994) as updated (USDA, NRCS 1999) with vascular plant species concepts and identifications based on Hitchcock and Cronquist (1973). Regional floristic guides (Hitchcock and Cronquist 1973, Klinka et al. 1989, Hickman 1993, Pojar and MacKinnon 1994) provided further information about species origins (native or exotic), natural histories, and preferred habitats.

Analytical Methods

We calculated (1) mean cover for each species, species richness (the number of species/plot), Shannon-Wiener diversity (H'), and evenness (E), the ratio of observed H' to the maximum H' that would occur if all species in the plot were equally abundant for each site (Magurran 1988); (2) the percentage of vascular plant species that were exotic; (3) basal area (m^2/ha) and densities of trees > 10 cm dbh; and (4) number of saplings and seedlings for each tree species. We used the midpoint for each dbh category for basal area calculations except for the largest category where we used the category value; thus basal areas might be biased downwards where trees were large—few oaks were >50 cm dbh (Table 1). We report means ± standard errors (SE) except where otherwise noted. We used presence-absence data for species or groups to calculate prevalence values by site and by plot. We assessed the correlation between oak height and dbh based on the two largest oak trees per 250-m^2 plot.

To assess native and exotic species contributions to total species richness and to contrast richness of sampled oak sites to similar areas in prairies and Douglas-fir forests, we generated species accumulation curves, including all understory and overstory species. We plotted the cumulative number of 25-m^2 plots versus the cumulative number of vascular plant species (McCune and Mefford 1999). Direct comparisons with prairies and forests were possible because all sampling efforts used 25-m^2 plots and 25 m^2 is an appropriate area with which to sample vegetation in grass, weed, and shrub communities (Gauch 1982). Prairie data are from Thomas and Carey (1996); managed-forest data are from Thysell and Carey (2000). We calculated the correlation between the total number of vascular plant species and the total number of exotic species on the oak sites.

We performed Bray-Curtis (BC) ordination with square-root transformed percent-cover values for all species encountered on all 176 plots. We chose BC ordination because it is easy to interpret ecologically as environmental or compositional gradients and it has documented utility for plant community data (Beals 1984). In BC, as in other indirect ordination methods (Kent and Coker 1994), ordination axes are derived from the floristic data and are initially undefined in terms of ecological or environmental variables. We used variance-regression endpoint se-lection and the Sorenson distance measure. The amount of variance explained by each ordination axis was computed by subtracting the ratio of the sum of squares of the residual distance matrix to the sum of squares of the original distance matrix from one and expressing it as a percentage. For combinations of species or selected derived variables of interest and each ordination axis, we calculated the value of the Pearson product moment correlation coefficient, r. Using $n = 176$ ($df = 174$), the critical value (two-tailed) of r at $\alpha = 0.01$ was 0.251 (Zar 1984). We report only correlations with $P < 0.01$.

To further assess species relations, we performed an ordination on all species and used weighted averaging to locate the average position of each species in the BC plots-ordination space (McCune and Mefford 1999). We grouped species with the Sorenson distance measure in the farthest neighbor linkage method of cluster analysis to identify recurring vegetation site types and used this site-type membership as a variable in the ordination. Weighted averaging was based on all species, but we graphed only locations of species found on ≥10% of the 176 plots. Then we used indicator species analysis to identify species characteristic of site types (Dufrene and Legendre 1997, McCune and Mefford 1999). We evaluated statistical significance of maximum indicator values (IV-max) for the resulting groups with a Monte Carlo method employing 1,000 permutations of the data where the resultant P-value was the proportion of permutations in which the IV-max from the randomized data set equaled or exceeded the observed IV-max. Thus, a significant IV-max indicated a species that was characteristic of a site type and that the indicator value was larger than would be expected by chance in a permutation set (Dufrene and Legendre 1997, McCune and Mefford 1999). All calculations were made with the SPSS statistical program release 9.0.1 (Norusis 1999) or with PC-ORD, a program for multivariate analysis of ecological data (McCune and Mefford 1999).

Results

Adjoining Landscape Features and Disturbance

All the oak communities we sampled (all the large areas of oak) were on level to gently sloping ground (generally < 15 % slope), with various aspects (Table 1). All the communities could be considered ecotonal, with adjoining landscape features including roads, prairies, savannas, and forests (Table 1). The distance from plot centers to adjoining plant communities or landscape components averaged (mean of site means) 60 ± 5 m; means ranged from 24 to 125 m. Thus, oak communities were linear and narrow in form, on average. Douglas-fir or Douglas-fir/mixed hardwood forest was nearest to 39%, prairies to 38%, and wetlands to 16% of plots (n = 176 plots). The remaining 7% were nearest to roads (4%) and shrub lands (3%) (Table 1).

Disturbance, as sampled by plots, was not widespread in the communities we sampled. We observed stumps of recently felled Douglas-fir (part of oak restoration efforts) on 23% of plots (< 1 % relative cover). We found evidence of homesteads (e.g., orchards, ornamental species such as periwinkle [*Vinca major*], or old foundations) on 22% (<1 % relative cover). Roads crossed 15% of plots (13 % relative cover) and excavations (e.g., army foxholes) were in 10% (4% relative cover). On plots in four areas, however, we found 8 mature oaks (>15 cm dbh and >40 years old) that appeared to have been killed by intense fire resulting from burning of Scot's broom. During our study, we actually observed crown fires in one oak-Douglas-fir stand and in one ponderosa pine stand during prescribed bums.

Overstory Trees and Regeneration

Total basal area averaged 22 ± 1 m^2/ha with a range of 7-38 m^2/ha (Table 1). Oak basal area averaged 14 ± 1 m^2/ ha, 66 ± 3 % of the total basal area. All but one of the sites contained trees other than oaks (Table 1). Douglas-fir was the second most abundant tree species, averaging 7 ± 1 m^2/ ha or 28 ± 2% of the total basal area. All but three sites contained Douglas-fir, which accounted for >20% of total basal area in 64% of the sites (Table 1). Tree densities were 254 ± 15 oak/ha and 60 ± 7 Douglas-fir/ha, with site averages for oak ranging from 105 to 450 stems/ha (Table 2). Oregon ash, bigleaf maple, and the non-native sweet cherry (*Prunus avium*) were the next most common trees, found in seven, four, and four sites respectively; each represented <0.5% of total basal area (Tables 1 and 2). Ponderosa pine was on two sites; and black cottonwood (*Populus balsamifera trichocarpa*) and Pacific madrone (*Arbutus menziesii*) were on one site each. All in all, >25 % of plots in all but 1 site and 64% of all plots contained > 1 tree species besides Oregon white oak (Tables 1 and 2).

