United States
Department of
Agriculture

Forest Service

Pacific Northwest
Research Station

Research Paper
PNW-RP-527
September 2000

Modification of Mixed-Conifer Forests by Ruminant Herbivores in the Blue Mountains Ecological Province

Robert. A. Riggs, Arthur R. Tiedemann, John G. Cook,
Teena M. Ballard, Paul J. Edgerton, Martin Vavra,
William C. Krueger, Frederick C. Hall, Larry D. Bryant,
Larry L. Irwin, and Timothy Delcurto

Authors

Robert A. Riggs, wildlife and range scientist, Boise Cascade Corporation, Timber and Wood Products Division, 1917 Jackson, La Grande, OR 97850

Arthur R. Tiedemann, scientist emeritus, USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850

John G. Cook, research biologist, National Council of the Paper Industry for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850

Teena M. Ballard, technician, and **Timothy Delcurto**, assistant superintendent, Eastern Oregon Agricultural Research Center, P.O. Box E, Union, OR 97883

Paul J. Edgerton, ecologist (retired, USDA Forest Service), Friday Harbor, WA 98250

Martin Vavra, Starkey team leader, USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, and superintendent, Eastern Oregon Agricultural Research Center, HC 71, 4.51 Hwy. 205, Burns, OR 97720

William C. Krueger, department head, Rangeland Resources, Oregon State University, Corvallis, OR 97331-6704

Frederick C. Hall, senior plant ecologist, USDA Forest Service, Pacific Northwest Region, P.O. Box 3623, Portland, OR 97208-3623

Larry D. Bryant, national range ecologist, USDA Forest Service, 14th and Independence Ave. SW, Washington, DC 20250

Larry L. Irwin, wildlife program manager, National Council of the Paper Industry for Air and Stream Improvement, P.O. Box 68, Stevensville, MT 59870

Cover Photo: Conducting a grazing trial with tractable elk in the Blue Mountains of northeastern Oregon. Photo by Art Tiedemann.

Abstract

Riggs, Robert. A.; Tiedemann, Arthur R.; Cook, John G.; Ballard, Teena M.; Edgerton, Paul J.; Vavra, Martin; Krueger, William C.; Hall, Frederick C.; Bryant, Larry D.; Irwin, Larry L.; and Delcurto, Timothy. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. Res. Pap. PNW-RP-527. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 77 p.

Secondary plant succession and the accumulation of biomass and nutrients were documented at seven ruminant exclosures in *Abies* and *Pseudotsuga* forests variously disturbed by logging, burning, and grass seeding. Long-term (25 or more years) foraging by Rocky Mountain mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) suppressed the development of deciduous shrubs. Ruminant herbivores influenced vegetation to extents equal to those of the initial episodic disturbances. Food preferences of elk were linearly correlated with long-term development of plant taxa. Accumulations of understory and forest floor biomasses were greater inside exclosures than outside. Accumulations of nitrogen, phosphorus, calcium, magnesium, and potassium were greater inside exclosures than outside.

Keywords: *Abies*, biomass, *Bos*, *Cervus*, cycling, disturbance, ecosystem, fire, forest, herbivory, logging, nutrients, *Odocoileus*, *Ovis*, productivity, *Pseudotsuga*, seeding, shrubs, site, succession, understory.

Summary

Forest managers are routinely concerned with the effects of ruminant herbivores on forest vegetation and with the effects of episodic disturbance agents, such as fire and logging. Nonetheless, influences of episodic agents and herbivores on forest vegetation seldom have been evaluated in common temporal and spatial contexts. To better understand the implications of disturbance-agent interactions, we retrospectively studied succession and nutrient accumulation on seven upland mixed-conifer sites in the Blue Mountains of northeastern Oregon. These sites first were partitioned by different episodic disturbances (logging, fire, seeding) and then by herbivory regime in the 1960s. Sequential data were available to compare influences of herbivory regimes on the successions begun by the episodic agents.

Experimental herbivory regimes did not seem to influence richness, diversity, or evenness of forest understory communities, as reflected in frequency-based indices. Evenness was consistently low, however, throughout the experiments at three sites sharing a common history of heavy grazing by domestic sheep prior to the experiments. Areas accessible to wild herbivores exhibited suppressed shrub strata. Over time, livestock and wild-ruminant influences on development of plant canopy cover were typically as great as the influences of the initial episodic disturbances.

We observed highly significant correlations ($P \leq 0.002$) between dietary selections of elk (*Cervus elaphus*) and development of canopy cover among individual plant taxa. Modeled utilization rates for the various taxa indicated that several were predisposed to suppression by elk, even under rather light herbivory regimes. The reason seemed to be their low abundance relative to other plant species immediately after episodic disturbance coupled with relatively high palatability to elk. The majority of these taxa were shrubs, including some climax "indicator species" (e.g., *Acer glabrum*, *Taxus brevifolia*, and *Linnaea borealis*), early-seral structural dominants (*Acer glabrum*, *Amelanchier alnifolia*, *Salix* spp., and *Sorbus sitchensis*), and taxa that can replenish nitrogen pools after depletion by episodic fire (*Astragalus canadensis*, and *Ceanothus* spp. [*C. sanguineus*, *C. velutinus*]).

Total understory and forest-floor biomasses averaged 2.1 and 1.5 times greater inside the exclosures than outside at the end of study (27 to 30 years). Amounts of total and exchangeable calcium in the forest floor were greater inside exclosures than outside (18 and 11 percent, respectively). Amounts of total and exchangeable magnesium in the forest floor were greater inside the exclosures than outside (20 and 16 percent, respectively). The concentration of total nitrogen in the forest floor was 26 percent higher inside than outside, but mineral nitrogen did not differ significantly. Nutrient differences were observed in forest floor but not in soil.

Herbivores appeared to influence secondary succession in these forests principally through their selective suppression of preferred food plants. Consequences of this suppression may include (1) confounding seral and climax vegetations used in forest planning, (2) suppressing fauna linked to understory shrubs, and (3) suppressing forest site productivity by reducing nitrogen accretion after episodic fire.

Contents

Introduction

Ruminant herbivores are products of ecosystem management, but they also are protagonists that regulate ecosystem processes and attributes. Ruminants tend to feed selectively, which can alter the composition of plant communities by suppressing some plant species and thereby conveying competitive advantage to other plants that are not selected. Ruminants also regulate ecosystem processes by modifying the cycling and availability of nutrients crucial to plant growth (Frank and Evans 1997, McNaughton 1976, Pastor and Naiman 1992). They do this as they process the selected foods through their digestive tracts (Hobbs 1996), which accelerates the rate whereby nutrients bound in those foods are made available to decomposers at the forest floor (Pastor and Naiman 1992). Their dung and urine contribute directly to the pool of nitrogen (N) that is immediately available for plant growth (Frank et al. 1994, McNaughton 1992, Pastor et al. 1993, Ruess and McNaughton 1987) and decrease the carbon (C)-to-N ratio at the forest floor, thereby increasing litter decomposition by microbes and increasing N-mineralization (Pastor et al. 1993, Ruess 1987, Seagle et al. 1992). As a result, the flow of nutrients through the system is accelerated and the production of some plants can be enhanced. Selective feeding and nutrient processing and the response adaptations of plants are fundamental to the hypothesis of "herbivore optimization" (e.g., Dyer et al. 1993, Hilbert et al. 1981, Holland et al. 1992, McNaughton 1979, Williamson et al. 1989), which holds that herbivores can enhance their own food resources.

In forests, ruminants can influence tree growth and wood production (e.g., Gill 1992a, 1992b; Pastor et al. 1993; Weigand et al. 1993), reduce carrying capacity for their own populations (e.g., Irwin et al. 1994, McCullough 1979), and influence abundance of other fauna (e.g., Bowers 1997, deCalesta 1994, McShea and Rappole 1997). Ruminants influence succession, stability, and productivity of aspen (*Populus tremuloides*) communities (Bartos et al. 1994; Kay 1995, 1997; Kay and Chadde 1992), and they can alter production of shrubs in subarctic tree-line communities (Molvar et al. 1993). In boreal forests, their suppression of deciduous plants can hasten domination of sites by conifers and reduce forest productivity over time (Pastor and Cohen 1997, Pastor and Naiman 1992, Pastor et al. 1993).

Ruminant herbivory thus has been hypothesized to have both positive and negative influences. Which type of influence predominates likely depends on various factors, including the herbivore regime (i.e., type, density, season), climate, geophysical characteristics of the site, and plant composition and adaptations to herbivory. The effects of herbivory can be obscure where other disturbance agents are present as well. Where interactions occur between disturbance agents, the influence of one agent on the ecosystem is contingent on the regime of the other(s). Contingencies involving herbivores and fire have been described for grasslands (Hobbs et al. 1991) and aspen forests (Bartos et al. 1994), and probably are common across a broad range of environments.

In managed forests, herbivores can interact with several other disturbance agents. In *Abies* and *Pseudotsuga* forests, for example, the direction and rate of plant succession is predisposed by site conditions, past disturbance, and the reproductive strategies of individual plant species (i.e., seed banks, sprouting rootstocks).

Secondary succession is begun by episodic agents (e.g., silviculture, fire) and is initially determined by attributes of each episodic agent's regime, such as its frequency of occurrence, intensity, and size (Heinselman 1978, 1981; Kilgore 1981; Schimmel and Granstrom 1996; Turner et al. 1997). Subsequent episodic disturbances and herbivory regimes can, however, modify the succession of seral plant communities. The combination of disturbance agents and their sequence of occurrence thus is important to the development of seral vegetation. Nonetheless, only rarely have disturbance-agent interactions been explored in managed forests, where several disturbance agents typically are operative.

Exclosures have been used in various ecological settings to describe the influences of herbivory on vegetation. The influences observed in such experiments typically are interpreted, however, without respect to their potential link to episodic disturbances. Conversely, research concerned with influences of episodic agents typically is interpreted without respect for the potential modification by herbivory regime. Exclosure experiments nevertheless can provide insight to disturbance-agent interactions if they incorporate a range of disturbance regimes; moreover, they often provide the only means of exploring such effects with any experimental control.

We explored some influences of ruminant herbivory at seven long-standing exclosures on upland mixed-conifer sites in the Blue Mountains of northeastern Oregon. These exclosures comprise the entire set of extant exclosures in the Blue Mountains for which long-term data sets exist. The sites were subjected initially to different combinations of logging, fire, and grass seeding, and then were further partitioned with herbivore exclosures. Plant composition was recorded at the outset of each experiment and then monitored intermittently for 27 to 30 years. We analyzed these data for trends in some commonly used community indices and for evidence of disturbance-agent interactions on plant taxa by using analysis of variance (ANOVA) pro-cedures. We also modeled relations between dietary preferences of elk, a dominant herbivore in this ecological province, and the development of plant taxa over time. To these analyses, we added a comparison of nutrient profiles for forest floor and soil at the end of the experiments. This paper ends in a discussion of how herbivory is relevant to current management issues, including the use of classification schemes in forest planning, managing transitory wildlife habitat, and maintaining site productivity in disturbance-adapted forests.

Study Sites

Climate and Potential Vegetation

We studied seven exclosures in three localities (fig. 1) in the Blue Mountain ecological province (Franklin and Dyrness 1973): Mottet (one exclosure), Hoodoo (three exclosures), and Hall Ranch (three exclosures). Mottet and Hoodoo are in the Blue Mountains on lands administered by the Umatilla National Forest. At High Ridge Barometer Watershed (the nearest climatological station), annual precipitation averages 142 cm with 87 percent deposited in winter, and temperature ranges from -10 to 30 °C (Fowler et al. 1979). The Hall Ranch is in the Wallowa Mountains on lands administered by the Oregon Agricultural Experiment Station, Eastern Oregon Agricultural Research Center. Annual precipitation averages 66 cm with about 60 percent deposited in winter, and temperature ranges from -18 to 38 °C. Other characteristics of these sites are summarized in table 1.

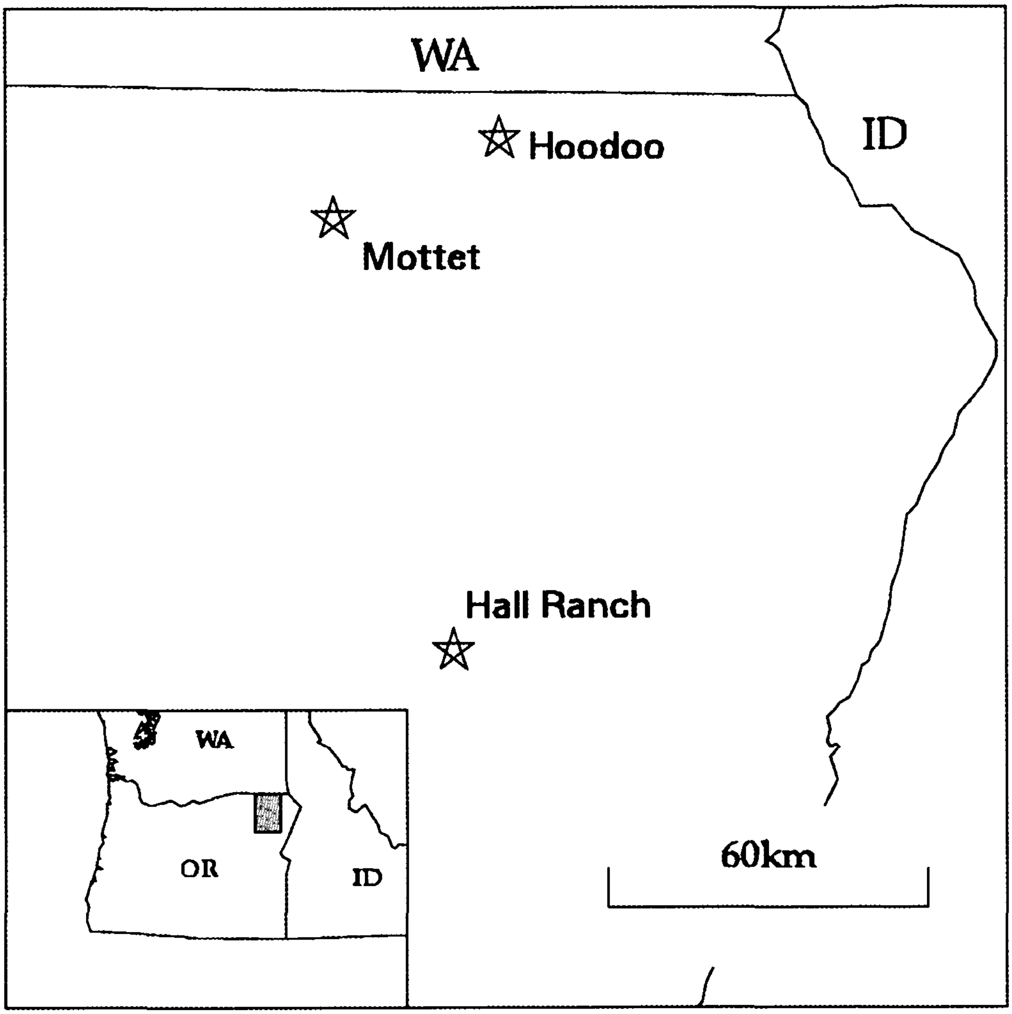

Figure 1—Geographic location of study sites in northeastern Oregon, USA. One exclosure was located at Mottet, three at Hoodoo, and three at the Hall Ranch.

Climax vegetation at six of the seven sites represented variations within the *Abies grandis* series of forest habitat types, but variants in the *Pseudotsuga menziesii* series were represented at two of the Hall Ranch sites (table 2). Earlier research at these and closely related sites is published elsewhere (Edgerton 1966, 1971, 1972, 1987; Edgerton and McConnell 1976; Erickson 1974; Hedrick et al. 1968; Krueger and Winward 1974, 1976; Pettit 1968; Strickler and Edgerton 1976; Young et al. 1967a, 1967b).

Table 1—Location, size of treatment areas, topography, and soils at study sites, northeastern Oregon

Exclosure site	UTM[a]	Size	Elevation	Slope	Aspect	Soils
		Ha	*m*	---- *Degrees*	----	
Mottet	5072654N 425453E	0.8	1341	10	130	Alfic Udivitrand, ashy over loamy, mixed, frigid
Hoodoo clearcut	5086788N 453265E	.8	1189	15	160	Typic Vitrandept, medial over loamy, skeletal, mixed, frigid
Hoodoo selective cut	5086500N 454250E	.8	1280	16	120	Typic Vitrandept, medial over loamy, skeletal, mixed, frigid
Hoodoo no cut	5086411N 453450E	.8	1311	11	80	Typic Vitrandept, medial over loamy, skeletal, mixed, frigid
Hall Ranch clearcut	4997221N 446217E	.8	1180	14	10	Typic Vitrandept, silt loam
Hall Ranch selective cut 1	4997537N 446077E	.4	1204	4	220	Typic Vitrandept, silt loam
Hall Ranch selective cut 2	4996951N 442605E	.4	1230	5	8	Typic Vitrandept, silt loam

[a] UTM = universal transverse mercator coordinates.

Table 2—Climax plant associations documented on or adjacent to study sites, northeastern Oregon

Exclosure site	Climax plant association	Classification authority
Mottet	*Abies grandis/Pachistima myrsinites*	Daubenmire and Daubenmire 1968[a]
	Abies grandis/Vaccinium membranaceum	Hall 1973
	Abies grandis/Linnaea borealis/forb	Hall 1973
	Abies grandis/Taxus brevifolia/Clintonia uniflora	Johnson and Clausnitzer 1992
Hoodoo (all 3 sites)	*Abies grandis/Taxus brevifolia/Clintonia uniflora*	Johnson and Clausnitzer 1992
	Abies grandis/Vaccinium membranaceum/Clintonia uniflora	Johnson and Clausnitzer 1992
Hall Ranch clearcut	*Abies grandis/Vaccinium membranaceum*	Johnson and Simon 1987
	Pseudotsuga menziesii/Physocarpus malvaceus[b]	Johnson and Simon 1987
Hall Ranch selective cut 1	*Pseudotsuga menziesii/Physocarpus malvaceus*[c]	Johnson and Simon 1987
Hall Ranch selective cut 2	*Abies grandis/Acer glabrum/Physocarpus malvaceus*[d]	Johnson and Simon 1987

[a] Used by Edgerton (1987), but subsequently replaced by Hall (1973) and by Johnson and Clausnitzer (1992).
[b] Occurs as a minor upper slope inclusion.
[c] Krueger and Winward (1974) report a grazing disclimax of *Pseudotsuga menziesii-Pinus ponderosa/Poa pratensis.*
[d] Krueger and Winward (1976) report a grazing disclimax of *Abies grandis/Physocarpus malvaceus/Calamagrostis rubescens.*

History of Herbivore Use

All seven sites had long histories of use by wild and domestic herbivores. Although undocumented, Native Americans may have grazed the sites with horses in the 18th and 19th centuries. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) were indigenous, but these wild ruminants were nearly extirpated between 1870 and 1900. Domestic ruminants increased dramatically during the same period (Irwin et al. 1994). All seven sites probably were grazed by domestic sheep in the first half of the 20th century.

Domestic sheep were grazed in the vicinity of Mottet during the experiment,[1] but no evidence was actually observed at the study site during the 27-year experiment (table 3). We thus assumed that the Mottet site probably lay outside the normal herding pattern and was seldom if ever grazed by sheep. We found no record of domestic sheep using any of the Hoodoo exclosures. Sheep grazing persisted at all three Hall Ranch sites until 1955 (table 3). During the experiments, cattle were the dominant livestock at all sites except Mottet (table 3). Records indicate that since 1964, cattle grazing occurred at Hoodoo only in odd-numbered years, between 1 June and 15 July (table 3).[2] Cattle replaced sheep at Hall Ranch in 1956, but cattle were not controlled there until the experiments began.

All seven study sites were subject to use by elk and deer (primarily *Odocoileus hemionus* and a few *O. virginianus*) during the study. They usually occupied the Mottet and Hoodoo vicinities during the 6-month snow-free period, roughly early June to late November. At Hall Ranch, they typically began to use the exclosure vicinities somewhat earlier, early April or May, and then remained into early December. Elk and deer would occasionally occupy the Hall Ranch sites throughout the year when mild winters occurred. Wild ruminants were more prevalent than livestock during the experiments (table 3). Only use by wild ruminants was recorded at Mottet. At Hoodoo, cattle stocking (ha/AUM [animal unit month]) was more intense than the estimated equivalent for elk or deer, but only in June and July, and even then only in odd-numbered years (elk and deer occupied the area every year for roughly 6 months). Livestock grazing was most consistent and intense at the Hall Ranch sites. There, cattle stocking (ha/AUM) was more intense than the equivalent for elk or deer in most years, but for only 1 to 3 months each year.