Douglas-fir trees large enough (≥30 cm dbh) to dominate mature oaks were found on 40% of plots. Dominant oaks (n = 340) averaged 33 ± 1 cm dbh (maximum = 84 cm dbh) and 16 ± 1 m tall (maximum = 30 m), with 80% of the dominants ≤20 m tall (Table 1, Fig. 1). Height and dbh of dominants was strongly correlated (transformed by the natural logarithm, r= 0.80). Most oaks were ≤30 cm dbh (5% were ≥40 cm dbh) while Douglas-firs >50 cm dbh were common (Fig. 1). Almost all (94%) plots con-tained more than one single-stemmed oak tree (0 ± SE, 5 ± 1) and 61 % contained more than one cluster-stemmed tree (4 ± 1 clustered stems) that may have arisen as suckers from the base of a stump or root collar.

Oak seedlings or saplings were present on all sites (N = 22) but in <50% of plots (n = 176) (Table 2). Of the four other common tree species, only Douglas-fir saplings were on >50% of sites or >20% of plots. Douglas-fir seedlings, while locally abundant, were observed in only 5% of plots (Table 2). Oregon ash seedlings or saplings were locally abundant (present in 45% of sites and 17% of plots). Bigleaf maple and sweet cherry seedlings and saplings were common on some sites, but were found in 510% plots (Table 2).

Species-area Curves

Cumulative number of species increased more rapidly in oak communities than in prairies or Douglas-fir forests. Furthermore, the species-area for oak communities was not asymptotic, even after accumulating 171 species, whilst the other communities reached asymptotes of approximately 100 (prairie) and 90 (Douglas-fir forest) species (Thomas and Carey 1996, Thysell and Carey 2000, Fig. 2). Exotics composed 31 % of the species in oak communities and the exotic-species curve was more asymptotic than the native-species curve (Table 1,

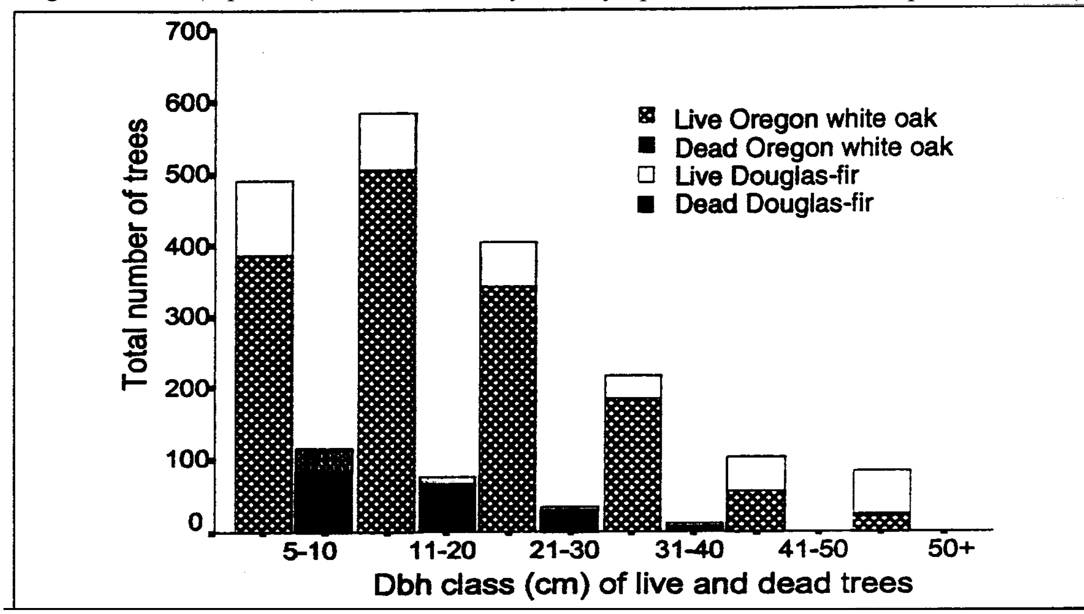

Figure 1. Diameter-class distributions of live and dead Oregon white oak (*Quercus garryana*) and Douglasfir (*Pseudotsuga menziesii*) trees on 176 250-m^2 plots in 22 oak communities on Fort Lewis, Washington, 1999.

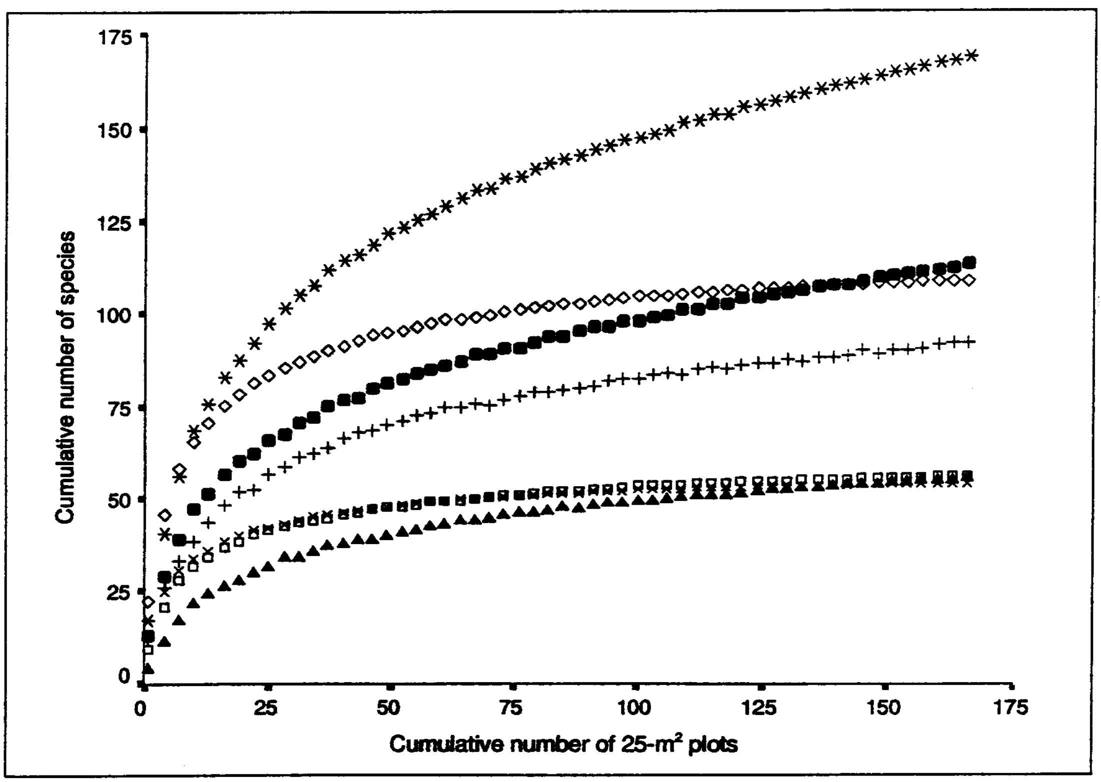

Figure 2. Species accummulation curves for Oregon white oak (Quercus garryana) communities (* = all species, ■ = native species, > = exotic species); prairies (' = all species, ~ = native species, X = exotic species); and managed Douglas-fir (Pseudotsuga menziesii) forests (+ = all species) on Fortr Lewis, Washington, 1992-1999.

Fig. 2). Native and exotic species were equally represented in prairie communities, but exotics were only 18% of the species in Douglas-fir forests.

Understory

We found 171 species (overstory and understory) in the oak communities; 53 (31%) were exotic (Tables 1 and 3). Oak communities contained numerous infrequent species; only 46 (27%) were found on >10% of plots and 103 (60%) were found on <5% of plots. Exotics were 28% of both the 46 most frequent species and the 103 infrequently encountered species. Plot-level species richness (n = 176) averaged 17.2 ± 0.4 (range 6-37) in oak communities and was intermediate between that of prairies (22.4 ± 0.5, n = 168) and that of man aged Douglas-fir forests (11.8 ± 0.3, n = 240). Exotics averaged 23 ± 1 % (range 0-78%) of total species across the 176 plots. Average species richness in oak communities ranged from 11 to 27 species/plot/site (Table 3). The total number of exotic species/site was positively correlated with the total number of species per site (r = 0.66). Plot-level species richness, diversity (H'), percent exotics species, and percent cover of common understory species varied greatly within and among sites (Table 3). Much of the variance encountered across all 176 plots also was contained within each of the 22 sites. Except for common snowberry, understory species were found at low average covers and frequencies; only 10 understory species were found on >50% of the 176 plots. The ten most common understory species included nine native species and one exotic species; all were widespread but variable in distribution (Tables 1, 3).

TABLE 3. Means (± 1 SE) and range of means for understory species richness, percent exotics, diversity, and evenness, and percent cover of 10 common species (found on > 50% of 176 plots) in 22 oak communities on Fort Lewis, Washington, 1999.

Variable	Value[a] Mean ± SE	Range
Species richness	17 ± 1	11-27
Exotics[b] (%)	23 ± 3	4-55
Shannon-Wiener diversity (H')	2 ± 0	1-2
Shannon-Wiener evenness (E)	1 ± 0	1-1
Cover (%)		
Symphoricarpos albus	20 ± 3	2-55
Galium aparine	2 ± 1	0-10
Mahonia aquifolium	2 ± 1	0-17
Rubus ursinus	3 ± 1	0-15
Oemleria cerasiformis	4 ± 1	0-18
Nemophila parviflora	1 ± 0	0-4
Carex inops	4 ± 1	0-20
Polystichum munitum	2 ± 1	0-12
Cytisus scoparius[c]	2 ± 1	0-12
Amelanchier alnifolia	4 ± 1	0-14

[a]Mean and range of 22 site means of 8 plots/site.
[b]Exotic species richness as a percentage of total species richness.
[c]Exotic species are emboldened.

Ordination, Cluster Analysis, Indicator Species

Our ordination (Fig. 3) produced a two-dimensional model that explained 81 % of total variance. Axis 1 explained 47% and Axis 2 explained 34% of the variance in cover of 171 species. Plots within the 22 communities were widely distributed in ordination space (Fig. 3a), except for oak sites 28, 92, and 314. Thus, we evaluated gradients and processes across all 176 plots in 171-species space rather than examining statistics averaged for the 22 communities sampled. In addition to oak and snowberry, only eight species were found on >50% of the plots. However, numerous native and exotic species were correlated with ordination Axes 1 and 2 (Table 4).

Of 18 species correlated with Axis 1 with r > 0.35, 12 were positively correlated; of these, 9 were exotic. The remaining six species were negatively correlated with Axis 1 and were native (Table 4). Weighted averaging of the 46 most frequent species revealed two broad groups of species (Fig. 3b). Of the 16 species that grouped on the right of Axis 1, 11 were exotic. Of 30 species that grouped on the left of Axis 1, only 2 were exotic. Axis 1 was positively correlated with percent exotic species, percent exotic cover, graminoid cover, and oak sapling density. Among native species, the graminoids long-stolon sedge (*Carex inops*) and blue wildrye (*Elymus glaucus*) had the strongest positive correlations (Fig. 3a). The species most negatively correlated with Axis 1 were Saskatoon serviceberry (*Amelanchier alnifolia*), Indian plum, common snowbeny, small enchanter's nightshade (*Circaea alpina*), and western swordfern (*Polystichwn munitum*). Tree species richness, oak height, tall shrub cover, and native shrub richness also were negatively correlated with Axis 1 (Fig. 3a, Table 5). Thus, we interpreted