---

[1] Unpublished data for the North End Sheep Allotment, Swamp Creek Unit, Jubilee Subunit. On file with: Umatilla National Forest, 2517 SW Hailey Ave., Pendleton, OR 97801.

[2] Unpublished data for the Eden Grazing Allotment. On file with: Umatilla National Forest, 2517 SW Hailey Ave., Pendleton, OR 97801.

Table 3—Wild herbivore densities[a] and cattle-equivalent stocking levels[b] for wild and domestic herbivores in the general vicinity of study sites, northeastern Oregon

	Elk		Deer		Livestock		
Site	Density	Cattle AUM equivalent	Density	Cattle AUM equivalent	Type	Equivalent	Years and dates of use
Mottet	0.9-3.7	45-11[c]	0.8-2.9	123-34[c]	sheep	unknown	1964-71, 1 pasture without rotation
						31 b.d.[d]	1972-81, 3-pasture deferred rotation
						34-4[d]	1982-92, 3-pasture deferred rotation
Hoodoo (all 3 sites)	.9-3.7	45-11	.8-2.9	123-34	cattle	6.3[e]	1964-79, odd years only; 6/1-7/15
						3.0[e]	1980-92, odd years only; 6/1-7/15
Hall Ranch clearcut	.8-2.8	51-15	1.7-13.4	57-7	sheep	heavy	through 1955[f]
					cattle	1.6	1956-63; 5/1-7/1
						0	1964, no livestock grazing
						.5	1965-94; start 6/15-7/15, + 30 days
Hall Ranch selective cut 1	.8-2.8	51-15	1.7-13.4	57-7	sheep	heavy	through 1955[f]
					cattle	1.8	1956-77; 5/1-7/1
						2.8	1978-94; start 5/25-6/30, to 8/1
Hall Ranch selective cut 2	.8-2.8[b]	51-15	1.7-13.4	57-7	sheep	heavy	through 1955[f]
					cattle	2.4	1956-80; 6/20-9/20
						2.8	1981-95; 8/1-9/15

[a] Summer range densities (animals per square kilometer) were projected from population estimates in the previous winter, assuming uniform distribution of animals over the summer range, and do not include young of the year. (Source: personal communication, Leonard Erickson, Oregon Department of Fish and Wildlife.)

[b] All stocking levels are in terms of hectares per cattle-equivalent animal-unit-month (ha/AUM) of range occupancy. For conversions, 1 cattle unit equals 2.5 elk units, 6 deer, or 6 sheep units. Cattle equivalencies (ha/AUM) decrease as the density of animals on summer range increases. At Mottet, for example, 0.9 elk per km^2 represents 45 ha per cattle-equivalent AUM, and 3.7 elk per km^2 represents 11 ha per cattle-equivalent AUM; 11 ha per AUM represents a stocking level roughly 4 times higher than that of 45 ha per AUM. Conversion to cattle-equivalent units is based on body size and not on dietary habits of the various herbivores.

[c] Edgerton (1987) reports that fecal pellets of elk were twice as abundant as those of deer at this site.

[d] The 1972-81 stocking level was loosely defined at ≤ 31 band days (b.d.) across all 3 Swamp Creek pastures. Thereafter, planned stocking in the Jubilee pasture was ≥ 4 ha/AUM in years when grazing occurred and 34 ha/AUM in deferred years (some trailing of stock occurred even in deferred years). Annual visits to Mottet revealed no evidence of sheep grazing in the immediate vicinity of the exclosure. We inferred that livestock grazing was not operative at Mottet despite its potential to occur under the area grazing plan.

[e] Stocking was 131 cow/calf pairs (193 AUM), 1964-79, and 239 pair (398 AUM) thereafter.

[f] Sheep grazed the Hall Ranch for some time before 1956, perhaps from as early as 1939. Early grazing was heavy, especially near bed grounds. The exclosure in selective cut 1 was on a site previously used as a sheep bed ground (Krueger and Winward 1974). Cattle replaced sheep at Hall Ranch in 1956.

Exclosure Design and Treatments

Mottet—A 3.2-ha area was clearcut in summer 1964. Logging slash was left in place. Half the clearcut was broadcast burned in autumn 1965, and a 1.6-ha exclosure was built that straddled the boundary between the burned and unburned areas. This created four 0.8-ha treatments: a burned area accessible to wild ruminants (burn, graze), a burned area protected from ruminants (burn, protect), an unburned area accessible to wild ruminants (unburned, graze), and an unburned area that was protected (unburned, protected). In spring 1966, conifer seedlings (*Pseudotsuga menziesii, Abies grandis, Picea engelmanii*) were planted in all four treatments, and pasture grasses (*Dactylis glomerata, Phleum pratens*) were broadcast seeded in the fire line (Edgerton 1987). This site typically received a heavy snowpack and its fence was lowered in autumn. Thus some grazing by wild ruminants could have occurred during the snow-free period when the fence was down.

Hoodoo—In 1965, a 0.8-ha exclosure was constructed in each of three logged areas: a clearcut from which all merchantable timber was removed, a selective cut area from which 50 percent of merchantable timber was removed, and an unharvested area. Pasture grass (*Phleum pratens*, 0.5 kg/ha) and conifers (*A. grandis*, 4.4 kg/ha; *Picea* sp., 0.1 kg/ha) were aerially seeded in autumn 1964. In May 1965, 2-year-old *Pinus ponderosa* were planted on a 3- by 3-m spacing. All logging debris was left onsite. The sites were not burned. Six treatments were thus created: clearcut, graze; clearcut, protect; selective cut, graze; selective cut, protect; no cut, graze; and no cut, protect. Exclosure fences were not lowered in winter.

Hall Ranch—A 4.9-ha area was clearcut in 1963. All merchantable trees were removed, and all nonmerchantable trees were felled perpendicular to the slope. The site was broadcast burned in 1964, and half was seeded with pasture grasses (*Arrhenatherum elatius, Bromus inermis, B. marginatus, Dactylis glomerata, Elymus glaucus, Phleum pratens*) at an average rate of 7 kg/ha. In spring 1965, conifers (*Larix occidentalis, Pinus ponderosa, Pseudotsuga menziesii, Pinus monticola*) were planted by hand, and the exclosure was constructed. The exclosure created three 1.6-ha grazing areas: an unfenced area accessible to both cattle and wild ruminants (dual use); an area fenced to exclude wild ruminants but not cattle (cattle only); and an area fenced to exclude cattle but not wild ruminants (game only). Each contained seeded and unseeded portions, creating six 0.8-ha treatments: dual use, seed; dual use, no seed; cattle only, seed; cattle only, no seed; game only, seed; game only, no seed. Fences were not lowered in winter.

Selective cut 1 was in an area of *Pseudotsuga menziesii* habitat type from which mature *Pinus ponderosa* were selectively logged in the 1930s. The exclosure was constructed in 1958, to create three experimental treatments: an unfenced area accessible to cattle and wild ruminants (selective cut, dual use); fenced (0.4 ha) to allow wild ruminants but exclude cattle completely (selective cut, game only); and fenced (0.4 ha) for protection from all ruminants (selective cut, protect). Grasses were not seeded. Fences were not lowered in winter.

Selective cut 2 was in mixed-conifer forest of *Abies grandis* habitat type. It was logged in summer 1960 to remove (1) all *Abies grandis* and 70 percent of *Larix occidentalis* and *Pseudotsuga menziesii* >41 cm in diameter at breast height (d.b.h.), (2) 50 percent of old-growth *Pinus ponderosa,* and (3) all weak or diseased trees. The exclosure was built in 1960 after harvest to create the same three treatments as at selective cut 1: selective cut, dual use (no fence); selective cut, game only (0.4 ha); and selective cut, protected (fenced, 0.4 ha).

Methods

Sampling

Plant communities—At Mottet and Hoodoo, vegetation was inventoried seven times from 1966 to 1992: Mottet in 1966, 1967, 1969, 1973, 1976, 1986, and 1992; and Hoodoo in 1966, 1967, 1969, 1974, 1977, 1987, and 1992. Each time, canopy cover and frequency were recorded by plant taxon with a modified Daubenmire (1959) scheme. Three parallel transects spanned each treatment. Each transect contained 10 plots, and each plot contained four nested subplots. Plot and subplot dimensions were 0.3 by 2.4 m and 0.3 by 0.6 m, respectively. Transects were located at random, and plots were located systematically along transects. Transects and plots were permanently marked with metal stakes. Canopy cover of forest overstory was usually estimated with densiometers (Strickler and Edgerton 1976), but in 1992 cover was estimated by ocular tube readings at each plot to avoid densiometer bias (Cook et al. 1995). Further detail regarding procedures is available elsewhere (Edgerton 1966, 1971, 1987).

Vegetation was inventoried six times at the Hall Ranch clearcut (1965, 1966, 1967, 1977, 1982, and 1995). Frequency of plant taxa was inventoried each time, but canopy cover was inventoried only in 1966, 1967, and 1995. Data initially were collected by using a modified Daubenmire (1959) technique in which twenty-five 32.8-m transects were randomly established in each treatment, with each transect containing one hundred 0.3- by 0.3-m plots. In 1977 the inventory scheme was altered to ten 0.3- by 0.6-m quadrats. Transect locations were rerandomized for each inventory at this site.

Vegetation at the Hall Ranch selective cuts was inventoried in 1972 and 1995. Frequency data were collected in 1972, and both frequency and canopy cover were recorded in 1995. Six transects were established in each treatment of selective cut 1, and four transects were established in each treatment of selective cut 2. Transect length was 30 m, each containing ten 0.3- by 0.6-m plots at 3-m intervals. Conifer cover was estimated in 1995 with an ocular tube at 10-m intervals.

Plant association (i.e., potential climax vegetation) for each site was determined by using area-specific keys (Daubenmire and Daubenmire 1968, Hall 1973, Johnson and Clausnitzer 1992, Johnson and Simon 1987). These keys were applied to either the site (only the Hoodoo no-cut site could be keyed directly), or applied to the nearest adjacent uncut forest site of similar topography and soil. Hitchcock and Cronquist (1981) was the authority used for identification and nomenclature of individual plant taxa.

Herbivore dietary relations—We conducted diet-selection trials at Mottet and Hoodoo in 1992. Given our small sample of exclosures, limited replication of treatments, and imprecise knowledge of site-specific grazing intensities, we hoped that explicit knowledge of grazing behavior might provide insight. Grazing trials ideally would have incorporated samples for each herbivore species, but small size of the exclosures precluded meaningful sampling with all three species; securing an adequate sample of diet selection with any one species in an exclosure would have grossly influenced the dietary choices available to the other species in the trial. Thus we were forced to limit our sampling to a single herbivore species. Both tractable cattle and elk were available, but we used elk for two reasons: (1) elk are intermediate between cattle and deer in dietary selectivity and metabolic requirements, and (2) elk herbivory was common to both the Mottet and Hoodoo herbivory regimes (see table 3).

Exclosure size also limited replication and the number of animals that could be used. A hand-reared yearling male and a 2-year-old female were habituated to native vegetation for 2 months prior to data collection. The trials were conducted in late May, mid-July, and early September. Each month, three trials were conducted at each exclosure over two days. Trials were conducted in morning and evening of the first day and morning of the second day. Each trial involved grazing inside and outside each exclosure, with grazing time partitioned equally. Sampling order (inside versus outside) was randomized for the first trial and alternated thereafter. Grazing time in each treatment area was limited to a maximum of 20 minutes to minimize the effect of gut fill on appetite. If necessary, elk were checked with a lead rope to prevent movement beyond the sampling area when outside the exclosures (Wickstrom et al. 1984), but their movement was unrestricted within sampling areas. To enhance familiarity with the sample areas, animals were allowed to roam freely at each location in afternoon and evening prior to the first sample day. Supplemental food was provided at night between trial days, but not on trial days, to maintain appetite and minimize nonfeeding behavior during the trials (Wickstrom et al. 1984).

Diet composition was estimated from bite counts (Canon et al. 1987, Schwartz and Hobbs 1985, Wickstrom et al. 1984). Bites were recorded by plant taxon, and 10 simulated bites of each taxon were clipped, ovendried, and weighed to estimate dry-matter content. Taxon-specific consumption was calculated as the product of the number of bites recorded and mean bite mass.

Biomass and nutrient pools—Biomass and nutrients were estimated in 1995. Samples were collected only where it was possible to contrast a grazed area against a protected area. Thus Mottet, all three Hoodoo sites, and the two Hall Ranch selective cuts were sampled (the Hall Ranch clearcut was not sampled because it did not include an area protected from all ruminants). Samples were collected from only the protected and dual use areas of the Hall Ranch selective cuts. Samples were collected from all four treatments at Mottet, and soil and nutrient variables were compared between the two herbivory regimes in both the burned and unburned areas. All samples were collected between mid-June and mid-July.

Total biomass of nonconiferous understory and forest floor were sampled on twelve 0.5-m^2 plots randomly located over vegetation plots. Nonconiferous vegetation was clipped at ground level in a vertical projection extending through the forest understory over each plot. Samples of forest floor down to mineral soil were collected for nutrient analysis in a 0.093-m^2 frame centered on each biomass plot. Soil samples were collected with an auger to depth of 20 cm in 10-cm increments. Volume mass (bulk density) was not determined. Samples were ovendried to constant mass at 70 °C. Standing biomass and forest-floor samples were weighed separately, and understory biomass was separated into graminoid, forb, and shrub components. Shrub biomass was further separated into stem and leaf components. Plot-based estimates of dry mass were expanded to kilograms per hectare. Forest-floor estimates were corrected for mineral soil content by multiplying mass by organic C content (percent), thus reflecting accumulation of organic C.

Proportional samples of each biomass and soil component were composited at each site for nutrient analysis. Forest floor and soil composites were analyzed for concentration of total C, total and available N, phosphorus (P), sulfur (S), and total and exchangeable calcium (Ca), potassium (K), and magnesium (Mg). Vegetative composites were analyzed for total N, P, S, Ca, K, and Mg, but not C. Total N was determined by Kjeldahl procedure (Bremner and Mulvaney 1982). Total P of forest floor and vegetation was determined by magnesium nitrate dry-ashing and vanadate- molybdate yellow color development (Chapman and Pratt 1961); hydrofluoric acid digestion and ammonium molybdate-ascorbic acid color development were used for total P in soil (Bowman 1988). Total S and total C were assayed by dry combustion (Nelson and Sommers 1982, Tiedemann and Anderson 1971) and total cations by perchloric acid digestion and ICP spectroscopy (Barnes 1977). Available N (NH_4-N + NO_3-N) was determined by 2 N KCl extract and Mg_2O and Devardas alloy steam distillation (Keeney and Nelson 1982); available P (inorganic PO_4-P) by 0.5 M sodium bicarbonate extraction and ascorbic acid color development (Olsen and Sommers 1982); and available S (soluble SO_4-S) in a 1:1 soil-to-water extract followed by ion chromatography (Dick and Tabatabai 1979). Exchangeable Ca, K, and Mg were determined by 1 N ammonium acetate extraction. Mass of standing biomass and forest floor (kilograms per hectare) were multiplied by individual nutrient concentrations to obtain the accumulation of nutrients in each biomass component (kilograms per hectare). Comparable calculations were not made for soil nutrients because we did not determine soil bulk density.

Analysis

Plant communities—We began our analysis by using distance-weighted least-squares procedures (Statsoft 1994) to approximate trajectories for three common community indices across years (y): richness of plant taxa (R_y), general diversity among plant taxa (A_y; after Shannon and Weaver 1963), and evenness among plant taxa (E_y; after Pielou 1966a, 1966b). The R_y was determined by count of unique plant taxa in the monitoring data. The A_y and E_y were calculated on taxon-specific frequencies of occurrence as follows:

$$A = -\sum^{t} (i/\Sigma i) \log (i/\Sigma i) \quad , \tag{1}$$

where

A = general diversity of plant taxa,
i = importance (frequency of occurrence), and
t = number of plant taxa recorded.

$$E = \frac{A}{\log (t)} \quad , \tag{2}$$

where

E = evenness among plant taxa,
A = general diversity, and
t = number of plant taxa recorded.

We analyzed for time-specific, intertreatment differences in canopy cover at five sites for which sequential estimates had been made. The five were Mottet, the three Hoodoo sites, and the Hall Ranch clearcut. In this phase of analysis, we first tested for differences among treatments in terms of aggregate canopy cover of five growth forms of vegetation: coniferous trees, woody shrubs, subshrubs and vines, graminoids, and forbs. These five forms can be distinguished based on stature in forest understory and on structural and chemical attributes relevant to food selection by herbivores (Pastor and Naiman 1992, Shipley 1999). After testing for differences in aggregate cover, we analyzed for differences within individual taxa.

Canopy cover estimates for Mottet and Hoodoo were true repeated measures, because transects and plots at these sites were permanently marked with stakes throughout each experiment. We analyzed these data with repeated-measures multivariate analysis of variance (MANOVA). For Mottet, we defined the experimental factors to be prescribed burning (fire, F), herbivory (H), year (Y), and transect (T). We combined data from the three Hoodoo exclosures and defined the experimental factors to be logging intensity (L), herbivory (H), year (Y), and transect (T). Transects and plots at the Hall Ranch clearcut were not permanently marked and thus were not true repeated measures. These data therefore were analyzed in factorial ANOVA; factors were herbivory (H), seeding (S), year (Y), and transect (T). Only plant taxa appearing sequentially in each data set were analyzed. Tests were conducted with fixed-effects general linear models (SAS Institute, Inc. 1988).

We primarily used MANOVA and ANOVA as convenient tools for calculating treatment means and variances for canopy cover over time and as aids to identifying plant taxa that may have been responsive to the various experimental treatments. We wished to identify as many potentially responsive plant taxa as possible. Thus we were sensitive to type II errors (i.e., failing to identify an effect when one indeed exists), but we were relatively insensitive to committing occasional errors of type I (i.e., falsely concluding an effect when one does not exist). Because of our relative insensitivity to type I error, we did not adjust the MANOVA or ANOVA to guard against experimentwise type I error, and we noted results significant to $\alpha = 0.10$. Rather than screen species by an arbitrary error probability, we screened on magnitude of the apparent treatment effect, assuming that those least likely to constitute type I errors would be of the greatest biological magnitude. We thus distinguished between statistically significant results and those that could be considered substantial in terms of biological magnitude; we defined "substantial" as statistically significant, time-specific, intertreatment differences of magnitude ≥5 percent canopy cover. We interpreted all the substantial effects by growth form, but for individual taxa the two-way effects were interpreted only in absence of a significant three-way effect. We also compared the observed occurrence of substantial two-way and three-way effects to their expected occurrence under chance (Neu et al. 1974, Roscoe and Byars 1971).

These experiments presented designs typical of most long-term exclosures in that each constituted a nonreplicated case study rather than a replicated experiment (see Hurlbert 1984). As such, the inferential space of each MANOVA or ANOVA must be limited to its own site and time frame.

Herbivore diets and understory succession—We conducted two analyses to explore relations between elk herbivory and the development of plant cover. These analyses were based solely on data collected at Mottet and Hoodoo, because only these sites had sequential estimates of canopy cover in grazed and protected communities. We needed one variable that could reflect both the magnitude and the direction of these differences over time. For this we defined an index to relative change (r_i) as follows:

$$r_i = c_{pi} - c_{gi} \ , \tag{3}$$

where

r_i = relative change for the ith taxon,
c_{pi} = cover change over time by the ith taxon in a protected area,
c_{gi} = cover change over time by the ith taxon in a grazed area,

where

$c = \log_e[(\acute{c}_2 + k)/(\acute{c}_1 + k)]$, if $\acute{c}_2 - \acute{c}_1 > 0$;
$= -\{\log_e[(\acute{c}_2 + k)/(\acute{c}_1 + k)]\}$, if $\acute{c}_2 - \acute{c}_1 < 0$; and
$= 0$, if $\acute{c}_2 - \acute{c}_1 = 0$;

and where

$\acute{c}_2$ = canopy cover at the terminus of a time period,
$\acute{c}_1$ = canopy cover at start of a time period, and
k = 0.02 (the minimum cover recorded for any taxon).