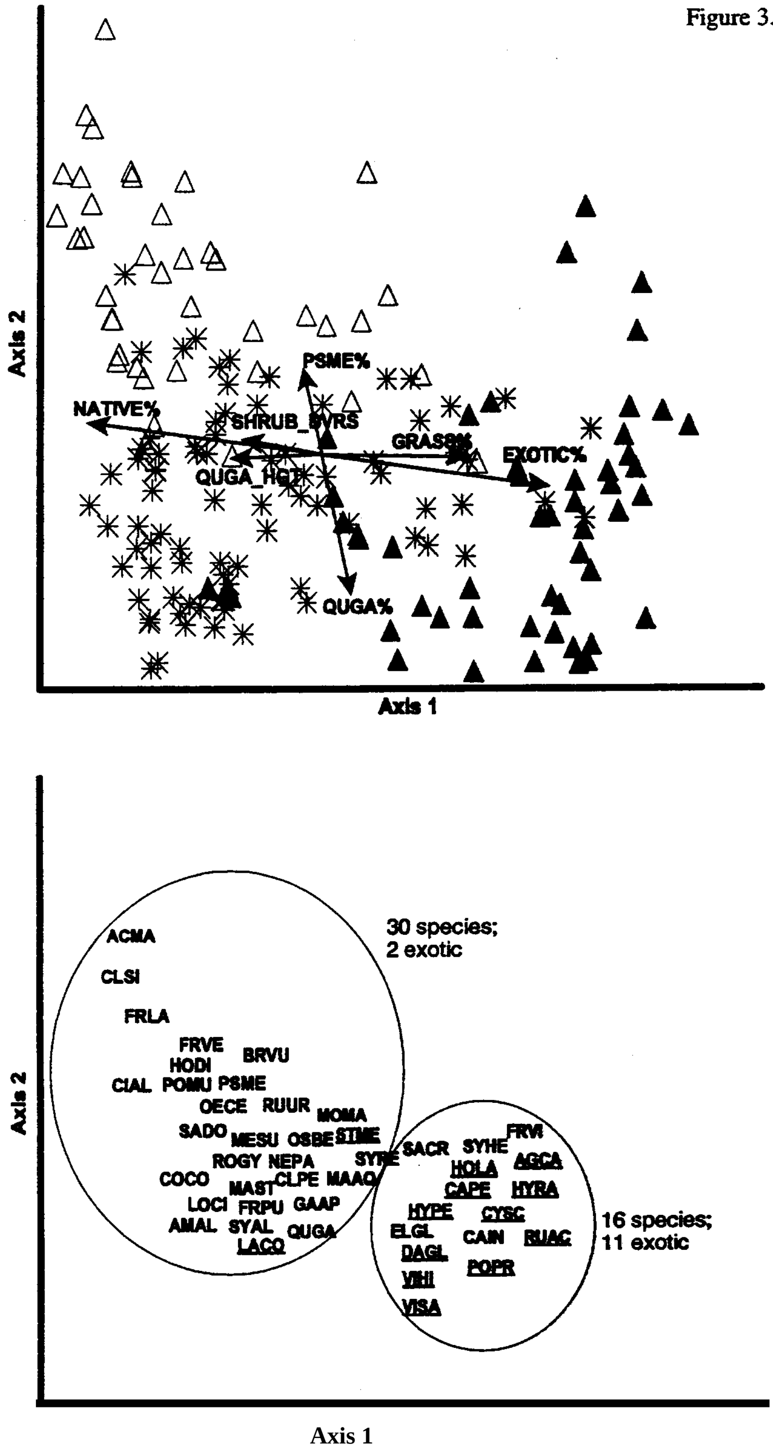

Figure 3. Bray-Curtis ordination of 176 sample plots (a) and weighted averaging of the 46 most common species (b) from 22 large oak communities on Fort Lewis, Washington, 1999. Axis 1 is increasing dominance of exotic species and Axis 2 is dominance changing from Oregon white oak (*Quercus garryana*) to Douglas-fir (*Pseudotsuga menziesii*) and sites grading from dry to mesic. Sample plots are displayed in vegetation site types derived from cluster analysis. Vectors indicate the direction and strength of correlations between axes and the variables: EXOTIC%, exotic richness as % of total richness; GRASS%, % grass cover; NATIVE%, native richness as % of total richness; PSME%, Douglas-fir basal area (BA) as a percentage of total BA;QUGA%, oak BA as a percentage of total BA; QUGA_HGT, height of largest oaks; SHRUB DVRS, richness of native shrubs. Acronyms are plant names (exotic species are underlined): ACMA, *Acer macrophyllum*; AGCA, *Agrostis capillaris*; AMAL, *Amelanchier alnifolia*; BRVU, *Bmmus vulgaris*; CAIN, *Carex inops*; CAPE, *Cardamine pensylvanica*; CIAL, *Circaea alpina*; CLPE, *Claytonia perfoliata*; CLSI, *C. siberica*; *COCO, Corylus cornuta*; *CYSC, Cytisus scoparius*; DAGL, *Dactylis glomerata*; ELGL, *Elymus glaucus*; FRVE, *Fragaria vesca*; FRVI, *F. virginiana*; FRPU, *Frangula purshiana*; FRLA, *Fraxinus latifolia*; GAAP, *Galium aparine*; HODI, *Holodiscus discolor*; HOLA, *Holcus lanatus*; HYPE, *Hypericum perforatum*; HYRA, *Hypochaeris radicata*; LACO, *Lapsana communis*; LOCI, *Lonicera ciliosa*; MAAQ, *Mahonia aquifolium*; MAST, *Maianthemum stellatum*; MESU, *Melica subulata*; MOMA, *Mohringia macrophylla*; NEPA, *Nemophila parviflora*; *OECE, Oemleria cerasiformis*; OSBE, *Osmorhiza berteroi*; *POMU, Polystichum munitum*; POPR, *Poa pratensis;* PSME, *Pseudotsuga menziesii;* QUGA, *Quercus garryana*; ROGY, *Rosa gymnocarpa*; RUAC, *Rumex acetosella*; RUUR, *Rubus ursinus*; SACR, *Sanicula crassicaulis*; SADO, *Satureja douglasii*; STME, *Stellaria media*, SYAL, *Symphoricarpos albus*; SYHE, *Symphoricarpos hesperius*; SYRE, *Syntheris reniformis*: *VIM- Vicia hirsuta*: VISA. *V. sativa.*

Axis 1 as a gradient of increasing dominance of exotic species, with Scot's broom, sod-forming colonial bentgrass and Kentucky bluegrass (Poa *pratensis*), common St. John's-wort (*Hypericum perforatum*), and common sheep sorrel (*Rumex acetosella*) most positively correlated (Tables 4, 5).