The value calculated for r_i indexes the comparison of vegetal canopy development observed for a given plant taxa inside an exclosure to that observed for the same taxa outside the same exclosure and over a specified period. Here, the period was 27 years. A positive r_i indicates greater canopy development inside the exclosure relative to that observed outside the same exclosure. A positive r_i can result from any of three conditions: (1) a taxon increased inside and outside the exclosure, but to the greater extent inside; (2) the taxon was diminished over time both inside and outside the exclosure, but to the lesser extent inside; or (3) the taxon increased inside the exclosure but decreased outside. Reverse arguments apply to negative values of r_i (i.e., canopy development was greater over time outside the exclosure than inside). The absolute value of r_i reflects the magnitude of divergence in canopy cover between treatments for the ith taxon.

We calculated r_i for each taxon at each site and then analyzed to see if the divergence it reflected could be related to the dietary preferences of elk. We used Ivlev's (1961) electivity index (e_i) to reflect preference, after Manley et al. (1993:10):

$$e_i = (o_i - \hat{\pi}_i)/(o_i + \hat{\pi}_i) \quad , \tag{4}$$

where

e_i = electivity exhibited by elk for the ith plant taxon,
o_i = sample proportion of bites taken of the ith taxon, and
$\hat{\pi}_i$ = sample proportion of total canopy cover attributed to the ith taxon.

We pooled dietary data across animals to calculate monthly values of e_i for each taxon, both inside and outside each exclosure. If the plant taxon was present both inside and outside the exclosure, then we set monthly e_i equal to the average for the two treatments. If the taxon was not detected in both treatments, its monthly e_i was set equal to the value calculated in the treatment where it occurred. The three monthly values for e_i were averaged over time and then across sites. We also averaged r_i across sites.

Averaged values of e_i and r_i were used for cluster and regression analyses. For clustering, we used a standardized Q-analysis (Romesburg 1984). In a Q-analysis, objects (here, plant taxa) are clustered by their attributes (here, r_i and e_i). This provided a view of how various plant taxa relate to one another in the two-dimensional space defined by e_i and r_i. Clustering was performed by using the unweighted pair-group method based on average Euclidean distance (the resemblance coefficient, d_{jk}) (Statsoft 1994). We used linear regression to test the hypothesis that r_i and e_i were not related.

We also examined the data for evidence of a relation between r_i and taxon-specific utilization rates. We lacked actual utilization data, however, and so we modeled it based on elk dietary preferences, elk forage demand, and community composition and production. An array of preference coefficients α_i (after Chesson 1978) was generated from data collected in the feeding trails. Elk forage demand was assumed constant at 7.68 kg/day (i.e., 130 $\text{gDM}\cdot\text{day}^{-1}\cdot\text{kgBW}^{0.75}$, for a 230-kg, lactating cow elk [Robbins et al. 1981]). Community composition was defined by canopy cover recorded in 1966 and 1967 and averaged across years.[3] Community production was adapted from estimates for open-, moderate-, and closed-canopy *Abies gran-dis* forest (Young et al. 1967a). Thus a recent clearcut was assumed to produce 856 kg/ha, of which 89 kg (10.3 percent) was shrub growth and 767 kg (89.7 percent) was herbage. A selective cut was assumed to produce 502 kg/ha consisting of 156 kg (31.1 percent) shrub and 346 kg (68.9 percent) herbage, and uncut forest was assumed to produce 175 kg/ha consisting of 78 kg (44.6 percent) shrub and 97 kg (55.4 percent) herbage. The available production in each forest was then partitioned among the i plant taxa according to the proportion of total canopy cover attributed to each in the shrub and herbage groups (shrub = shrubs, subshrubs, and vines; and herbage = graminoids and forbs). We ignored coniferous vegetation because elk did not use conifers during the grazing trials.

From these input data, we simulated taxon-specific consumption and utilization rates. A FORTRAN program was parameterized to deplete 1 ha of forest understory at a constant rate (7.68 kg/day), partitioned among i plant taxa in each community according to α_i. We ran the program as a "graze-out" simulator. This simply involved daily reparameterization of the α array and taxon-specific forage availability (to account for the effect of forage utilization) and then calculation of taxon-specific forage use (based on the reparameterized α array). This process was repeated on a 1-day time step until all available forage production was consumed (Chesson 1978). Model output included taxon-specific vectors for daily depletion and usage as functions of the number of elk-days of use per hectare. When conjugated over time, these vectors form profiles consistent with empirical utilization curves used by range managers (see Smith 1965).

With model output in hand, the plant taxa were cluster-analyzed again, this time on r_i and model utilization rates (u_i). The u_i was expressed as mean daily usage, calculated over the number of days required for complete utilization of the ith taxon. We performed separate cluster analyses for clearcut forests (Mottet and Hoodoo, averaged), selective cut forest (Hoodoo), and uncut forest (Hoodoo).

Biomass and nutrient accumulations—For each site, differences in understory biomass and forest-floor biomass were tested with a Wilcoxon two-sample test using normally approximated P values (Steel and Torrie 1960). Across sites, t-tests were used to assess the significance of differences between grazed and protected areas for (1) understory and forest-floor biomass; (2) nutrient mass in understory and forest-floor biomass; and (3) nutrient concentration in understory biomass components, forest-floor biomass, and soil. We report test results to $P \leq 0.10$.

---

[3] We modeled on the first 2 years, assuming that grazing influences would be most pronounced then, for two reasons: (1) young plants and sprouts dominate recently disturbed communities, and (2) low productivity per unit area immediately after an episodic disturbance (and coincidentally, in the uncut forest) intensifies the influence of any given level of herbivory. Ideally, we would have preferred that our estimate of α be based on observations made concurrent with the estimates of composition for the community being modeled, but this option was not available to us.

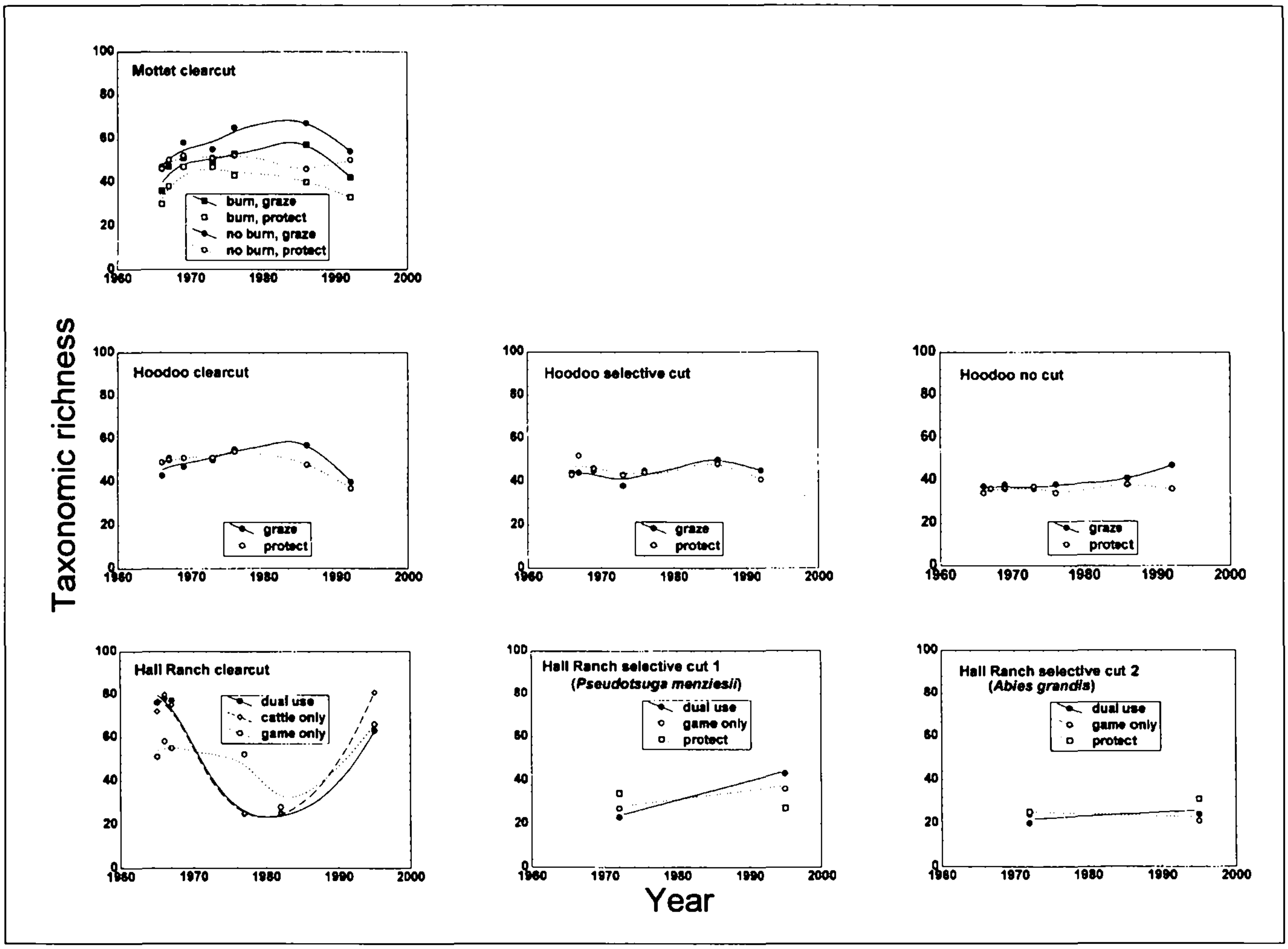

Figure 2—Distance-weighted, least-squares trajectories for taxonomic richness (R_y) under different disturbance regimes at seven exclosures in the Blue Mountains, 1965-95.

Results

Community Indices

Trajectories for richness (R_y, fig. 2) and diversity (A_y, fig. 3) appeared more dynamic in clearcuts than in the selective-cut or uncut areas. These trajectories were not consistent in treatment, however, and time-specific variations in these indices among treatments were generally less than or equal to the variation exhibited within individual treatments over time. We did not use statistics to test hypotheses regarding these indices.

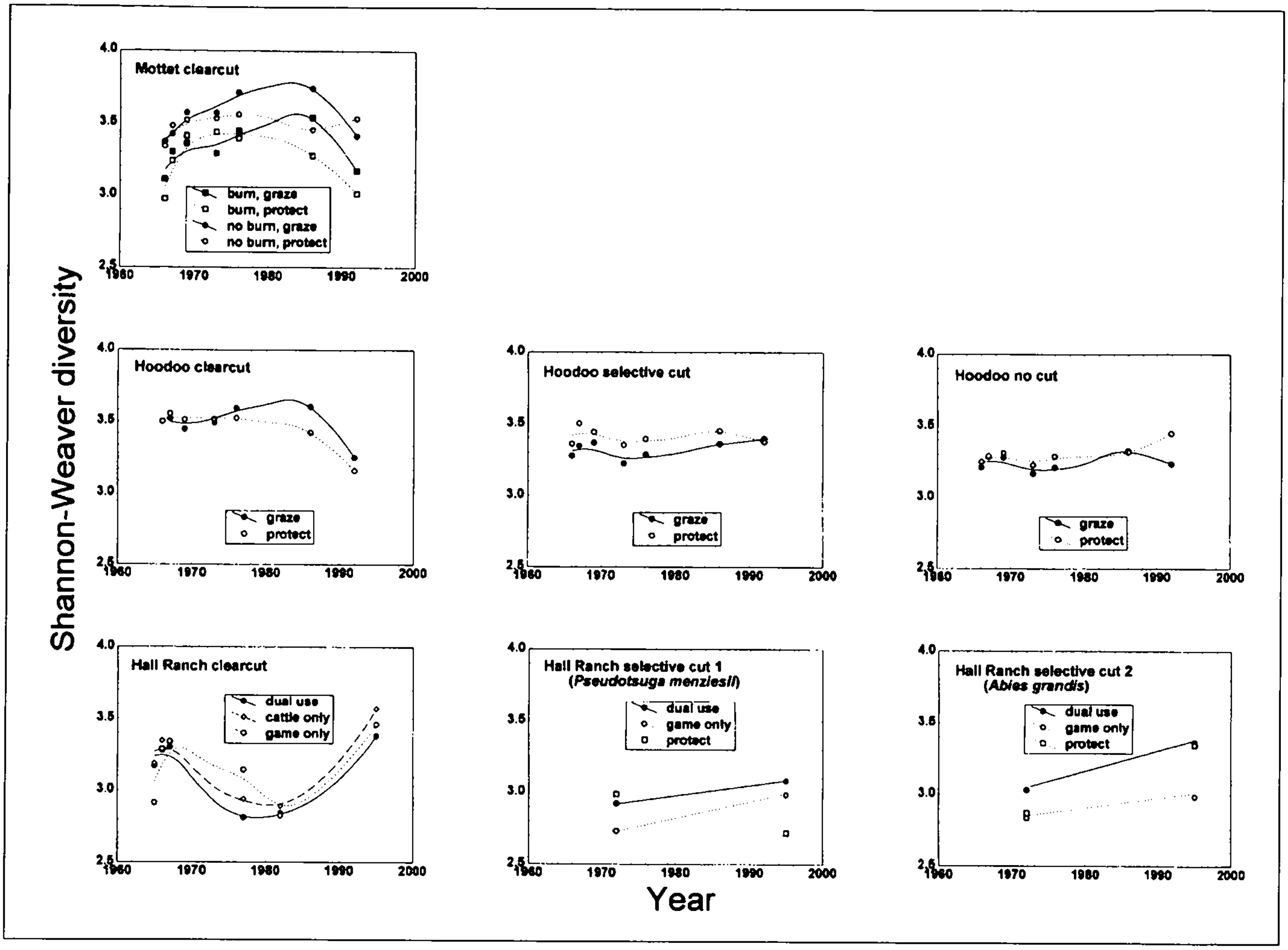

Figure 3—Distance-weighted, least-squares trajectories for diversity (A_y; Shannon and Weaver 1963) under different disturbance regimes at seven exclosures in the Blue Mountains, 1965-95.

The only clearly consistent difference among communities was observed in their evenness (E_y), which was consistently lower in all communities at the three Hall Ranch exclosures than in those at Mottet and Hoodoo (fig. 4). Differences in evenness among the treatments at each site were small compared to the differences among sites (Mottet and Hoodoo versus Hall Ranch). Average E_y (across treatments) for Mottet and Hoodoo was twice that for Hall Ranch sites; the ranges of E_y at Mottet and Hoodoo were virtually identical and mutually exclusive of the ranges observed at Hall Ranch sites.

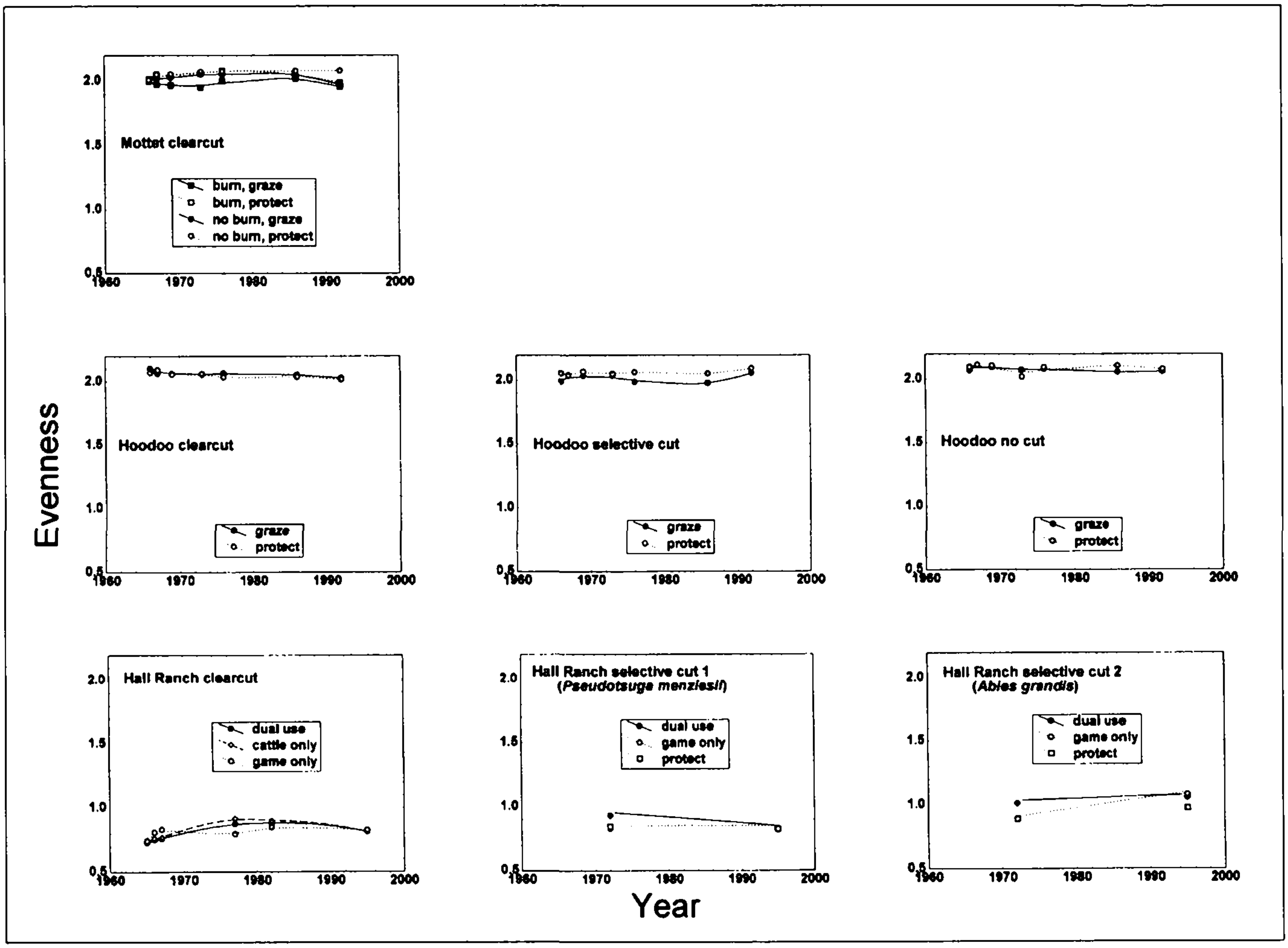

Figure 4—Distance-weighted, least-squares trajectories for evenness (E_y, Pielou 1966b) under different disturbance regimes at seven exclosures in the Blue Mountains, 1965-95.

Canopy Cover Dynamics

Results of the MANOVA and ANOVA tests conducted on canopy cover over time are reported for plant taxa at Mottet, Hoodoo, and the Hall Ranch clearcut. For each experiment, we first will focus on illustrating variation in canopy development by growth forms (woody shrubs, subshrubs and vines, graminoids, and forbs) and then on variation exhibited by individual plant taxa. Throughout, we will focus on disturbance-agent interactions. For Mottet and Hoodoo, these interactions are defined by the MANOVA within-subject effects (i.e., *YxFxH*, *YxLxH*, *YxF*, *YxL*, *YxH*). For Hall Ranch, these are defined by ANOVA temporal-interaction effects (i.e., *YxSxH*, *YxS*, *YxH*). These interactions are the only model effects relevant to detecting divergence in canopy cover among treatments over time. For shrubs, subshrubs, and vine taxa, we present all significant effects ($P \leq 0.10$), but we distinguish between effects on shrubs that were both significant (unadjusted for experimentwise type I error, at $P < 0.10$) and substantial (of magnitude > 5 percent), versus those that were merely significant but not substantial. For graminoids and forbs we report only results that were significant and substantial.