Axis 2 was a bipolar gradient representing shifts in dominance from oak to Douglas-fir and from dry to mesic sites (Fig. 3a, Tables 4, 5). All nine species correlating with Axis 2 with $r > |0.35|$ were native. Seven were associated with wet to mesic forest-Oregon ash, bigleaf maple, Siberian

TABLE 4. Correlation coefficients between plant species and Bray-Curtis ordination axes, and their indicator values for three vegetation site types found in 22 oak sites on Fort Lewis, Washington, 1999. Species shown have $r > 0.35$, indicator values ≥20, or frequencies ≥20% ($n = 176$ plots).

	r		Indicator Value for Site Types			
Species[b]	Axis 1	Axis 2	type 1 ($n = 84$)	type 2($n = 40$)	type 3($n = 52$)	*P*[a]
Acer macrophyllum	-0.24	0.42	0	26	0	<0.01
Agrostis capillaris	0.61	0.07	6	0	48	<0.01
Amelanchier alnifolia	-0.41	-0.16	41	12	1	<0.01
Bromus vulgaris	-0.20	0.26	5	24	2	<0.01
Cardamine pensylvanica	0.36	-0.01	2	2	21	<0.01
Carex inops	0.68	-0.22	8	4	61	<0.01
Circaea alpina	-0.42	0.31	6	6	34	<0.01
Claytonia siberica	-0.31	0.43	1	32	0	<0.01
Corylus cornuta	-0.21	0.04	6	12	13	0.49
Cytisus scoparius	0.62	-0.12	10	4	46	<0.01
Elymus glaucus	0.45	-0.17	5	3	36	<0.01
Fraxinus latifolia	-0.31	0.37	3	23	0	<0.01
Galium aparine	-0.06	-0.09	36	34	19	0.11
Geranium columbinum	0.32	-0.19	0	0	22	<0.01
Holcus lanatus	0.35	0.02	4	0	19	<0.01
Hypericum perforatum	0.61	-0.02	10	5	38	<0.01
Lapsana communis	-0.07	-0.12	23	3	1	<0.01
Leucanthemum vulgare	0.36	0.08	0	0	24	<0.01
Lonicera ciliosa	-0.30	-0.09	27	12	2	<0.01
Mahonia aquifolium	0.09	0.02	15	24	26	0.48
Melica subulata	-0.17	0.12	7	21	1	<0.01
Nemophila parviflora	-0.20	0.05	32	24	6	<0.01
Oemleria cerasiformis	-0.39	0.36	18	51	4	<0.01
Osmorhiza berteroi	-0.10	0.09	6	7	19	0.02
Poa pratensis	0.41	-0.24	2	0	30	<0.01
Polystichum munitum	-0.40	0.36	19	48	1	<0.01
Pseudotsuga menziesii	-0.37	0.54	16	60	1	<0.01
Quercus garryana	0.03	-0.74	41	18	38	<0.01
Rubus ursinus	-0.17	0.24	24	34	9	<0.01
Rumex acetosella	0.42	-0.08	1	1	20	<0.01
Symphoricarpos albus	-0.40	-0.41	41	31	17	<0.01
Teesdalia nudicaulis	0.36	0.06	0	0	16	<0.01
Tellima grandiflora	-0.31	0.43	0	29	0	<0.01
Vicia hirsuta	0.23	-0.28	4	0	27	<0.01
Vicia sativa	0.36	0.06	0	0	16	<0.01

[a]*P*-values based on Monte-Carlo simulations (McCune and Mefford 1999).
[b]Exotic species are emboldened.

springbeauty (*Claytonia sibirica*), Indian plum, western swordfem, Douglas-fir, and bigflower tellima (*Tellima grandiflora*) (Klinka et al. 1989, Pojar and MacKinnon 1994)—and were positively correlated with Axis 2. Axis 2 was positively correlated with native shrub richness, tree richness, percent basal area that was Douglas-fir, basal area of bigleaf maple and Oregon ash, and density of Douglas-fir ≥ 30 cm dbh. Only Oregon white oak and common snowberry were negatively correlated with Axis 2. Percent basal area that was oak and density of oaks ≥10 cm dbh were negatively correlated with Axis 2 (Table 5). The species most highly correlated with Axis 2 were Douglas-fir ($r = 0.54$) and Oregon white oak ($r = -0.74$).

Cluster analysis produced three groups of plots representing three vegetation site types that made up the oak communities (Fig. 3a). The eight plots sampled in each of the 22 oak communities were widely variable as to site-type membership and on average occurred in 2.4 vegetation site types.

TABLE 5. Correlation coefficients between selected variables and Bray-Curtis species ordination axes for 22 oak communities on Fort Lewis, Washington, 1999.

	r	
Variable	Axis 1	Axis 2
Total understory cover	-0.09	-0.15
Percent exotic cover	0.46	-0.05
Percent graminoid cover	0.70	-0.15
Percent tall shrub cover	-0.52	0.16
Total species richness	0.15	0.25
Percent exotic species	0.82	-0.29
Native shrub richness	-0.49	0.52
Tree species richness	-0.54	0.53
Shannon-Wiener diversity (H=)	0.05	0.37
Shannon-Wiener evenness (E)	-0.08	0.35
Total basal area (BA, m^2/ha)	-0.43	0.13
Quercus garryana BA	-0.20	-0.34
Pseudotsuga menziesii BA	-0.32	0.40
Fraxinus latifolia BA	-0.24	0.38
*Acer macrophyllum*BA	-0.25	0.37
Density of live oaks >1 0 cm dbh	-0.12	-0.43
Q. garryana sapling density	0.37	-0.04
Q. garryana seedling density	0.24	-0.16
Density of dead *Q. garryana* >10 cm dbh	-0.30	0.03
Density of *P. menziesii* >30 cm dbh	-0.33	0.37
Height of tallest *Q. garryana*	-0.52	-0.10

Indicator species analysis revealed that each site type had characteristic species (Table 4), while a number of species, notably beaked hazelnut (*Corylus cornuta*), stickywilly (*Galium aparine*), and hollyleaved barberry [tall oregongrape] (*Mahonia aquifolium*), were common to all three vegetation site types. Site type 1 contained 48% of plots, and was characterized by oak in the overstory and the native shrubs servicebeny and snowberry in the understory. The native vines, orange honeysuckle (*Lonicera ciliosa*) and California blackberry (*Rubus ursinus*), were also common in this site type. The native herbs stickywilly and smallflower nemophila (*Nemophila parviflora*) were common in site type 1 but did not distinguish this group from other groups. Except for common nipplewort (*Lapsana communis*), exotic species were rare in site type 1 (Fig. 3a,b; Table 4, 5). Thus we labeled site type 1 the white oak/native shrub group.