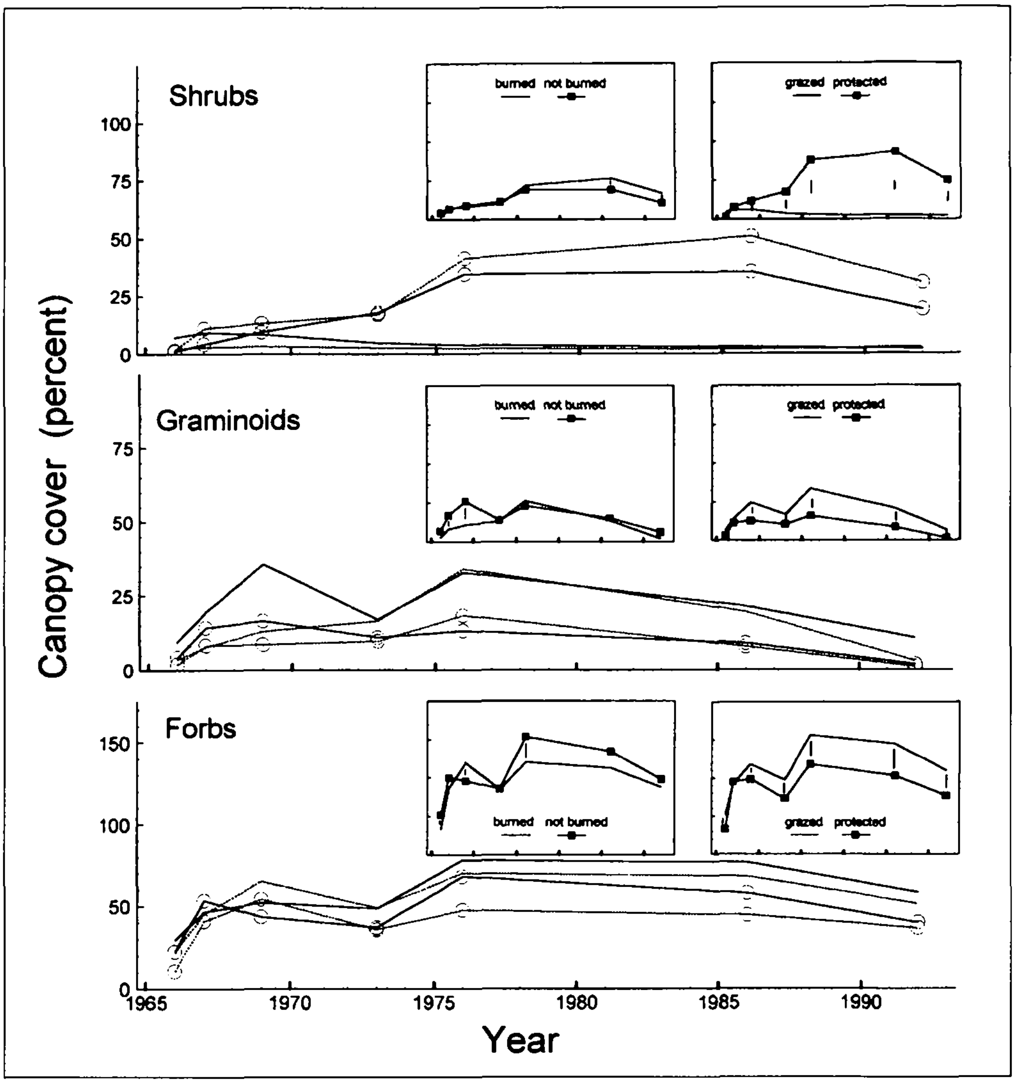

Figure 5—Aggregate canopy cover for shrubs, graminoids, and forbs in the Mottet clearcut: burn, graze (······); burn, protect (--⊖-); no burn, graze (—); and no burn, protect (–⊖–). Inset graphs contrast the observed influence of burning with that of herbivory. Vertical bars in the inset approximate year-specific $LSD_{0.05}$ values for significant differences between means.

Mottet—

Coniferous trees—Neither herbivores nor fire influenced development of conifer cover significantly. It was < 1 percent in all four treatments through 1969, increased to 3 percent in 1973, and then increased to 27 to 36 percent in 1992 with no significant differences among treatments ($P \geq 0.26$).

Shrubs—Broadcast burning enhanced development of aggregate shrub cover ($P_{Y\times F} = 0.06$), but the burning effect was not apparent until 1986 (see inset, fig. 5). Herbivores suppressed shrub cover at this site early in the experiment ($P_{Y\times H}$ < 0.01, fig. 5). Aggregate cover increased in protected areas (both the burned and

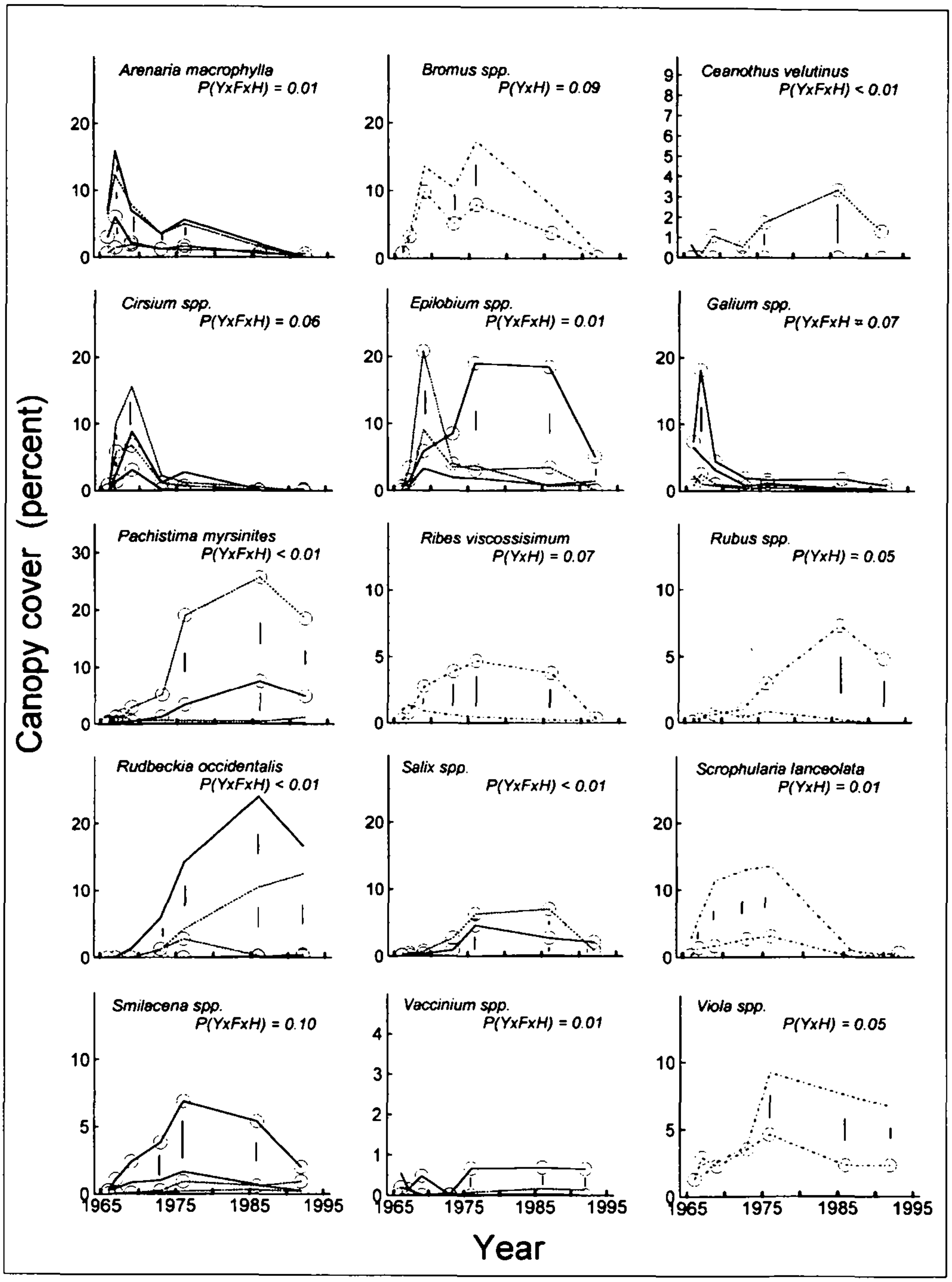

Figure 6—Canopy cover trajectories for Mottet taxa exhibiting *YxFxH* effects (burn, graze ----; burn, protect--⊖--; no burn, graze ——; no burn, protect —⊖—), for *YxF* effects (burn ----; no burn ——), and *YxH* effects (graze - - -, protect - ⊖ -). Vertical bars approximate year-specific *LSD* values at the significance level indicated in each graph.

unburned) to 43 percent in 1986. The maximum canopy cover in the two grazed areas (burned and unburned) was only 6 percent, however, and it was recorded within 4 years of burning. The three-way within-subject effect was not significant for shrubs in the aggregate ($P_{Y \times F \times H} = 0.16$).

Twenty-two shrub taxa were recorded at Mottet and 13 of these were analyzed for development of intertreatment differences in cover over time.[4] Thus, the most within-subject effects that potentially could be identified in the analysis was 39 (i.e., three different effects for each of 13 taxa). Fifteen significant effects were detected (i.e., unadjusted, $P \leq 0.10$, two-way or three-way). Six of the 15 effects were interpretable (i.e., not confounded by a higher order effect), but only 4 of those were substantial (i.e., ≥ 5 percent). *Ceanothus velutinus, Pachistima myrsinites, Salix* spp., and Vaccinium spp. each exhibited the *YxFxH* effect, but it was interpreted as substantial only for *Pachistima* and *Salix. Ribes viscosissimum* and *Rubus* spp. each exhibited the *YxH* effect. Each taxa developed more cover in protected areas than in grazed areas (fig. 6).

Graminoids—Aggregate cover was similar among areas initially but for a brief time more developed in the unburned areas than in burned areas ($P_{Y \times F} = 0.04$; fig. 5). The *YxH* effect was not significant ($P_{Y \times H} = 0.14$), but cover was greater in grazed areas than in protected areas throughout the experiment ($P_H < 0.01$; fig. 5). The three-way effect was not significant ($P_{Y \times F \times H} = 0.15$).

Twenty-five taxa were recorded during the experiment, but only eight of these were sufficiently represented in the plot data to allow analysis of their cover development over time. Thus, 24 within-subject effects were potentially detectable in the analysis. Only four were significant, and only one was substantial. *Bromus* spp. (*B. inermis, B. carinatus, B. vulgaris*) exhibited the *YxH* effect by developing more cover in grazed areas than in protected areas (fig. 6).

Forbs—The *YxFxH* effect was not significant for aggregate cover ($P_{Y \times F \times H} = 0.21$), but the *YxF* ($P_{Y \times F} = 0.01$) and *YxH* ($P_{Y \times H} = 0.05$) effects were each substantial (fig. 5). With a sole exception in 1969, the aggregate cover appeared to be greater in the unburned area than in the burned area. Herbivory had a more persistent influence on aggregate forb cover than did broadcast burning; forb cover was significantly greater in the grazed area than in the ungrazed area by 1969, and this condition persisted through 1992.

Among 102 recorded taxa, 37 could be analyzed for differences in cover development over time. Thus, 111 different within-subject effects were possible. We detected 36, among which only 19 were interpretable and only eight of these were of substantial magnitude (fig. 6). Six taxa exhibited substantial *YxFxH* effects (*Arenaria macrophylla, Cirsium* spp., *Epilobium* spp., *Galium* spp., *Rudbeckia occidentalis, Smilacina* spp.), and two exhibited the *YxH* effect (*Scrophularia lanceolata, Viola* spp.). Among these, *Epilobium, Galium,* and *Smilacina* responded negatively to herbivory.

---

[4] Complete data lists are available for all study sites from (1) USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR, 97850; or (2) Eastern Oregon Agricultural Research Center, P.O. Box E, Union, OR 97883.

Hoodoo—

Coniferous trees—In the clearcut, conifer cover increased from 0 percent in 1966 to 8.8 percent in 1977, declined to 0.3 percent in 1987, then increased to 3.5 percent by 1992. Throughout the experiment, understory conifer cover was stable in the selective-cut and uncut forests (averaging 2.9 and 0.9 percent, respectively). In 1992, understory conifer cover was 3.5 percent in the clearcut, 8.5 percent in the selective cut, and 1.3 percent in uncut forest. At no time did understory cover differ among treatments ($P > 0.10$). Overstory cover was similar among treatments in 1992, ranging from 46 to 53 percent ($P \geq 0.25$).

Shrubs—The three-way effect was not significant for aggregate cover ($P = 0.65$). Shrubs appeared, however, to benefit similarly from protection in all three logging treatments ($P_{Y \times H} = 0.03$, fig. 7), but to a lesser extent than at Mottet. Shade-intolerant taxa remained suppressed by conifer overstory in the Hoodoo selective-cut and uncut forests. Hoodoo treatments were not burned, whereas all were burned at Mottet; this may explain the weaker response of several shrubs at Hoodoo.

Twenty-five shrub taxa were recorded, and 13 were sufficiently represented for analysis. Thirteen of the 39 possible within-subject effects were significant, but only six of these were interpretable (fig. 8). *Lonicera utahensis, Ribes* spp., *Symphoricarpos albus*, and *Vaccinium* spp. each exhibited the $Y \times L \times H$ effect. *Rosa gymnocarpa* exhibited $Y \times L$ and $Y \times H$ effects (but not to a substantial extent) and did not exhibit the three-way effect. Each taxa developed greater cover at some point in time in one or more of the protected areas, but the apparent responses to herbivory were not as consistent as those observed for shrubs at Mottet, and their magnitude appeared to be contingent on the previous logging regime. *Symphoricarpos* and *Lonicera*, for example, developed substantially higher cover in only the protected area that had been previously clearcut, and *Ribes* developed higher cover only in the protected area that had been selectively harvested. These effects may reflect differences in shade tolerance.

Subshrubs and vines—All the within-subject effects were significant. The $Y \times L \times H$ effect ($P = 0.06$) was attributed to greater cover in selective cut, grazed forest but only in 1974 (fig. 7). The $Y \times L$ effect ($P = 0.06$) reflected greater development in the uncut and selective cut forests than in the clearcut. The $Y \times H$ effect ($P = 0.03$) reflected greater cover development in grazed areas on average than in protected areas early in the experiment, followed by a contrast reversal.

There were only four taxa in this group and thus 12 possible within-subject effects. Seven were significant. Five were interpretable and only three of these were substantial (fig. 8). *Chimaphila umbellata* exhibited the $Y \times L \times H$ effect; *Linnaea borealis* exhibited $Y \times L$ and $Y \times H$ effects but not the three-way effect. *Berberis repens* exhibited a significant $Y \times L$ effect that was not substantial, and *Lonicera ciliosa*, a climbing vine, exhibited a significant $Y \times H$ effect that was not substantial. *Chimophila* developed substantial cover only on the uncut and select-cut treatments that were grazed. *Linnea* and *Lonicera* each developed more cover in protected areas.

Graminoids—Both the $Y \times L \times H$ and $Y \times L$ effects were significant for aggregate cover ($P < 0.01$). The $Y \times L \times H$ effect was apparent only in 1974 when cover was greatest in clearcut, grazed forest (fig. 7). The $Y \times L$ effect reflected substantially greater development of graminoids in the clearcut than in selective-cut or uncut forest over time.

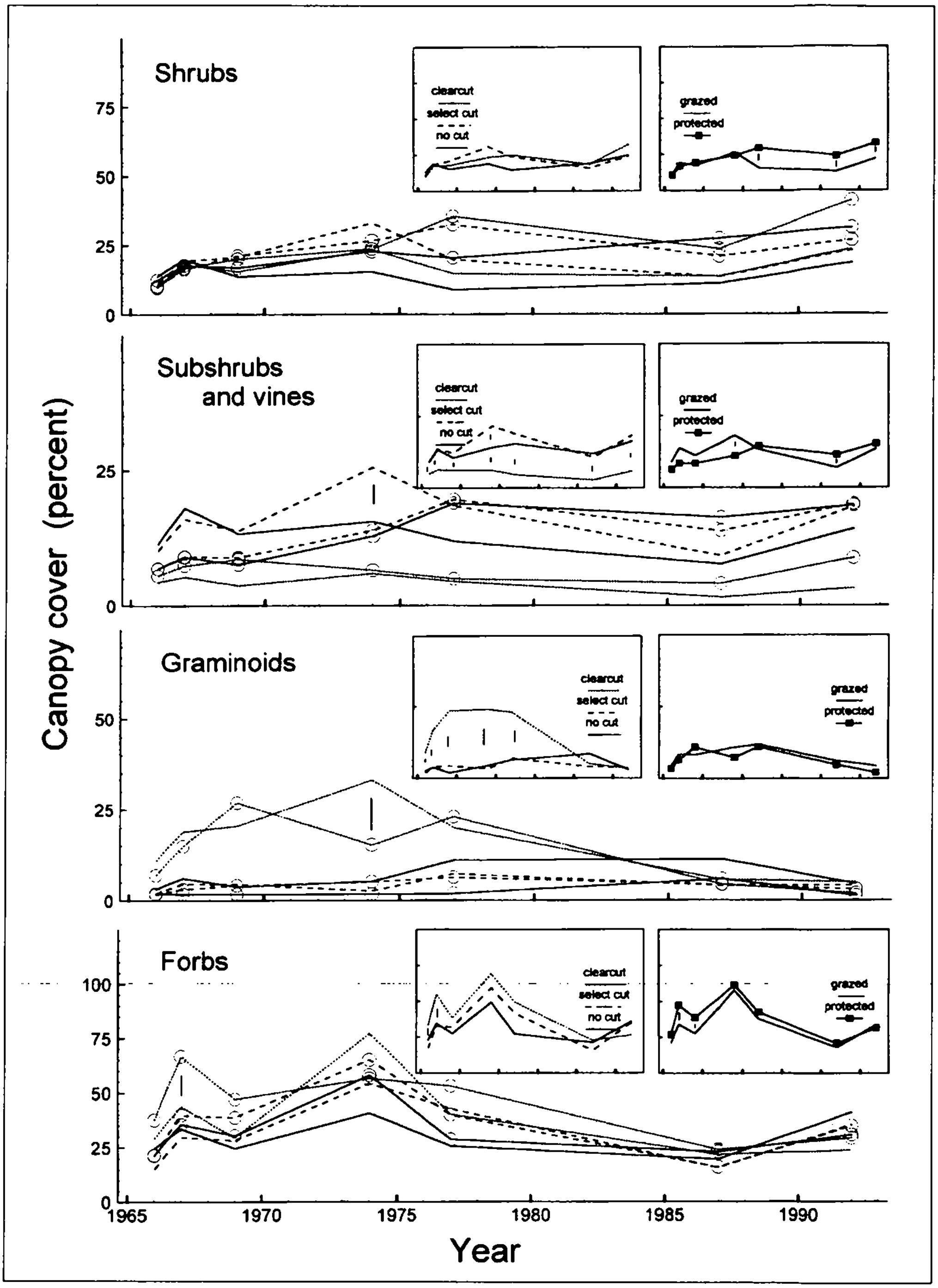

Figure 7—Aggregate canopy cover trajectories for shrubs, subshrubs and vines, graminoids, and forbs, at Hoodoo: clearcut, graze ( ); clearcut, protect ( ); selective cut, graze ( ); selective cut, protect (—○—); no cut, graze(——); and no cut, protect (—⊖—). Inset graphs contrast the observed influence of logging intensity with that of grazing. Vertical bars in the insets approximate $LSD_{0.05}$ values for year-specific differences between treatment means.

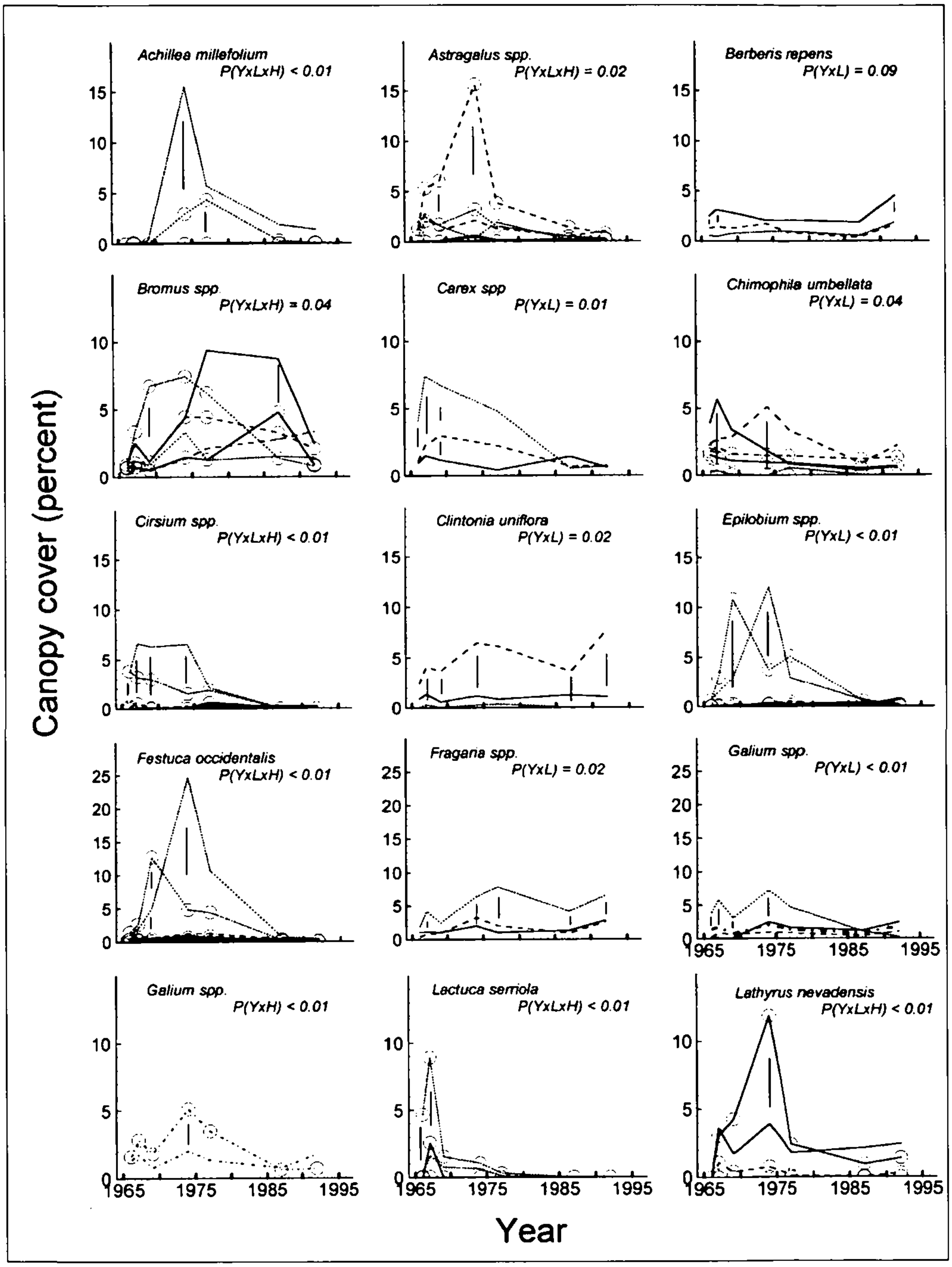

Figure 8—Canopy cover trajectories for Hoodoo taxa exhibiting *YxLxH* effects (clearcut, graze ·····; clearcut, protect ··⊖··; selective cut, graze – –; selective cut, protect –⊖–; no cut, graze ——; no cut, protect —⊖—), for *YxL* effects (clearcut ·····, selective cut – –, no cut ——), and *YxH* effects (graze - - -, protect - ⊖ -). Vertical bars approximate year-specific *LSD* values at the significance level indicated in each graph.

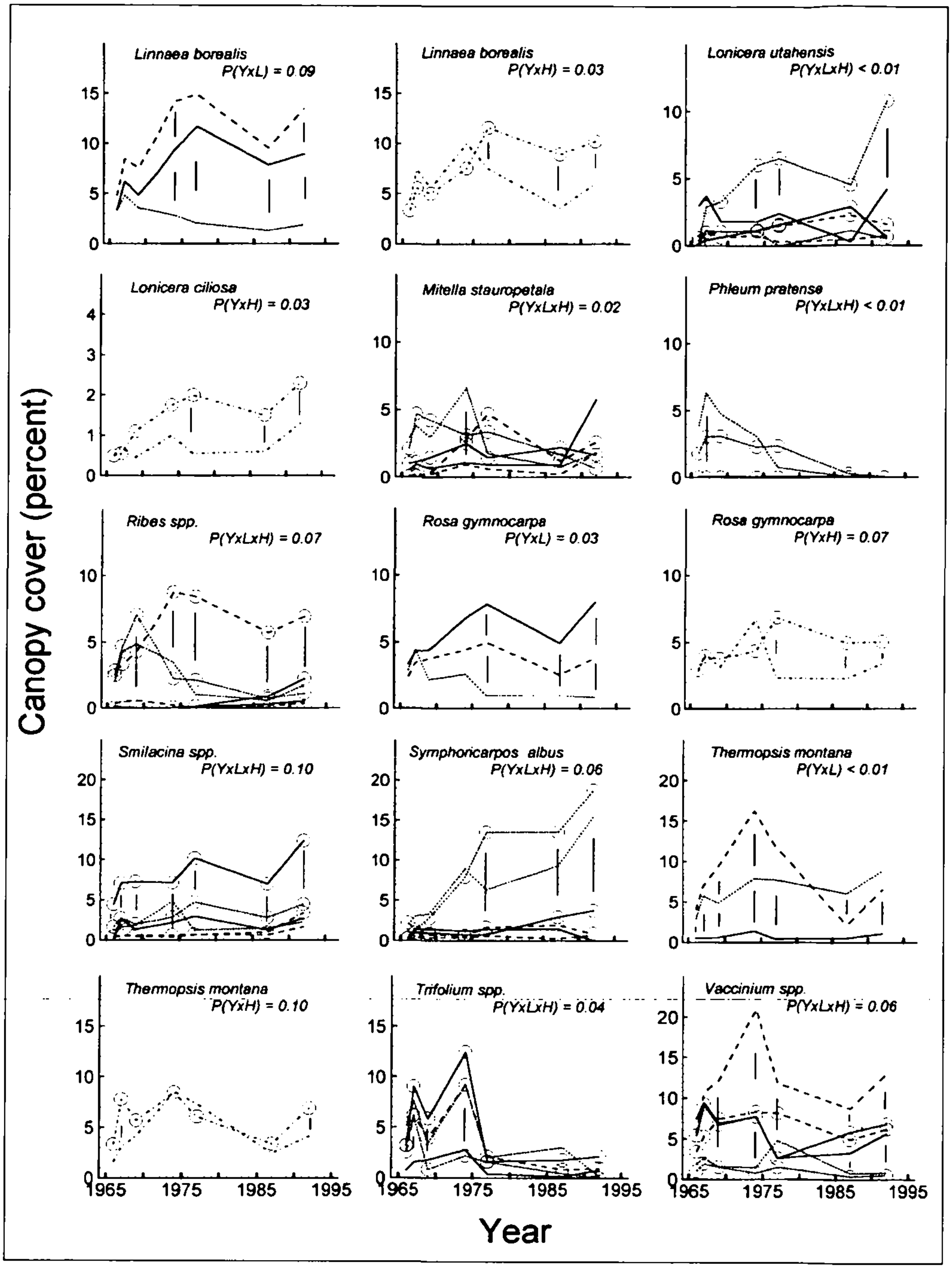

Figure 8—(continued)

Twenty-two taxa were recorded, and eight of these were analyzed for differences in cover development. Fourteen effects were detected of a possible 24, and 4 were substantial (fig. 8). *Bromus* spp. (*B. carinatus* and *B. vulgaris*), *Festuca occidentalis*, and *Phleum pratense* exhibited the *YxLxH* effect. *Bromus* spp. initially appeared to

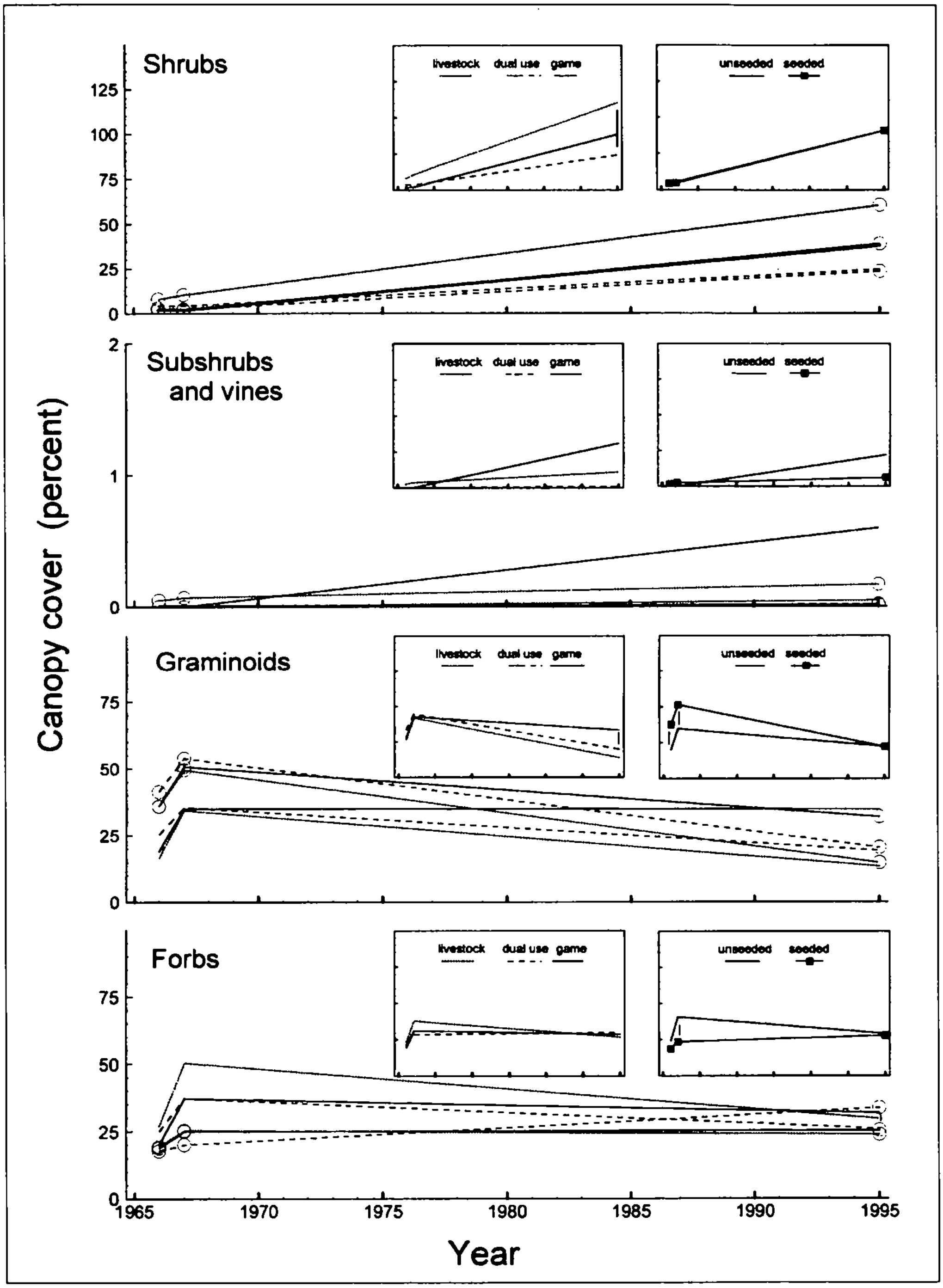

Figure 9—Aggregate canopy cover trajectories for shrubs, subshrubs and vines, graminoids, and forbs, at the Hall Ranch clearcut: cattle only, no seed ( ); cattle only, seed ( ); dual use, no seed (– –); dual use, seed ( ); and game only, no seed ( ); game only, seed ( ). Vertical bars in the insets approximate year-specific $LSD_{0.05}$ values for differences between means.

benefit from grazing protection in the clearcut, but over time it appeared more responsive to the logging treatments than to the herbivory regimes. *Festuca* and *Phleum* each developed more cover in the grazed clearcut. *Carex* spp. exhibited the $Y{\times}L$ effect.

Forbs—The $Y{\times}L{\times}H$ effect ($P_{Y{\times}L{\times}H} = 0.05$) was apparent only in 1967 when cover was substantially greater in the clearcut, protected treatment (fig. 7). Also early in the experiment, aggregate cover was greater in the clearcut than in selective cut or uncut areas ($P_{Y{\times}L} = 0.01$) and greater in protected versus grazed areas ($P_{Y{\times}H} = 0.03$).

Among 101 recorded taxa, 35 were analyzed for differences in cover development. Fifty-five significant effects were detected. Twenty-eight of these effects were interpretable, but only 15 were substantial (fig. 8). Nine taxa exhibited the $Y{\times}L{\times}H$ effect (*Achillea millefolium*, *Astragalus* spp., *Cirsium* spp., *Epilobium* spp., *Lactuca serriola*, *Lathyrus nevadensis*, *Mitella stauropetala*, *Smilacina* spp., and *Trifolium* spp.). Two exhibited only the $Y{\times}L$ effect (*Clintonia uniflora* and *Fragaria* spp.), and two others exhibited $Y{\times}L$ and $Y{\times}H$ effects (*Galium* spp., *Thermopsis montana*) absent the three-way effect.

Hall Ranch clearcut—

Coniferous trees—Conifer cover increased in all treatments over time, from 0 percent in 1965 to 38 to 50 percent in 1995 but without significant differences among treatments ($P \geq 0.67$).

Shrubs—Only the $Y{\times}H$ interaction was significant for aggregate cover ($P_{Y{\times}H} = 0.07$); more cover developed in the cattle-only area than in the dual use or game-only areas (fig. 9). Sixteen shrub taxa were recorded and all were sufficiently represented to allow analysis of their cover development. Thus there were 48 possible interactions. Eleven were significant, but only seven were interpretable and only four of these substantial (fig. 10). *Rosa nutkana* exhibited a significant $Y{\times}H{\times}S$ effect, but the intertreatment difference was not substantial. Four taxa exhibited significant effects that were substantial for the $Y{\times}H$ effect (*Ceanothus velutinus*, *Holodiscus discolor*, *Physocarpus malvaceus*, and *Symphoricarpos albus*), and two other taxa exhibited a significant $Y{\times}H$ effect that was not substantial (*Rosa gymnocarpa* and *Salix* spp.). No shrubs exhibited a significant $Y{\times}S$ effect.

Graminoids—The $Y{\times}H$ and $Y{\times}S$ effects were significant for aggregate cover ($P < 0.02$) but not the $Y{\times}H{\times}S$ effect ($P_{YxHxS} = 0.97$). Graminoids showed more development under game-only grazing than under dual use or cattle only, and more where grass seeding occurred than where it did not occur (fig. 9).

Thirty-three graminoid taxa were recorded and analyzed, thus presenting 99 possible interaction effects. Eighteen significant interactions were detected. Thirteen were interpretable, but only eight of these were of substantial magnitude (fig. 10). Four

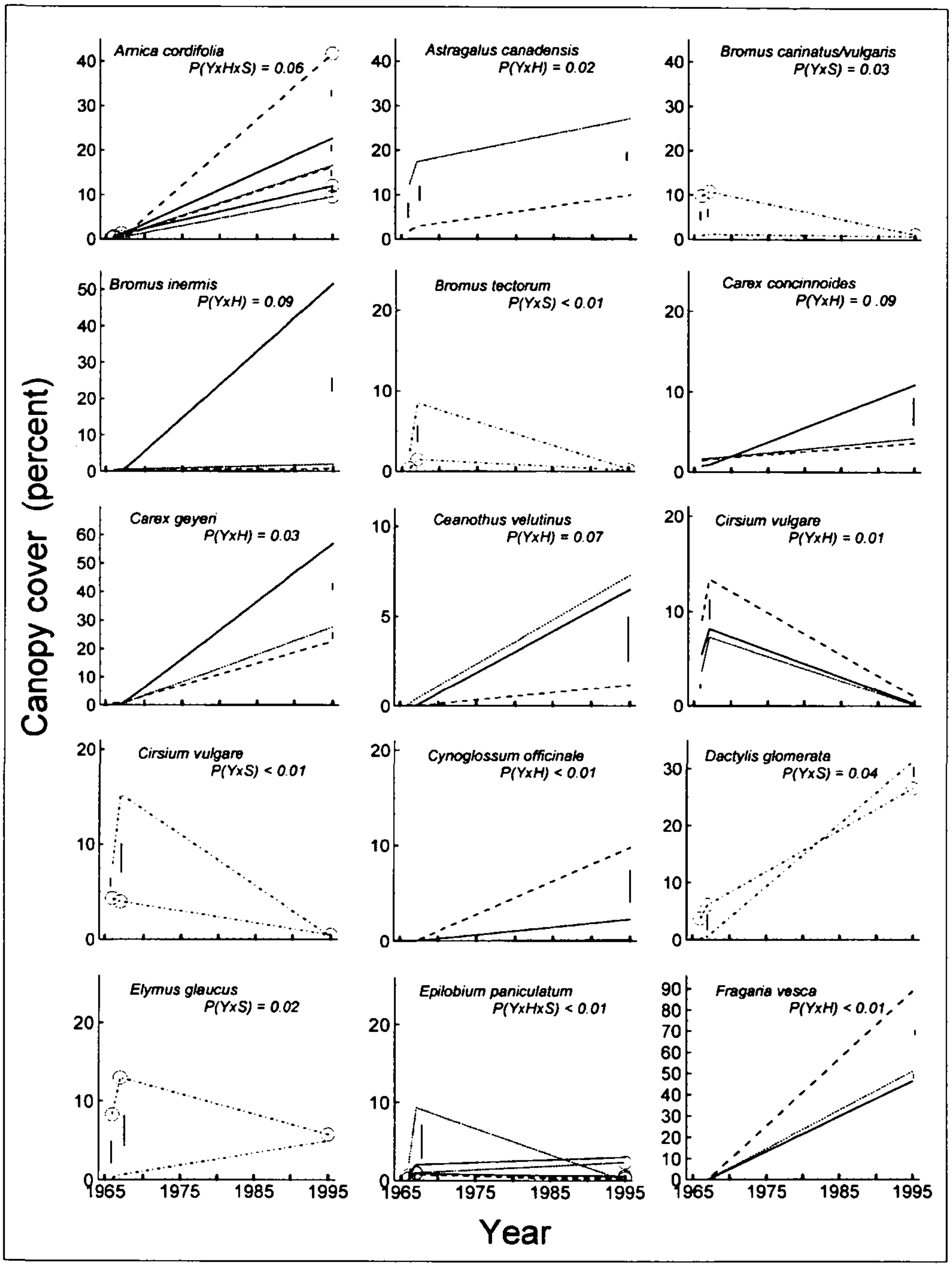

Figure 10—Cover trajectories for Hall Ranch taxa exhibiting *YxSxH* effects (cattle only, no seed ·····; cattle only, seed ··⊖··; dual use, no seed – –; dual use, seed –○–; game only, no seed ——; game only, seed –⊖–), *YxH* effects (cattle only ····· , dual use – –, game only ——), and *YxS* effects (no seed -·-·-, seed -·⊖·-). Vertical bars approximate year-specific *LSD* values at the significance level indicated in each graph.