The three species characteristic of site type 2 were Douglas-fir, Indian plum, and western swordfern, with the moist-site herbs small enchanter's nightshade, Siberian springbeauty, and bigflower tellima (Klinka et al. 1989, Pojar and MacKinnon 1994) also common; site type 2 contained 23% of the plots. Site type 2 had the lowest density and basal area of oaks, the lowest frequency and abundance of exotic species, the highest tree species richness (and the largest non-oak hardwood component), and the highest Shannon Wiener diversity (H') and evenness (E) of the three site types (Fig. 3a,b; Tables 4, 5). We labeled site type 2 the Douglas-fir-oak/moist herb site type.

Site type 3, with oak as its overstory indicator species, contained 29% of plots. Its understory was characterized by native graminoids (long-stolon sedge and blue wildrye) and by exotics (colonial bentgrass, Scot's broom, and St. John'swort). Other exotics such as long-stalk cranesbill (*Geranium columbinum*), common velvet-grass (*Holcus lanatus*), oxeye daisy (*Leucanthemum vulgare*), Kentucky bluegrass, common sheep sorrel, barestem teesdalia (*Teesdalia nudicaulis*), and vetches (*Vicia hirsuta,* and *V. sativa*) also were characteristic of site type 3 and virtually absent from the other site types. Diversity (H') and evenness (E) were less in site type 3 than in other site types and, in sharp contrast to site types 1 and 2, exotic species were a substantial portion of total species richness. Oak seedlings and saplings were more abundant in site type 3 than in site types 1 and 2 (Fig. 3a,b; Tables 4, 5). We labeled site type 3 as the pioneer oak/grassland-exotic site type.

Discussion

Status of Oak Communities

Oak sites cover <4% of Fort Lewis (Ryan and Carey 1995*a,b*); few are >5 ha and many contain few oaks. Most are ecotones with sharper gradients and greater influences from adjacent communities than in the 22 large sites we describe. Early in the 20th century, Rigg (1918) described the oaks of Fort Lewis as forming a "fringe around the edge of the prairie, next to the forest. The forest is evidently advancing slowly upon the prairies." Eighty years later, our assessment is similar, but human dominance of the landscape has resulted in establishment of exotics and advancement of Douglas-fir into woodlands and prairies and, off Fort Lewis, a continuing loss of woodlands, e.g., >25% from 1982-1992 (McGinnis et al. 1997).

The status of the oak communities is still primarily a result of human activities: fire exclusion, introduction and spread of exotic species, military activities, and conservation activities. Disturbances affectting Fort Lewis woodlands and prairies are dominated by military activity and conservation efforts. Tveten and Fonda (1999) described one fire policy on Fort Lewis: 80% of the area under fire exclusion, 8% under annual, artillery induced, fire, and 8% under a 3—°5-year rotation of low intensity prescribed bums. But various efforts employ diverse techniques to address different conservation objectives on (and off) Fort Lewis (Dunn and Ewing 1997 provide a partial compendium). Goals include reduction of Scot's broom, maintenance of the structural appearance of oak, pine, and prairie communities, restoration of the historical variety of oak, pine, or prairie communities, and maintenance of viable populations of various sensitive species of plants, invertebrates, and vertebrates.

Condition of Oak Communities

Although the large oak communities were influenced by adjacent communities, most remained structurally and compositionally dominated by oaks; most seedlings and saplings were oaks as well. Most sites averaged >200 oak trees/ha within the ranges of sizes, densities, and basal areas reported as normal by Stein (1990). Large oaks were rare-most oaks were <30 cm dbh and <20 m tall. Clusters of oaks, such as develop from cut stumps or root collars (Stein 1990), were common, but we saw almost no direct evidence of felling. Abundant small, clustered stems suggests that current oak densities may be higher, and average oak size smaller, than in the past (Stein 1990) and that natural, accidental, and prescribed fires had not been frequent enough to prohibit oak regeneration. Small oaks, while providing options for future management, are more susceptible to fire than large oaks (Stein 1990, Agee 1996, Tveten and Fonda 1999). Dense small oaks, small Douglas-firs, and Scot's broom in understories of oak communities create conditions whereby fire can be more damaging to mature oaks than where mature oaks are large and widely separated with grassy understories. In the former, understory, especially mature stands of Scot's broom, provides fuel for intense, high severity fire (Tveten and Fonda 1999) and a ladder to the crowns of mature oaks, whereas in the latter grasses support only a mild fire confined to the vicinity of oak trunks. Consequently, we observed fire-killed mature oaks, Douglas-firs, and ponderosa pines in some oak sites. Repeated burning on Fort Lewis has reduced fuel loads on some sites and low intensity fires have been shown not to affect mature oaks (Teveten and Fonda 1999). Fire mortality was not common among large Oregon white oaks; suppression by Douglas-fir was more common.

Ecological Uniqueness of Oak Communities

The ecological uniqueness of oak communities rests on the physical, architectural presence of Oregon white oak itself, its role in providing habitat for the threatened western gray squirrel (Ryan and Carey 1995*b*), and the contribution of the communities as elements of the PSA mosaic ecosystem—an ecosystem whose properties (e.g., species diversity) are greater than the sum of the unique characteristics of each component system. Few, if any, vascular plant species were found to be obligate associates of oaks. We did not study nonvascular plants or fungi, however. Nonetheless, oak communities had high plant species richness compared to similar areas of prairies or Douglas-fir forests, reflecting the transitional nature of the oak communities. Most species were "rare" species, in the tail of the rank-abundance curve. Only one, however, was "everywhere sparse" (Murray et al. 1999) and afforded special protective status in Washington (Washington Natural Heritage Program 1997)—the smallflower wakerobin. Other rare species were species more common in prairies, Douglas-fir forests, mixed hardwood forests, or wetlands (Thomas and Carey 1996; Carey et al. 1999*c*; Thysell and Carey 2000).

Oak communities used by the western gray squirrel on Fort Lewis were >2 ha, <0.6 km from water and had a mixture of tree species, including co-dominance by Douglas-fir, and a diversity of mast-producing native trees and shrubs Ryan and Carey (1995*a*,*b*). Western gray squirrels were negatively affected by fragmentation of oak communities. Thus, full function of oak communities in the greater ecosystem depends, in part, on their size, contiguity, and ecological context. The extant oak communities on Fort Lewis are small in size, relatively high in number, but widely dispersed (Ryan and Carey 1995*a*,*b*).

Conceptual Model and Oak Trends

Puget Sound oak communities were more extensive a few hundred years ago than today and occurred under a broader range of conditions than they do now (Stein 1990, Kruckeberg 1991, Ryan and Carey 1995*b*, Tveten and Fonda 1999). Thus, we constructed a conceptual model that incorporates a narrowing of the breadth of habitat conditions occupied by oak communities (Fig. 4). Present oak communities are physically narrower, more disjointed, and more influenced by Douglas-fir than in the past, a phenomenon apparent throughout the range of Oregon white oak (Thilenius 1968; Reed and Sugihara 1987; Barnhart et al. 1987, 1996; Stein 1990; Tveten and Fonda 1999). Consequently, the contribution of oaks to landscape and biological diversity in the PSA has diminished substantively. On Fort Lewis, oak communities are commonly bounded on one side by glacial outwash prairies—a major floristic influence that is increasingly dominated by exotic species (Clampitt 1993, Thomas and Carey 1996) and that was evident in our pioneer oak/grassland exotic vegetation type. Thus, one of the two chief influences on oak communities in our model (Fig. 4) is the prairie/exotic influence.

The other community exerting strong influence on oaks is Douglas-fir lowland forest. In the absence of fire and during years of above-average rainfall, Douglas-firs readily establish on prairies and among oaks. Rapid height and diameter growth of Douglas-firs can quickly transform prairie or oak sites into homogeneous fir forests (Leighton 1918; Reed and Sugihara 1987; Barnhardt et al. 1987, 1996). Our results also show this process

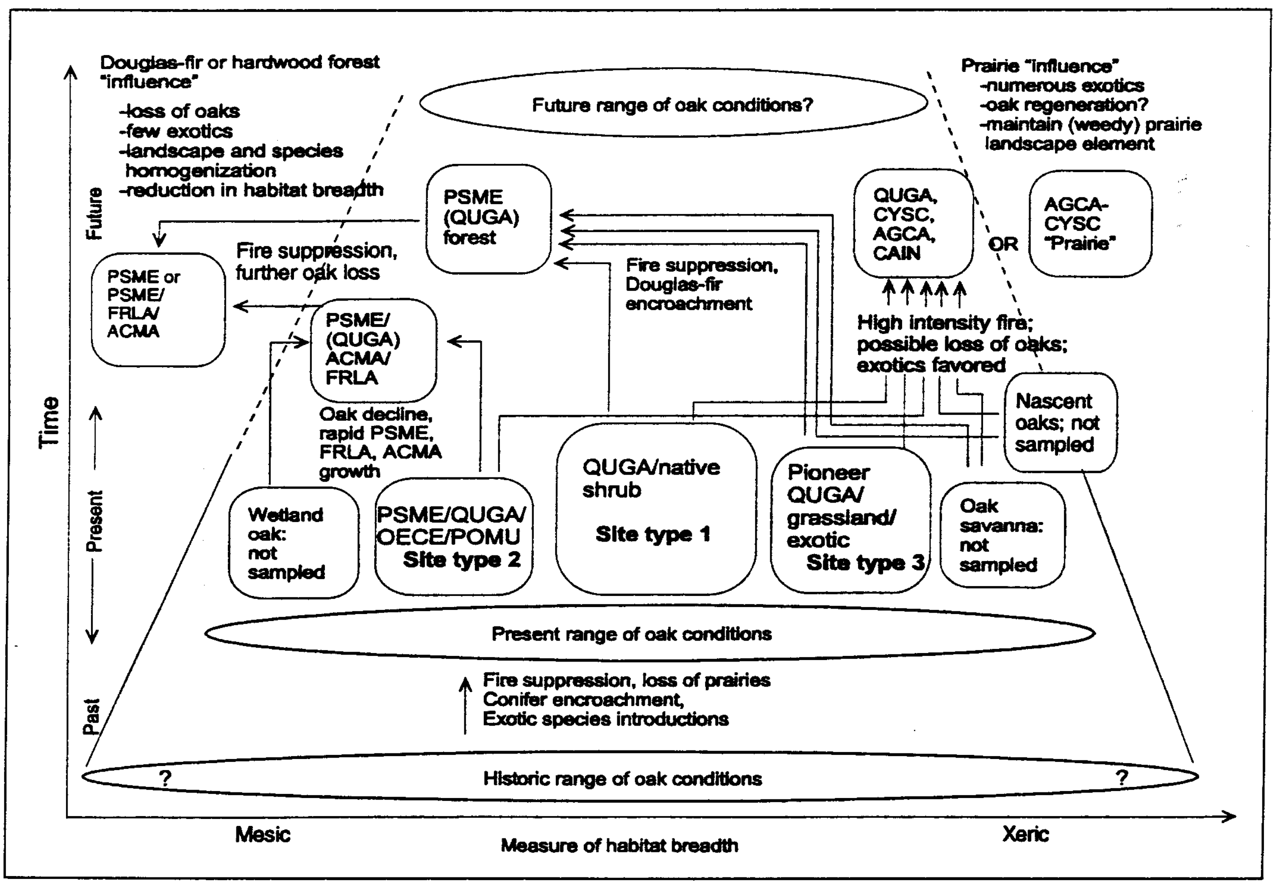

Figure 4. Conceptual model of Oregon white oak (*Quercus garryana*) community development on Fort Lewis, Washington. Gray boxes indicate non-oak communities. Site types 1, 2, and 3 refer vegetation site types that compose oak communities: oak/native shrub group, Douglas-fir-oak/moist herb group, and pioneer oak/grassland-exotic group. Acronyms are; ACMA = *Acer macrophylllum*; AGCA = *Agrostis capillaris*; AMAL = *Amelanchier alnifolia*; CAIN = *Carex inops*; CYSC = *Cytisus scoparius*; FRLA = *Fraxinus latifolia*; OECE = *Oemleria cerasiformis*; POMU = *Polystichum munitum*; *PSME* = *Pseudotsuga menziesii*; QUGA = *Quercus garryana*; SYAL = *Symphoricarpos albus*. Minor species are indicated by parentheses.

is ongoing in most large oak communities; we do not believe that any PSA oak site is immune from succession to Douglas-fir or Douglas-fir/ash/maple forest. Thus, the other major influence in our model is rapid succession to Douglas-fir or Douglas-fir/mixed hardwood forests with fire exclusion.