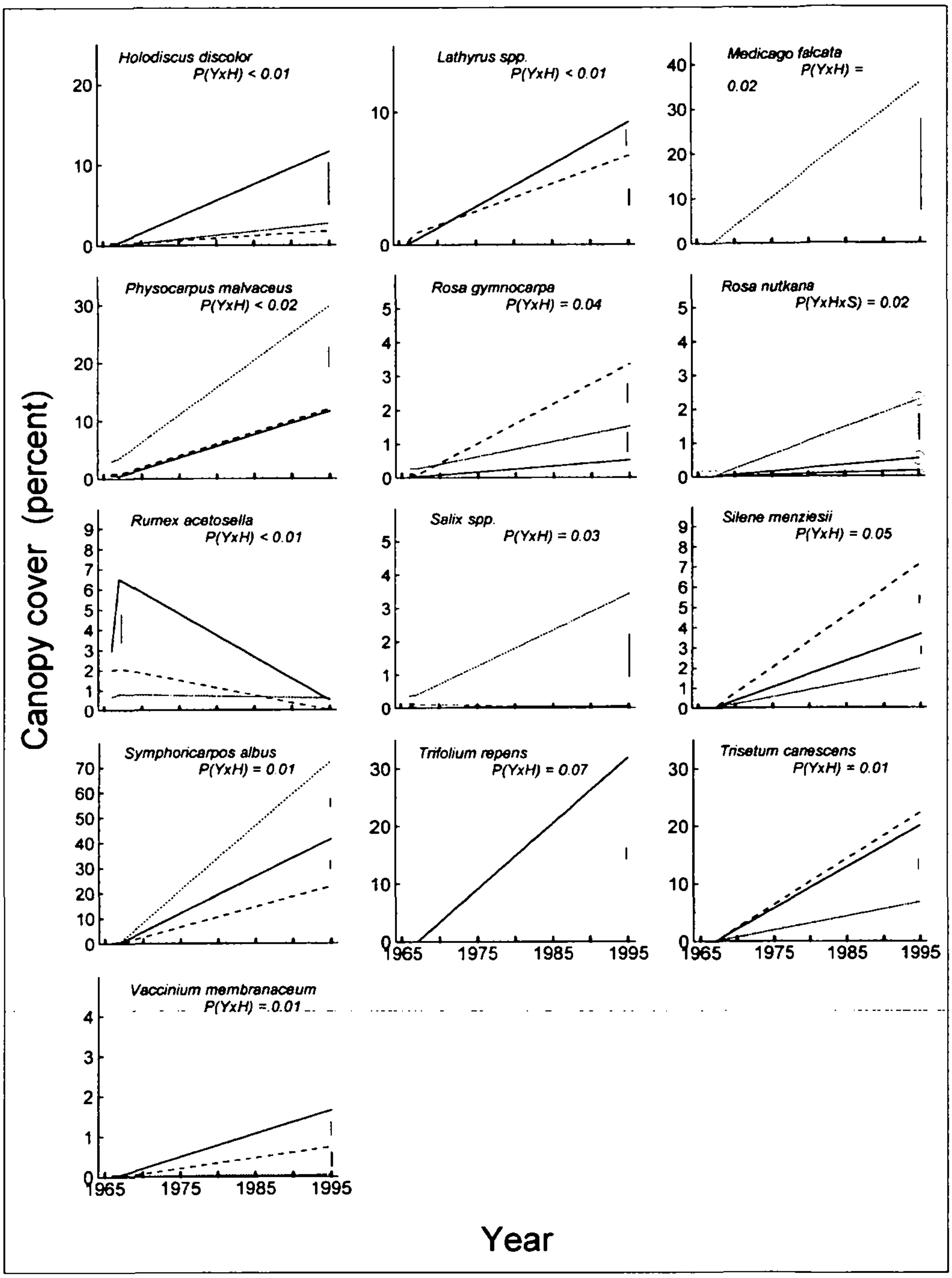

Figure 10—continued

taxa exhibited substantial *Y*×*H* effects (*Bromus inermis*, *Carex geyeri*, *C. concinnoides*, and *Trisetum canescens*), and each showed more development under game-only grazing than under cattle-only grazing; *Trisetum* developed similarly under game only and dual use. Four other taxa exhibited a substantial *Y*×*S* effect (*Bromus* spp. [*B. carinatus* and *B. vulgaris*], *B. tectorum*, *Dactylis glomerata*, and *Elymus glauca*). *Bromus* and *Elymus* exhibited canopy differences only early in the experiment, but *Dactylis* exhibited a contrast reversal over time. None of the graminoids exhibited substantial three-way effects.

Forbs—Aggregate cover exhibited a substantial *Y*×*S* interaction ($P_{Y\times S} = 0.04$). Aggregate cover increased rapidly in areas not seeded to grasses, but cover was similar among treatments at the end of the experiment (fig. 9).

Eighty-nine forbs were recorded and analyzed, presenting 267 possible interaction effects. Forty significant effects were detected. Twenty-seven of these were interpretable, but only 12 were substantial (involving 11 taxa; fig. 10). *Arnica cordifolia* and *Epilobium paniculatum* exhibited the *Y*×*H*×*S* effect. *Cirsium vulgare* exhibited the *Y*×*H* and the *Y*×*S* effect but not a three-way effect. *Cirsium* developed more cover under dual use grazing than under either game-only or cattle-only regimes and more cover where grasses were not seeded after disturbance. Eight taxa exhibited the *Y*×*H* effect only (*Astragalus canadensis*, *Medicago falcata*, *Rumex acetosella*, *Cynoglossum officinale*, *Fragaria vesca*, *Lathyrus* spp., *Silene menziesii*, and *Trifolium repens*). Among these taxa, *Lathyrus*, *Trifolium*, and *Rumex* developed their greatest cover under game-only grazing. The others developed greatest cover under either the dual use or cattle-only regimes.

Summary of MANOVA and ANOVA—We conducted a total of 256 MANOVA or ANOVA analyses for individual taxa, which in aggregate presented 768 possible within-subject or temporal interaction effects. Among these 768 possible interactions, 213 (28 percent) were significant (unadjusted for experimentwise error; $P \leq 0.10$); however only 65 of the 213 (8.5 percent) were interpretable (i.e., not precluded by a higher order interaction) and of sufficient magnitude to suggest potential relevance to management (i.e., indicating canopy-cover differences ≥ 5 percent). Most of the effects surviving this screening were indeed visually apparent in the field (see appendix), and we think few if any type I errors (i.e., false effects) exist in the set of 65.

The frequency with which the various temporal interactions were detected in the combined data set may be of interest. Table 4 compares observed occurrence of the various substantial effects (in the set of 65) to their expected occurrence under a null hypothesis that each should have been detected in proportion to its occurrence in the set of 768 (i.e., H_0: effects were detected at random). A chi-square test of this null hypothesis was soundly rejected ($X^2 = 44.42$, 6 *df*, $P < 0.001$). Substantial *Y*×*F* effects, which can be interpreted as fire effects not contingent on subsequent herbivory, did not occur in the data set (i.e., less than expected under the null). The *Y*×*L*×*H* effect was detected more often than would be expected by chance; the *Y*×*S* and *Y*×*S*×*H* effects occurred less often than expected.

Table 4—Expected and observed occurrence of 2-way and 3-way interaction effects in a set of 65 substantial effects,[a] and confidence intervals (95-percent family confidence coefficient) on the observed proportions

			In the set of 65 substantial effects								
Effect[b]	Total number	Number possible[c]	Number observed	Number expected	Proportion observed	Proportion expected	95% confidence interval on observed proportions in the set of substantial effects[d]				
Y×*F*	58	50	0	4.148	0.000	.064	0.000	≤	0.000	≤	0.000*
Y×*L*	60	43	8	3.567	.123	.055	.011	≤	.123	≤	.235
Y×*S*	138	136	5	11.283	.077	.173	-.014	≤	.077	≤	.168*
Y×*H*	256	229	25	19.000	.385	.292	.219	≤	.385	≤	.551
Y×F×*H*	58	58	8	6.172	.123	.095	.011	≤	.123	≤	.235
Y×*L*×*H*	60	60	17	6.328	.261	.097	.111	≤	.261	≤	.411*
Y×*S*×*H*	138	138	2	14.555	.031	.224	-.028	≤	.031	≤	.090*
	768	690	65	65.053	1.000	1.000					

[a] A "substantial" effect is defined here as an effect exhibiting statistical significance ($P \leq 0.10$), for a difference in canopy cover between treatments of magnitude ≥ 5 percent.

[b] Y = year, F = burning, L = logging, S = grass seeding.

[c] The number of possible 2-way effects reflects the observed number of precluding 3-way effects.

[d] * = the expected proportion was not contained within the confidence interval calculated for the observed proportion.

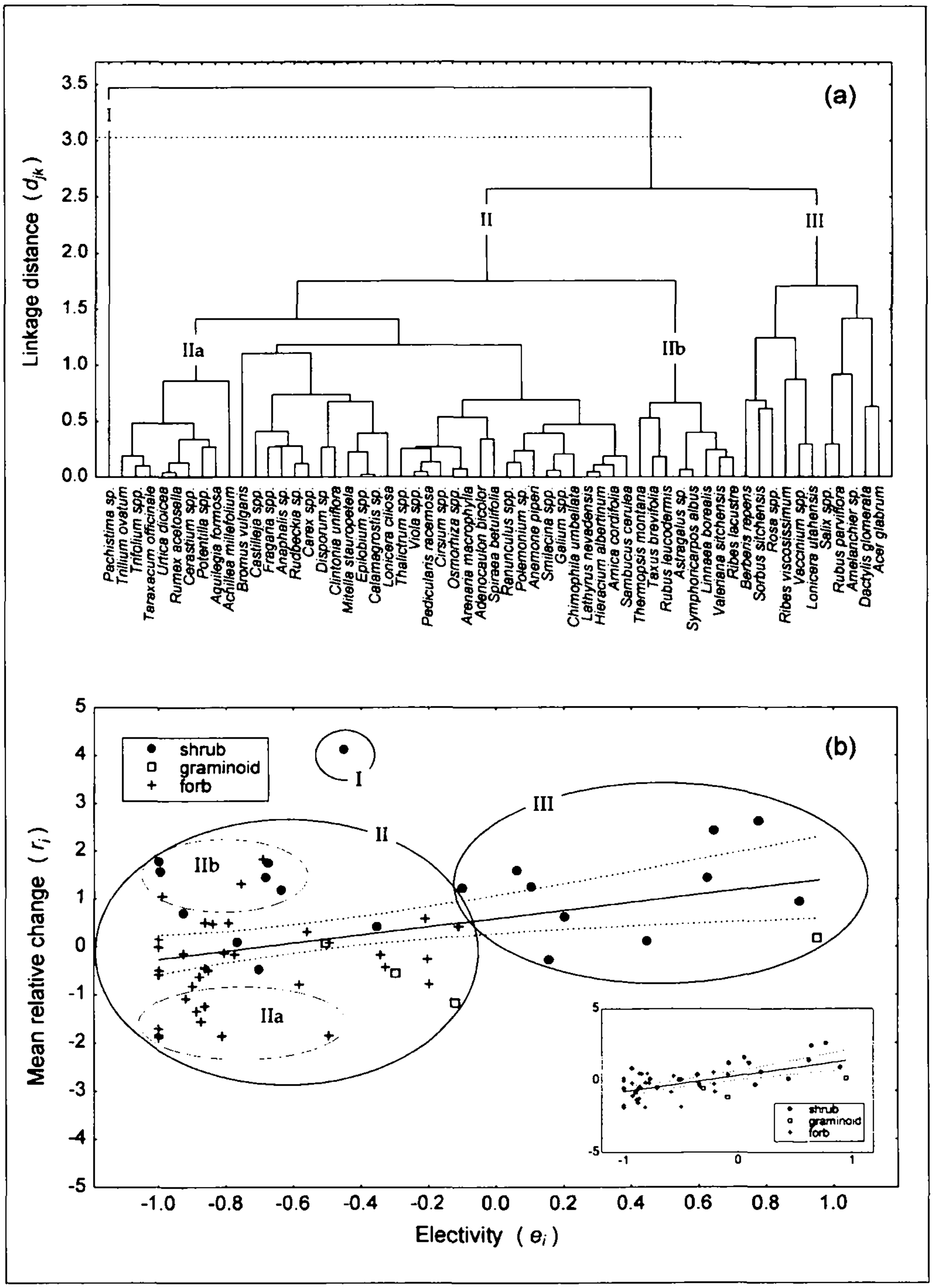

Figure 11—Joining tree (**a**) and scatter plot (**b**) for cluster analysis of plant taxa (n = 59); roman numerals in (a) correspond to those in (b). The joining tree illustrates relations among taxa. The scatter plot illustrates composition (shrubs, graminoids, forbs) of clusters and regression relations. In (b), the main graph illustrates regression of r_i on e_i for all taxa excluding group I ($r_i = 0.501084 + 0.808696[e_i]$, $P = 0.002$, $r^2 = 0.14$, $SE = 1.038$); the graphic inset illustrates the regression after exclusion of taxa in groups I and IIb ($r_i = 0.378316 + 1.119127[e_i]$, $P = 0.000003$, $r^2 = 0.37$, $SE = 0.832$).

Elk Diets and Secondary Succession

Fifty-nine taxa were clustered on dietary electivity (e_i, of elk) and relative change (r_i) (fig. 11). For 53 of these taxa, both e_i and r_i were calculated for two or more sites; exceptions for which calculations could be performed for only one site were *Acer glabrum*, *Pachistima myrsinites*, *Rubus leucodermis*, *Sambucus cerulea*, *Sorbus sitchensis*, and *Rumex acetosella*.

Robustness of general-purpose classifications is maximized by cutting hierarchical trees within the maximum range of resemblance coefficients for which the number of clusters remains constant (Romesburg 1984). Here that range was $2.6 < d_{jk} < 3.5$, and within this range, all taxa clustered into one of two groups (fig. 11a) based primarily on r_i (fig. 11b). The first group contained only one taxon, *Pachistima myrsinites*. The second group [II,III] contained the remaining 58 taxa. Taxa belonging to this group exhibited a highly significant but weak positive correlation between e_i and r_i ($r_i = 0.501084 + 0.808696[e_i]$, $P = 0.002$, $r^2 = 0.14$, $SE = 1.038$). Separate regressions for shrubs, graminoids, and forbs in this group were not significant ($P \geq 0.50$).

The next cut in the hierarchical tree was at $1.7 < d_{jk} < 2.6$. Here the 58 taxa in group [II,III] clustered into group II or group III, primarily based on e_i (fig. 11). Group II contained 47 taxa, all characterized by negative e_i, and only 8 of the 47 were shrubs. Conversely, group III was comprised of 11 taxa; all but one of these were characterized by positive e_i, and 10 of the 11 taxa were shrubs.

One more cut of this tree, at $1.4 < d_{jk} < 1.7$, presented two clusters of further interest. Group IIa consisted of nine forbs exhibiting the lowest values of e_i and r_i. Group IIb contained taxa that exhibited among the lowest values of e_i but high values for r_i. Ordination of group IIa was logical. The ordination of group IIb was illogical, however, because its members developed relatively high canopy cover inside exclosures (compared to outside) despite exhibiting the lowest electivities in elk diets.

We suspected that group IIb was an artifact of negatively biased estimates of e_i for at least some of its members. Palatability of evergreen taxa is often low in summer, only increasing in autumn and winter after deciduous taxa become senescent and reduced in availability (Irwin and Peek 1983a, 1983b; Pierce and Peek 1984). We conducted our grazing trials in summer, and thus our estimates of dietary electivity for the evergreen taxa may be biased. *Linnaea borealis* and *Taxus brevifolia* (group IIb) and *Pachistima myrsinites* (group I) are evergreen species; had we collected data into autumn and winter, average e_i for these taxa may have been estimated at somewhat higher levels, which would have shifted their ordinations to the right in fig. 11.

We recalculated the regression of r_i on e_i after deleting data for all members of group IIb. This calculation yielded a stronger relationship between r_i and e_i among the remaining taxa ($r_i = 0.378361 + 1.119127[e_i]$, $P = 0.000003$, $r^2 = 0.37$, $SE = 0.832$), with slope approximating 1 ($SE_{b1} = 0.211966$; $CI_{b1(.05,48df)} = 0.6837363 \leq b_1 \leq 1.5362636$).

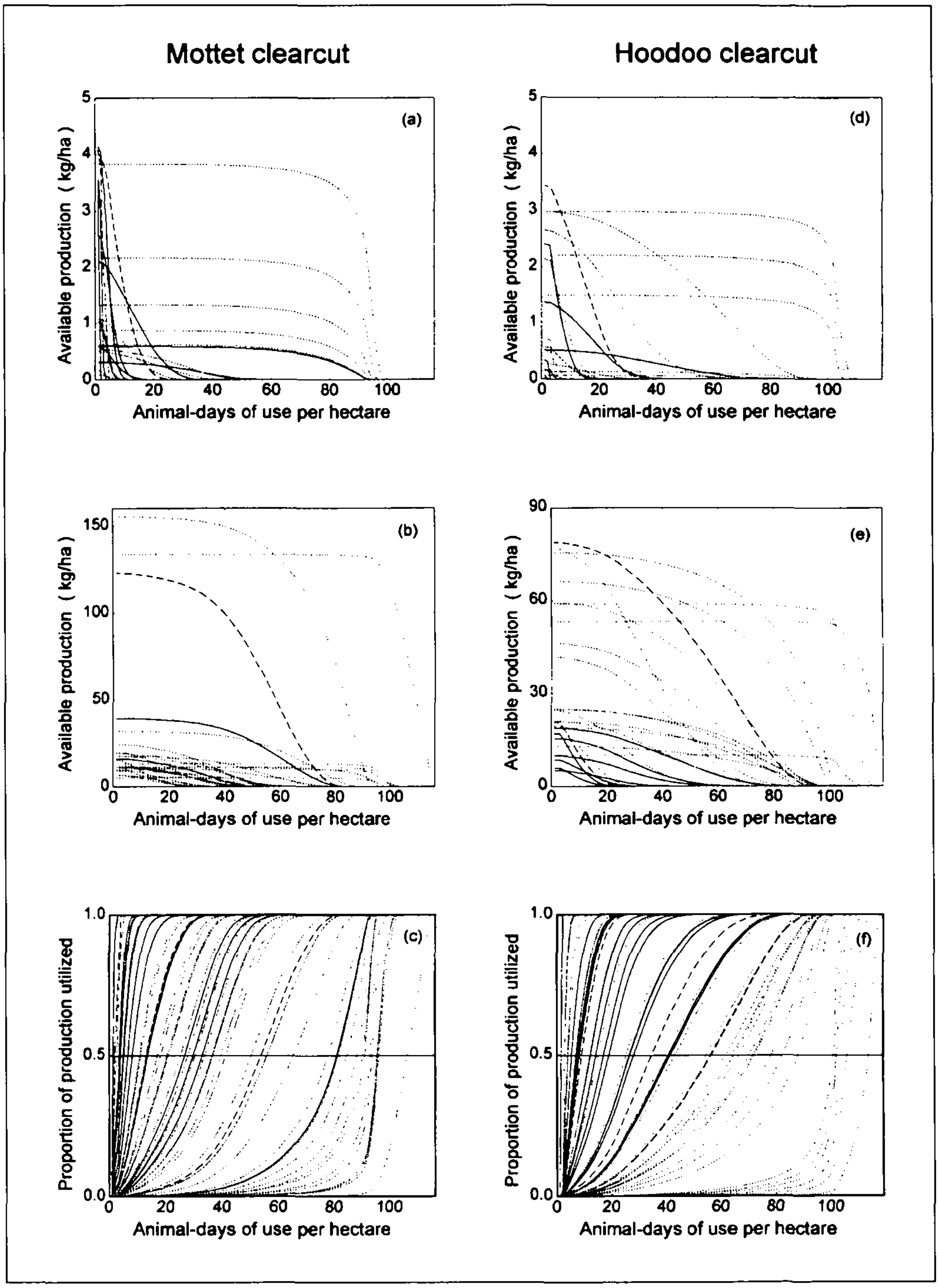

Figure 12—Modeled depletion and utilization profiles (panels c, f, i, and l) for plant taxa at the Mottet and Hoodoo sites, as functions of the number of animal-days of forage use by elk. For each site, the taxon-specific depletions are illustrated separately for those taxa accounting for ≤ 5 kg/ha (panels a, d, g, and j) and those accounting for > 5 kg/ha (panels b, e, h, and k).

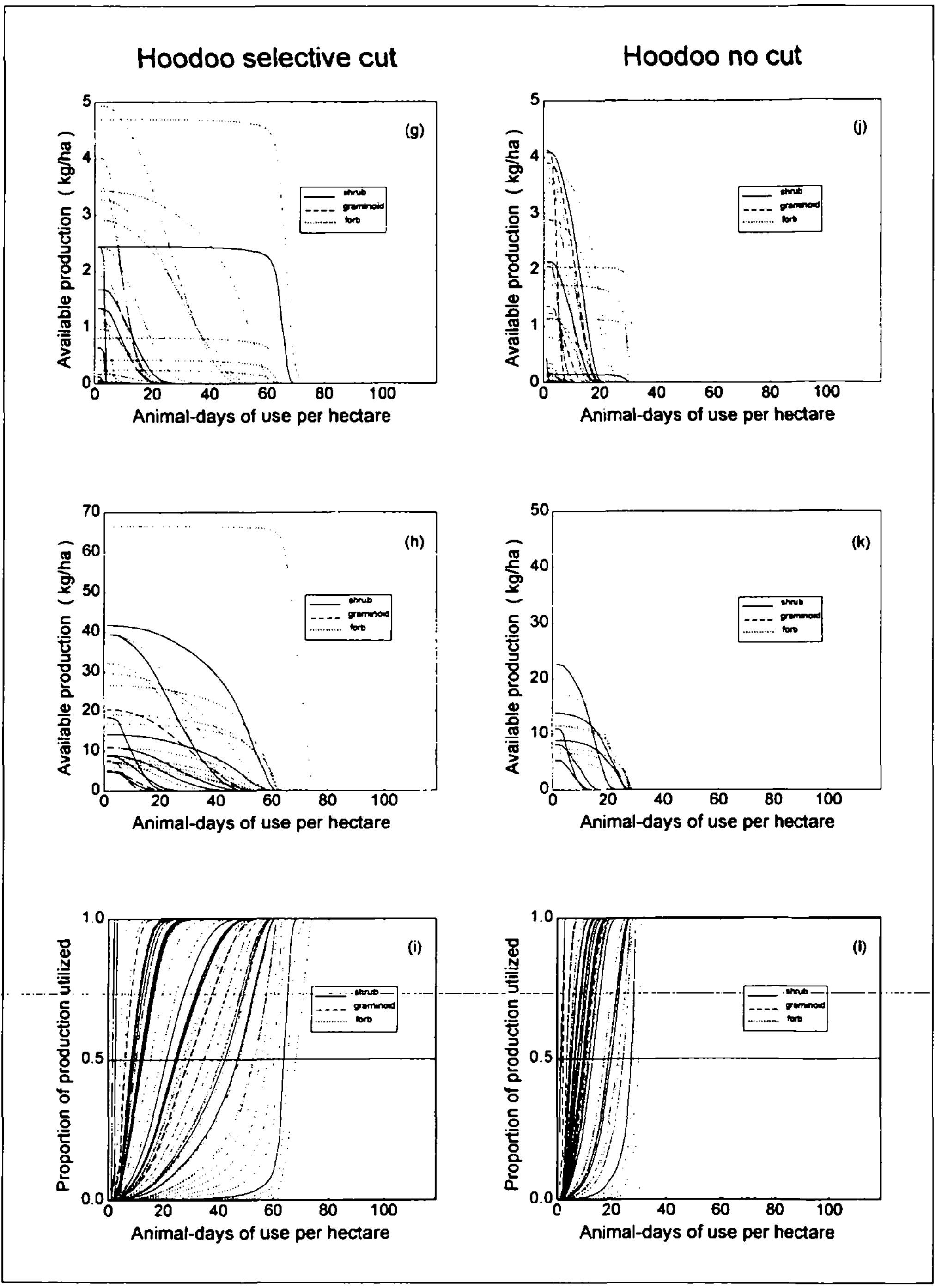

Figure 12—continued

Utilization modeling projected broad variation in depletion rates of the various plant taxa at the four sites we modeled, but shrubs tended to be depleted faster than herbs in each simulation (fig. 12). Cluster analysis based on mean daily utilization rates (u_i) and on r_i produced similar results for taxa in clearcut, selective cut, and uncut forest.

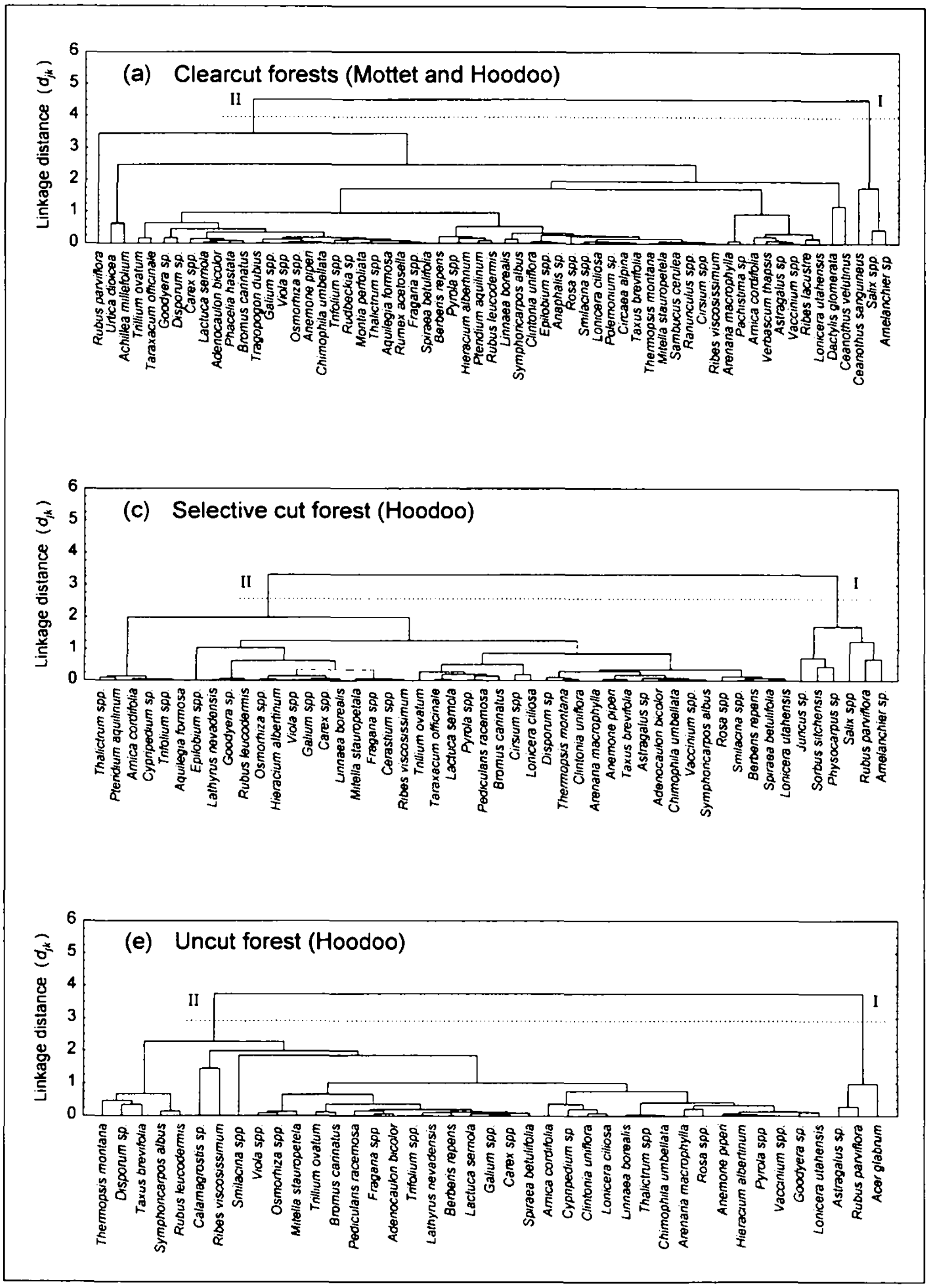

Figure 13—Joining trees and scatter plots from cluster analyses of taxa at clearcuts (a, b), selective cut (c, d), and uncut (e, f) forest sites, based on daily utilization rate immediately after episodic disturbance (u_i, modeled for 1966-67) and long-term relative change (r_i, estimated for 1966-92). Joining trees illustrate hierarchical relations. Scatter plots illustrate major clusters and class membership of shrubs, graminoids, and forbs. Roman numerals cross-reference hierarchical trees with scatter plots.

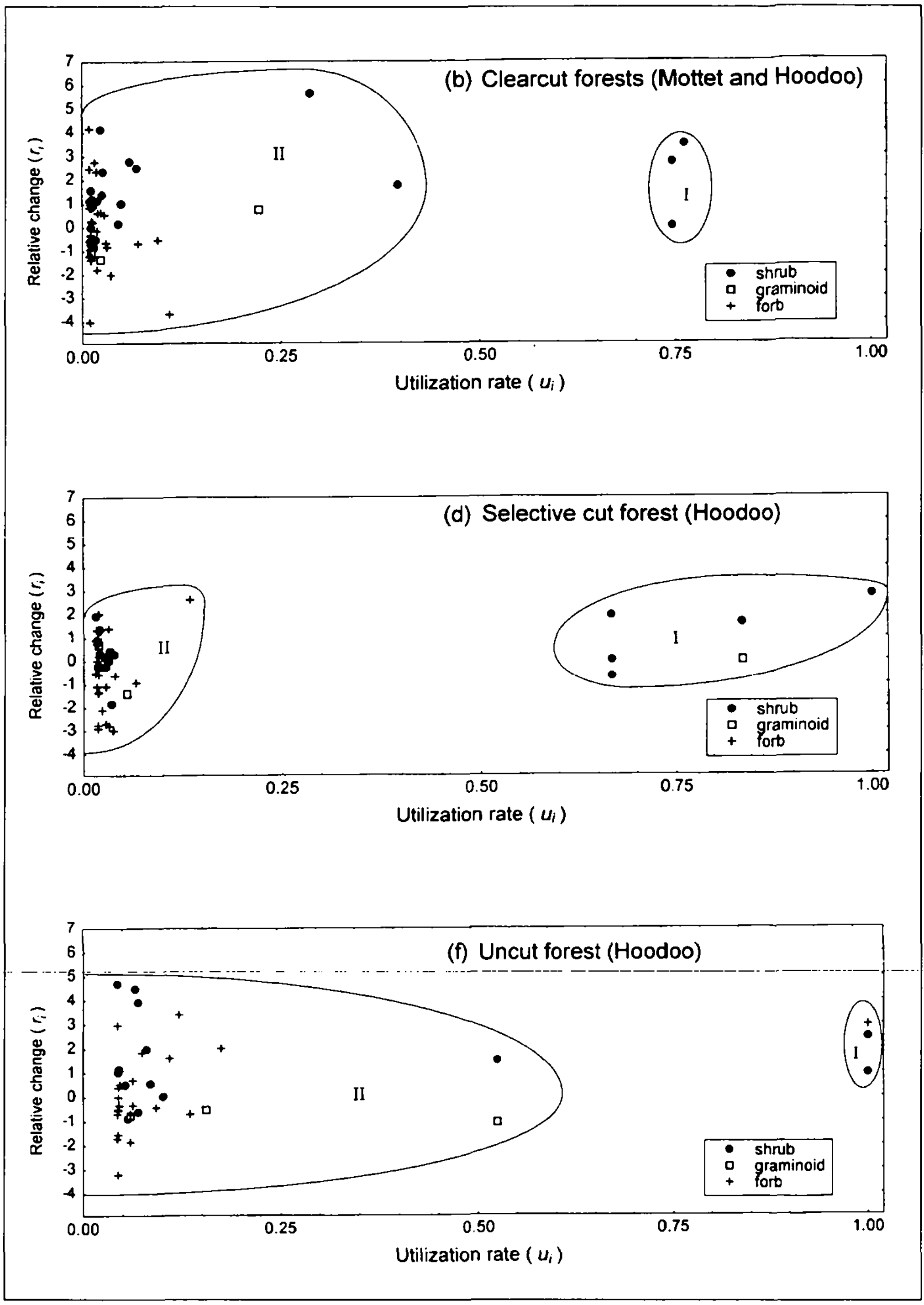

Figure 13—continued

All three analyses clustered taxa into two groups. *Amelanchier alnifolia*, *Ceanothus sanguineus*, and *Salix* spp. clustered separately from all other taxa in clearcuts (group I, 3.4 < d_{jk} < 4.5; fig. 13, and b). *Amelanchier alnifolia*, *Physocarpus*

Table 5—Mean biomass and nutrient accumulation in understory vegetation and forest floor, outside and inside 7 exclosures, northeastern Oregon

Component	Outside	Inside	*P*
	--Kilograms per hectare--		
Understory vegetation:			
Graminoids	187	133	NS[a]
Forbs	409	426	NS
Shrubs	1,042	2,858	0.05
Total, understory	1,638	3,417	.05
Forest floor	8,896	13,735	.05
Nutrients:			
Nitrogen	190	313	.01
Phosphorus	32	45	.01
Sulfur	10	14	NS
Calcium	273	446	.01
Magnesium	28	50	.01
Potassium	53	81	.05
Total, nutrients	586	949	.01

[a] NS = not significant; difference between outside and inside the exclosure was not significant ($P < 0.10$).

Table 6—Nutrient concentrations (percentage of mass) in foliage of grasses, forbs, and shrubs in study exclosures, Blue Mountains of northeast Oregon, expressed as means for samples collected inside and outside exclosures[1]

Nutrient	Graminoids	Forbs	Shrubs
Total nitrogen	1.03^{a}	1.41^{b}	1.46^{b}
Total phosphorus	$.29^{a}$	$.36^{b}$	$.42^{c}$
Total sulfur	$.06^{a}$	$.09^{b}$	$.09^{b}$
Total calcium	$.42^{a}$	1.11^{b}	1.24^{b}
Total magnesium	$.11^{a}$	$.20^{b}$	$.23^{b}$
Total potassium	$1.82^{a,b}$	2.12^{b}	1.40^{a}

[1] Nutrient concentrations of the individual foliage types inside the exclosures did not differ significantly from those outside. Different superscripts indicate significant differences in nutrient concentration among the foliage types ($P \leq 0.05$).

Table 7—Concentrations (percentage of mass) of total amounts of nutrients in forest floor and soil samples, outside versus inside 7 exclosures, northeastern Oregon[1]

	Carbon		Nitrogen		Phosphorus		Sulfur		Calcium		Magnesium		Potassium	
Samples	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In
Forest floor	42.70	42.20	0.78	0.91^{a}	0.13	0.12	0.04	0.03	1.06	1.25^{b}	1.18	1.42^{b}	0.17	0.18
Soil 0-10 cm	4.34	3.90	.17	.15	.18	.18	.01	.01	.37	.38	.25	.25	.21	.23
Soil 10-20 cm	2.52	2.29	.07	.09	.16	.16	.01	.01	.30	.29	.26	.25	.19	.22

[1] Superscripts in the table indicate significance level for differences, outside versus inside the exclosure: $a = P \leq 0.10$; $b = P \leq 0.05$.

malvaceus, *Rubus parviflora*, *Salix* spp., *Sorbus sitchensis*, and *Juncus* sp. clustered separately from other taxa in selective-cut forest (group I, $2.0 < d_{jk} < 3.3$; fig. 13, c and d). *Acer glabrum*, *Rubus parviflora*, and *Astragalus canadensis* clustered separately in uncut forest (group I, $2.3 < d_{jk} < 3.7$; fig. 13, e and f). Not all group I taxa were characterized by positive r_j, but all group I centroids shared this characteristic (fig. 13, b, d, and f).

Biomass and Nutrient Accumulations

Biomass and nutrient differences across all sites—Graminoid and forb biomass accumulations inside the exclosures were similar to those outside the exclosures. Significant differences were evident, however, for aboveground shrub biomass, total understory biomass, and forest-floor biomass (table 5). Shrub biomass averaged 2.7 times greater inside the exclosures than outside. Forest-floor biomass averaged 1.5 times greater inside than outside. In understory vegetation and forest floor, accumulations of individual nutrients, except S, were greater inside the exclosures than outside, as was accumulation of total nutrients (N, P, S, Ca, Mg, and K, but excluding C; table 5). Excluding S, nutrient pools ranged from 1.4 to 1.8 times greater inside exclosures than outside.

Nutrient concentrations within foliage samples collected inside the exclosures did not differ significantly from those of samples collected outside exclosures, regardless of growth form (i.e., shrub, graminoid, or forb). There were significant differences, however, among growth forms (table 6). Concentrations of N, S, Ca, and Mg were significantly higher in dicot (shrubs and forbs) foliage than in that of monocots (graminoids). The largest difference occurred in concentration of Ca, which was roughly two to three times greater in shrub and forb foliage than in graminoid foliage. Concentration of foliar P, however, was higher in shrubs than in graminoids or forbs. Concentration of K was highest in forbs and lowest in shrubs.

In the forest floor, concentrations of total N, Ca, and Mg were greater ($P < 0.10$) inside exclosures than outside (table 7), but no differences were detected for total concentrations of other nutrients (S, P, K, or C). For exchangeable nutrients, only concentrations of Ca and Mg were greater inside than outside (table 8). No nutrient (total or exchangeable amounts) differed in either the upper (0 to 10 cm) or lower (10 to 20 cm) soil layers (tables 7 and 8).

Table 8—Concentrations (parts per million) of exchangeable nutrients in forest floor and soil, outside versus inside 7 exclosures, northeastern Oregon[1]

	Nitrogen		Phosphorus		Sulfur		Calcium		Magnesium		Potassium	
Samples	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In
Forest floor	105	92	156	135	81	73	5975	6603[a]	780	902[a]	1396	1378
Soil 0-10 cm	29	28	65	74	11	9	2872	2697	174	169	539	598
Soil 10-20 cm	17	15		55	7	6	2115	1994	142	155	443	475

[1] Letter denotes significant difference, outside versus inside ($P \leq 0.05$).

Table 9—Understory and forest floor biomass at the Mottet exclosure, northeastern Oregon

	Burned			Not burned		
Biomass	Out	In	*P*	Out	In	*P*
	--------*Kg/ha*--------			--------*Kg/ha*-------		
Understory:						
Graminoids	14	30	0.770	268	42	0.001
Forbs	890	586	.300	754	722	.772
Shrubs	4	5600	< .001	34	1520	< .001
Total, understory	908	6216	< .001	1056	2284	.026
Forest floor	5870	10 531	.097	1646	8390	< .001

Table 10—Understory and forest floor biomass at the 3 Hoodoo exclosures, northeastern Oregon

	Uncut forest			Selective cut forest			Clearcut forest		
Biomass	Out	In	*P*	Out	In	*P*	Out	In	*P*
	-------*Kg/ha*-------			-------*Kg/ha*-------			------*Kg/ha*------		
Understory:									
Graminoids	54	32	0.466	58	44	0.371	94	72	0.161
Forbs	264	238	.018	272	400	.663	390	292	.104
Shrubs	372	2178	< .001	830	1286	.147	3320	4880	.970
Total, understory	690	2448	< .001	1160	1730	.263	3804	5244	.999
Forest floor	13 590	13 531	.967	13 646	14 109	.300	5565	10 545	.257

Biomass differences at individual sites—

Mottet—Biomass differences were pronounced at Mottet (table 9). Shrub biomass was 1,400 and 45 times greater inside the exclosure than outside in the burned and unburned areas, respectively. Inside the exclosure, shrub biomass was 3.7 times greater in the burned area than in the unburned area, and outside the exclosure, it was 8.5 times greater in the unburned area. Graminoid biomass in the unburned area was significantly greater outside the exclosure than inside, but there were no other significant differences for either graminoid or forb biomass. Total understory biomass was significantly greater inside the exclosure than outside, in both the burned and unburned areas, with differences of 6.8 and 2.2 times, respectively. Forest-floor biomass was 1.8 and 5.1 times greater inside than outside in the burned and unburned areas, respectively.

Hoodoo—At the uncut forest site, shrub and total understory biomass were each significantly greater inside the exclosure than outside, but forb biomass was greater outside the exclosure. Shrub, total understory, and forest-floor biomasses each appeared to be somewhat higher inside than outside exclosures at both the clearcut and selective-cut forest sites, but the differences were not statistically significant (table 10).

Table 11—Understory and forest floor biomass on select-cut forest sites in *Abies grandis* and *Pseudotsuga menziesii* forest types at Hall Ranch, northeastern Oregon

	Abies grandis			*Pseudotsuga menziesii*		
Biomass	Out	In	*P*	Out	In	*P*
	---------*Kg/ha*--------			---------*Kg/ha*--------		
Understory:						
Graminoids	262	185	0.099	558	528	0.436
Forbs	160	632	.099	124	112	.149
Shrubs	2526	3588	.061	215	956	.026
Total, understory	2948	4405	.046	897	1596	.237
Forest floor	13 821	21 491	.099	8136	17 554	.069

Hall Ranch—Shrub, total, and forest-floor biomasses each were greater inside exclosures than outside at both the *Abies grandis* and *Pseudotsuga menziesii* selective-cut sites (table 11). At the *Abies* site, shrub biomass was 1.4 times greater inside the exclosure than outside; at the *Pseudotsuga* site it was 4.4 times greater inside than outside. At these two sites, respectively, total understory biomass was 1.5 and 1.8 times greater inside than outside, and forest-floor biomass was 1.6 and 2.1 times greater inside than outside. Neither graminoid nor forb biomass differed, inside versus outside, at the *P. menziesii* site. At the *A. grandis* site, however, graminoid biomass was 1.4 times greater outside the exclosure than inside, and forb biomass was 3.9 times greater inside the exclosure than outside.