The model incorporates our three vegetation site types (Figs. 3, 4) to suggest possible trends in future oak development. Although the types resemble community types (Thilenius 1968), they are not discrete communities. Rather, they represent responses of vegetation to environmental gradients and compose fine-grained mosaics within oak communities. Nearly 50% of plots were in the oak/native shrub type. This type is the least influenced by nearby plant communities and may be the most indicative of interior oak-dominated forests (and western gray squirrel habitat). Because these plots often contained Douglas-fir or were in close proximity to areas that did, this type will continue to convert to a Douglas-fir type in the absence of disturbance. The oak/native shrub type contained few exotic species.

The Douglas-fir-oak/moist herb type is in the process of conversion to Douglas-fir or Douglas-fir/ash/maple forest. Plots within this group contained large, rapidly growing Douglas-firs in close proximity to mature oaks. These Douglas-fir can rapidly overtop the slower-growing oaks. Although oaks are long-lived, they are shade-intolerant and decline rapidly when overtopped by Douglas-fir. Here, we often found oaks with small live crowns at the end of long, arcuate stems. We often encountered Douglas-fir, Oregon ash, and bigleaf maple seedlings and saplings but rarely oak regeneration. This vegetation type contained few exotic species.

The pioneer oak/grassland-exotic type represents areas that are most influenced by glacial-outwash prairies. This type has abundant and diverse exotic species, often dominated by sod-forming grasses and Scot's broom. Prior to introduction of Scot's broom and colonial bentgrass, frequent fires in grassy understories and at prairie-oak margins would have been patchy and of low intensity, but sufficient to kill invading Douglas-fir. In contrast, exotic understory species, especially Scot's broom, now have the potential to fuel higher intensity, more severe fires that could kill even mature oaks (Tveten and Fonda 1999, this study). Although less frequent than in the other two oak types, Douglas-fir was here also, suggesting that, with exclusion of fire, succession to Douglas-fir forests could occur here as well (Fig. 4).

Management Implications

Without appropriate managerial intervention, encroachment by Douglas-fir and other invasive species will continue and development of classical oak communities in the future is unlikely. Among the ever-increasing number of invasive plant species in the Pacific Northwest, Scot's broom and colonial bentgrass (Hitchcock and Cronquist 1973, Toney et al. 1998, Ussery and Krannitz 1998, Tveten and Fonda 1999, this study) present the greatest threat to oak communities by altering regeneration niches (Grubb 1977), promoting acorn decay and altering litter decomposition (Jackson et al. 1998), altering soil moisture, precluding oak seedling establishment (Danielson and Halvorson 1990), and increasing fire intensity and frequency (D'Antonio and Vitousek 1992, Agee 1996). Such complex relationships suggest that both a comprehensive set of conservation objectives and comprehensive assessment of techniques for promoting indigenous species, including oaks, and controlling individual exotic species is needed. For example, exclusion of fire, without other managerial intervention, leads to succession to a Douglas-fir community. On oak-prairie margins, fire used to control Scot's broom can pose risks to oaks unless it is used frequently enough to prevent excessive accretion of fuel. If fire is too frequent, however, exotic species may be favored over native species (Tveten and Fonda 1999). The frequency, intensity, and season of burning to control exotic species must be carefully chosen to avoid damaging native species and mechanical destruction of Scot's broom and Douglas-fir before burning will reduce the potential for negative effects on oaks (Tveten and Fonda 1999).

Currently management is not effectively addressing issues of decreasing land area available for natural communities, maintenance of landscape processes such as dispersal and colonization by western gray squirrels, landscape dynamics, or values attributable to the PSA mosaic *per se.* Such issues transcend any one management group. Landscape processes came to the fore in attempts to formulate management recommendations for the western gray squirrel, whose population viability may depend upon an interconnected network of low-density local populations that form a resilient metapopulation (Ryan and Carey 1995*a*,*b*). Ryan and Carey (1995*a*,*b*) recommended both community and landscape management.

Maintaining oaks as part of a dynamic landscape requires management of contemporary processes that are reducing the area of oak communities. Our model gives insight into some of these processes. But the model is inadequate to describe how either individual oak communities or a greater PSA system might behave under comprehensive landscape management. A more sophisticated model is needed to suggest hypotheses that could be tested in management experiments. This model would be necessarily complex and incorporate various submodels, perhaps like the qualitative model of fire and vegetation interaction presented by Myers (1985). Judicious use of fire is an important tool for sustaining values associated with Oregon white oak woodlands (Reed and Sugihara 1987, Ryan and Carey 1995*b,* Agee 1996, Tveten and Fonda 1999). Fire holds promise for reducing Scot's broom and preventing invasion of Douglas-fir. Douglas-fir, however, and various deciduous trees are important members of certain types of oak communities. If simple maintenance of oaks is the conservation goal, one could remove all other trees. If maintenance of either the oak-fir ecotonal community with its threatened flagship species, the western gray squirrel, or the landscape mosaic of oak woodlands, wetlands, prairies, and conifer forests with the attendant myriad of species is the conservation goal, then a balance of oaks, Douglas-fir, and various hardwood species must be maintained (Ryan and Carey 1995*a*,*b*). Not only could some existing communities be rehabilitated, but areas of especially desirable communities could be expanded and areas of undesirable communities could be decreased to help maintain a functional mosaic (Carey et al. 1999*b*), e.g., expanding oak communities in conjunction with prairie restoration or where small oaks have survived around kettle depressions at the expense of the excessively abundant mature Douglas-fir communities and the undesirable Scot's broom communities. The creation, improvement, and expansion of oak communities will require long-term adaptive management.

Acknowledgments

This research was funded by the Environmental and Natural Resources Division, Department of Army, Fort Lewis, and the Pacific Northwest Research Station, U.S. Department of Agriculture Forest Service. We thank Fort Lewis Military Reservation for assistance in selection and identification of the study sites. We thank personnel of the Environmental and Natural Resources Division, and members of the Ecological Foundations of Biodiversity Team of the Pacific Northwest Research Station for invaluable assistance during the study. We particularly thank Stacey Brewster for her assistance in the field. We thank Jim Agee, Allan Branscomb, Rich Fonda, David Ford, Jeff Foster, Betsy Kirkpatrick, and Ted Thomas for their valuable review comments on earlier drafts of the manuscript.

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Received 11 September 2000
Accepted for publication 27 March 2001