Discussion

Review and Discussion of Results

Individual exclosures typically define small inferential space (Hurlbert 1984), and their best use is not in making broad-ranging inferences but rather for generating hypotheses that may be corroborated in other case studies or tested with more complex research designs. Nonetheless, they often provide the only quantitative evidence of herbivore effects given strict experimental control; moreover, when their results are repeated across several sites, they can provide managers with robust information and can motivate better experiments having broader inferential relevance (Eberhardt and Thomas 1991). We examined all exclosures in *Abies* and *Pseudotsuga* forests for which baseline data were available in our area, but we recognize their design limitations and suggest caution when acting on our results.

We found no repeatable influences of herbivory on community richness, Shannon-Weaver diversity, or evenness. Using a more rigorous sampling methodology, Stohlgren et al. (1999) also found no differences in richness, diversity, or evenness attributable to herbivory in a larger sample of grassland exclosures. Evenness, however, was roughly twice as high at Mottet and Hoodoo than at the Hall Ranch throughout the experiments (fig. 4). The basis for this difference is obscure. Edaphic factors differed somewhat among the sites (tables 1 and 2), but there also were differences in grazing history prior to the experiments (table 3). Heavy sheep grazing before the Hall Ranch experiments may have reduced evenness to comparable levels that were subsequently sustained regardless of experimental herbivore regime. In either event, the indices we used did not reveal consistent herbivory influences during the experiments.

We detected 213 (28 percent of 768 total) significant within-subject or temporal interaction effects on canopy development by individual taxa. Sixty-five of these were interpretable and of sufficient magnitude to suggest importance to managers. Over time, substantial herbivory effects were often of equal or even greater magnitude than those of the episodic agents. Herbivory's effects were generally greatest in clearcuts. This probably reflects higher forage production in the clearcuts than in selective cuts or uncut stands, and the tendency of ruminants to feed where forage density is high (Canon et al. 1987, Collins et al. 1978, Gillen et al. 1984, Harris 1954, Miller et al. 1981, Pickford and Reid 1948, Roath and Krueger 1982, Young et al. 1967b). Together these two factors would facilitate development of clearly visible effects in clearcuts even under rather weak sampling designs. Herbivory effects were less apparent in selective-cut and uncut forests, but our utilization model showed that even light selective grazing could cause effects there because of low plant productivity.

The null hypothesis of chance occurrence of the ANOVA and MANOVA effects implicitly assumes that plant taxa comprising the communities were likely to manifest the various interaction effects equally. However, substantial *Y×L×H* effects were detected more often than expected, and substantial *Y×F*, *Y×S*, and *Y×S×H* effects were detected less often than expected under the null hypothesis (table 4). The infrequent occurrence of substantial seeding effects suggests that seeding was less important than other disturbance agents in causing divergence among communities. Results suggest another alternative hypothesis for the *Y×F* and *Y×L×H* effects, H_a: substantial effects of fire and logging on understory are more likely to be contingent on subsequent herbivory regime than to be independent of it. This alternative is consistent with the conclusion of Bork et al. (1997) that herbivory is more important than site and other disturbance factors in determining the composition of forest communities. Nevertheless, the expected effects of logging and prescribed fire on forest vegetation in the Blue Mountains are almost never conditioned on expectations of the herbivory regimes that may follow.

Shrub suppression has been a concern of managers in the Blue Mountains for at least 50 years (Mitchell 1951), and is a common finding in forest settings (Ammer 1996, Anderson and Katz 1993, Bobek et al. 1979, Chadde and Kay 1991, Chytrý and Danihelka 1993, Dzieciolowski 1980, Hernandez and Silva-Pando 1996, Kroll et al. 1986, Pastor and Naiman 1992, Tilghman 1989, Trumbell et al. 1989, Woodward et al. 1994). Our cluster analysis and regression indicated a continuum of vegetation response to elk dietary preference to explain this common empirical result. Palatable deciduous shrubs predominated at one extreme of this continuum and unpalatable herbs predominated at the other extreme (fig. 11).

In our simulations, several shrubs were predisposed to rapid utilization because they were not abundant immediately after disturbance and yet were highly preferred by elk. The fact that most large herbivores feed selectively when choices are available implies that in most settings some plant taxa will be predisposed to suppression by them, even under circumstances of low herbivore stocking. Young and others (1967a) observed that shrub production is relatively low compared to that of herbs in recently logged *Abies* forests, and several of the shrubs we studied were indeed highly preferred by our test animals. Suppression of these taxa outside the exclosures was not surprising to us in retrospect, particularly given that juvenile (i.e., grazing sensitive) plants tend to predominate in recently disturbed areas.

Our utilization model calculated each plant taxon's utilization rate based not only on elk forage demand but also on the forage preferences exhibited by elk (α_i) and the proportional availability of each taxon in the plant community ($\hat{\pi}_i$). Calculation of the α and $\hat{\pi}$ arrays was specific to our experimental communities and to the dietary preferences of our experimental animals. Modeling on communities of different composition, or on different dietary preferences (e.g., for other elk, cattle, or deer, or combinations of the three herbivores), would have produced somewhat different plant utilization profiles. More grazing trials will be required to fully understand the extent to which variation in community composition and herbivory regime (i.e., herbivore type, density, season of use) controls secondary succession. Incorporating the timing of herbivory in relation to the occurrance of episodic disturbance will be important to future experiments. Herbivory in the first months or years after episodic disturbance could be more important to the secondary succession than herbivory later in the time stream.

Our results demonstrated that herbivores strongly influence the accumulation of biomass in these forests. At the end of the experiments, total understory biomass averaged 2.1 times greater inside exclosures than outside, and forest-floor biomass averaged 1.5 times greater inside than outside. We are unaware of comparable information for total biomass, but the apparent suppression of biomass accumulation on the forest floor agreed with results of two other studies. Tiedemann and Berndt (1972) report that forest-floor biomass was 60 percent greater inside an exclosure in *Pinus ponderosa* forest than outside after 30 years of grazing exclusion. Similarly, Pastor et al. (1988) report that forest-floor biomass was about four times deeper inside a boreal-forest exclosure than outside, and that moose had reduced annual litterfall at two of three sites studied. Our results suggest that accumulation of shrub biomass is influenced by herbivores to a greater extent than that of grasses or forbs. The greater accumulation of shrub biomass inside exclosures probably accounts for the greater amounts of forest-floor and total biomass observed there. Pastor et al. (1988, 1993) also report that shrubs are the major source of forest-floor biomass in boreal forest.

Our results did not demonstrate strong herbivory influences on nutrient pools in soil. We composited our soil samples and thus could not test for herbivory effects on soil C or N pools within sites, but we did not detect herbivory effects on these nutrients or on P, S, or K in soil across sites. Tiedemann and Berndt (1972) did not detect differences in total C or total N in the upper 30 cm of soil after 30 years of grazing exclusion in a *Pinus ponderosa* forest. Similarity between pools of exchangeable nutrients in soil, inside versus outside the exclosures, may reflect rapid uptake of free nutrients or establishment of comparable equilibria in grazed and protected areas. Milchunas and Lauenroth (1993) summarize exclosure studies in which soil C ($n = 27$) and N ($n = 39$) was measured, observing that pools of these nutrients in grazed areas were greater than or equal to those in protected areas in about half the cases.

Although we did not observe herbivores to affect soil nutrients, we did observe herbivory effects on some forest-floor nutrient pools (total N, Ca, and Mg and exchangeable Ca and Mg). Shrubs were major contributors of litterfall inside the exclosures, particularly in clearcuts where the potential for shrub expression was greatest. Also, shrub foliage (and that of forbs) contained relatively high concentrations of N, P, S, Ca, and Mg compared to graminoids. Greater amounts of these nutrients inside exclosures probably reflects the contribution of shrub foliage to forest-floor biomass (Klemmedson 1975). Greater accumulation of forest-floor Ca inside exclosures may reflect a role of shrubs in translocating Ca from the lower soil profile (Binkley and Husted 1983).

Implications for Managers

Forest succession is a function of edaphic factors, the density and viability of seeds and sprouting rootstocks, episodic disturbance regimes, and herbivores. The influence of herbivory is a function of the operative herbivore species, seasonal timing and duration of grazing, and grazing intensity (Holechek et al. 1982, 1987; Krueger 1983; Rhodes and Sharrow 1990; Urness 1990; Vavra 1983, 1986; Vavra et al. 1989). Variation in herbivory regime alters the utilization profile of a plant community and thus can alter its successional trajectory. Variation in herbivory also can modify seed production and seed banks (Allison 1987, Kay 1995, Kay and Chadde 1992, Verkaar 1987) and alter nutrient dynamics (Pastor and Cohen 1997, Pastor and Naiman 1992, Pastor et al. 1993, this study), thereby influencing succession. Separation of feeding niches and density variation among herbivore species cause each herbivore species to have somewhat unique effects on plant communities. Nonetheless, the response of each plant community to herbivory is ultimately a response to the combined influences of all operative herbivores. The site conditions and herbivory regimes represented in our sample are common and widely distributed in the Blue Mountains, but our study still represents only a small subset of the possible ranges of plant potential and herbivory.

In some ecological settings, ruminants have been bestowed “keystone” status (e.g., Molvar et al. 1993), in the sense that they can control ecosystem properties (Mills et al. 1993). Even so, the importance of herbivory is not well recognized in the predominant management paradigms for western forest ecosystems. Management's attention has focused on influences of episodic agents such as logging and fire (e.g., Agee 1996, Aubry et al. 1999, Langston 1995, Quigley and Arbelbide 1997, USDA Forest Service 1996). Where some attention has been directed to herbivory, it has focused on influences of livestock grazing, without much respect for the potential influences of wild herbivores (e.g., Belsky and Blumenthal 1997, Fulé et al. 1997). In the Blue Mountains, however, long-term declines in livestock herbivory have been substantially compensated for by increases in elk and deer herbivory (Irwin et al. 1994). If ruminant herbivores do indeed exert widespread controlling influences, then we should be able to describe where those influences will be most relevant to managers and thereby identify where applied research will be most beneficial.

Management planning tools—Knowledge of herbivore effects is important to managers because matrix logic is being used increasingly for forest planning. By crossing or nesting seral vegetations with potential climax vegetations, planners hope to build matrices representing the array of vegetations one might expect to occur in a landscape. When mapped and linked with forest growth models, the cells in these matrices comprise ecological units that can be used to analyze landscapes in terms of such variables as timber inventories, vegetation mosaics, and wildlife habitat indices. By calculating responses of these variables to hypothetical or proposed management schemes, the forest planner can hope to identify management scenarios producing desirable outcomes (e.g., Roloff et al. 1999). "Ecosystem diversity matrices" (Haufler 1994, Haufler and Irwin 1993, Haufler et al. 1996), "GAP" analysis (Scott et al. 1993), "core reserve" (DellaSala et al. 1996), and "emphasis-use" (Everett and Lehmkuhl 1996) conservation strategies all use some matrix logic.

Knowledge of how herbivores influence forest vegetation is crucial to any matrix-based planning strategy because variation in herbivory regime can influence the stability of the planning matrix. When using a vegetation matrix for planning purposes, one must assume that the planning matrix is stable, meaning that the relations among seral and climax vegetations in the matrix are constant in space and over time. By varying herbivory regimes, however, managers can alter the pathway of seral vegetation to climax and even alter the composition of "climax" vegetations.

In conifer forests, the potential climax vegetation for any given site usually is assigned based largely on estimated differences in the abundance of "key" plant taxa generally assumed to reflect soil and climate (e.g., Daubenmire and Daubenmire 1968, Johnson and Clausnitzer 1992). Climax vegetations, or associations, are characterized by an overstory association of trees and an attendant association of understory taxa. Differentiation among the understory associations is generally based on differences in the abundance of key taxa as measured by presence or absence, reproductive success, or discrete variation in species-specific canopy cover (e.g., Johnson and Clausnitzer 1992, Johnson and Simon 1987). Our results show that herbivores can modify the abundance of several of these key taxa. Some of the susceptible taxa were *Acer glabrum*, *Alnus sitchensis*, *Linnaea borealis*, *Mitella stauropetala*, *Physocarpus malvaceus*, *Pteridium aquilinum*, *Spiraea betulifolia*, *Taxus brevifolia*, and *Vaccinium membranaceum*. Thus, variation in herbivory can influence the stability of the climax associations, which are keyed to the abundance of these taxa.

The uncut forest at Hoodoo provided an example of this herbivory effect. In 1995, we determined the potential climax vegetation for that site, first inside and then outside the exclosure, by using the relevant key to the forest vegetation (Johnson and Clausnitzer 1992). The keyed association was *Abies grandis/Taxus brevifolia/Linnaea borealis* inside the exclosure. We keyed the potential climax association outside the exclosure to *Abies grandis/Clintonia uniflora*. Thus, shrubs defined the apparent climax understory association inside the exclosure, but herbs defined the apparent climax outside the exclosure. We thus concluded that the *Clintonia uniflora* understory association is not a climax association at all, but more likely represents a variation of herbivore disclimax (Daubenmire and Daubenmire 1968), or a "grazing lawn" (McNaughton 1984), beneath mature forest canopy (fig. 17 in the appendix).

How many other herb-dominated understory associations are really herbivore disclimaxes? Evidence is growing that such modifications are not unique but actually rather widespread (Jenkins and Starkey 1996, Peek et al. 1978, Schreiner et al. 1996). Knowledge of them is fundamentally important to managers and planners, because their matrix logic assumes that vegetation on disturbed sites will consistently succeed to predictable climax associations. Clearly, the veracity of this assumption can be strictly dependent on the planner having accounted for an herbivory's site-specific influences on succession.

Wildlife habitat in transitory settings—If herbivore-induced modifications of succession are indeed widespread, then they profoundly affect links that forest managers assume to exist between their management practices and wildlife populations. Consider that Neotropical migrants are relatively well represented in the avifauna of *Abies grandis* forests in the Blue Mountains (Sallabanks and Riggs 1998). Even though some Neotropical migrants nest primarily in mature forest canopies, many nest in shrubs and saplings, either in burns and clearcuts or under mid- to late-successional coniferous canopy. However, some shrub-nesting species may be relatively unabundant in mixed-conifer forests of the Blue Mountains (Bunnell et al. 1997). Such observations appear to link the abundance of avifauna in mixed-conifer forests to herbivores in a manner similar to that already documented in Eastern deciduous forests (e.g., deCalesta 1994, McShea and Rappole 2000). If so, what is the relative importance of logging and fire to that of chronic herbivory in determining the composition and productivity of the regional avifauna? The manager cannot answer such questions without an understanding of how episodic disturbance and herbivory interactively influence forest vegetation at the landscape scale over time.

In temperate forests, ruminant carrying capacity (Caughley 1979, McCullough 1992) is strongly tied to the amount and quality of early seral vegetation (McCullough 1979). In this context, early seral vegetations have been referred to collectively as "transitory range" because of strong temporal dynamics in their production and composition profiles (Hedrick et al. 1968, Hett et al. 1978, Jenkins and Starkey 1996, Leege 1968, Pengelly 1963, Young et al. 1967a,). The quality of transitory communities for supporting herbivores is a function of the density of assimilatable nutrients in plant tissues, as compounded by the amount of vegetation produced. This quality can be reflected in the abundance of preferred plant taxa into which any community is partitioned. The most valuable plants and plant tissues typically comprise relatively small proportions of total community biomass (Hobbs and Swift 1985, McCullough 1979), and as the more valuable foods decline in abundance, herbivores are forced to increase their consumption of less valuable ones (Hobbs and Swift 1985, Smith 1965). Most herbivores typically forage selectively to acquire the more nutrient-rich foods to which their particular mouth parts and digestive system are adapted. Selective foraging is thus the core of a feedback mechanism through which herbivores influence their immediate energy balance and also the quality of their own food supplies over time.

Herbivores may enhance or diminish the quality of transitory range. They can enhance it by their fertilization effects (McNaughton 1976) and by stimulating the growth of some herbivore-adapted plants on which they feed (Molvar et al. 1993, Peek et al. 1978). The term "herbivore optimization" has become popular in referring to such effects. Herbivores can also diminish the quality of transitory range, however, by suppressing their preferred food plants.

It is not unreasonable to assume that some plants benefitted from herbivory outside our exclosures. Outside the exclosures, several plant taxa avoided by elk apparently benefitted from the suppression of those that were preferred. Plant production was probably enhanced, at least temporarily, at the microsites where herbivores deposited their urine and feces. It also is possible that some grazed plants may have enhanced their productivity through adaptations to cropping.

Despite the potential for such positive effects, selective suppression of preferred plant taxa probably had a dominant influence on these communities over time. Most of the suppressed taxa were shrubs. This is important because forest shrubs often are nutritionally superior to herbs, particularly late in the growing season (Cook, in press; Renecker and Hudson 1988) when herbaceous plants are senescent, even as lactating females and their offspring maintain high nutrient demands (Cook et al. 1996a, Irwin et al. 1994). Some deciduous shrubs offer ruminants long leaders having high leaf-to-stem ratios that facilitate high rates of intake of digestible nutrients (Canon et al. 1987). Intake rate is correlated with availability of acceptable foods (Hudson and Watkins 1986, Wickstrom et al. 1984), and daily consumption of assimilatable nutrients during seasons of high nutritional demand influences animal production more than any other factor (Minson and Wilson 1994).

One might therefore expect foraging efficiency to reflect the influences of herbivory on these transitory communities. Lower foraging efficiency outside exclosures, compared to inside, would indicate that the herbivore regimes had a negative influence on carrying capacity. Indeed, foraging efficiency of the elk used in our experiment was significantly lower outside exclosures than inside them (see Irwin et al. 1994). One can conclude, therefore, that over time these herbivory regimes negatively influenced the transitory resource. It remains unclear, however, the extent to which the long-term negative effect may have been balanced by any shorter term positive effects.

If selective use of plant taxa plays a crucial role in determining the dynamics of seral vegetation, then the balance between herbivory and seral vegetation is crucial to managing carrying capacity and herbivore productivity in these forests. This balance can be manipulated only by either controlling herbivore numbers or by controlling forest disturbance regimes (Cook et al. 1996b; DeByle 1979; deCalesta and Stout 1997; Irwin and Peek 1983a, 1983b; Regelin et al. 1974).

Managers typically try to maintain a static balance between herbivore numbers and food supply. They may monitor this balance via usage rates for selected plant species that typically exhibit moderate and relatively constant usage rates through the grazing season ("key species concept," Smith 1965). In doing so, managers seek to achieve more or less moderate use of the total plant community but with somewhat higher use of the more preferred and less abundant plant taxa and somewhat lower use of those taxa that are less preferred and more abundant (fig. 12, c, f, i, and l). We observed that a few highly preferred plant taxa may be particularly predisposed to suppression in seral *Abies* vegetations. Most of these are shrubs, and most are adapted to episodic disturbance. Nonetheless, they were suppressed early in secondary succession. We hypothesize that they were predisposed to suppression then by low abundance and high palatability, and possibly low resistance to grazing as well. Early suppression of these taxa precluded their contribution to the carrying capacity of the transitory communities over time.

These taxa may be used as indicators of herbivore effects, and it may make sense for managers to focus utilization monitoring on the plant communities occupying recently disturbed sites. Failure of these species to regenerate might then be used to trigger reductions in herbivore numbers or increases in local disturbance regimes (e.g., Debyle 1979, deCalesta and Stout 1997). An ecologically based rationale for managing the balance of herbivore numbers with episodic disturbance has yet to be developed for the Blue Mountains forest ecosystems (e.g., Oregon Department of Fish and Wildlife 1990, 1992; USDA Forest Service 1996). The lack of such an ecological rationale may be viewed as a major obstacle to reliable ecosystem-level planning. Maintaining diverse and well-distributed shrub-dominated successions may be a crucial consideration in developing one.

Finally, habitat evaluation indices for wild herbivores virtually ignore herbivory effects in transitory communities (e.g., Thomas et al. 1988, Wisdom et al. 1986). As applied, these models generally index habitat quality as a function of the amount and interspersion of cover types (among other factors) but usually without respect to forage composition, production, or quality, and also without respect to either animal density or nutrient demand of herbivore populations. Size of forest openings and distance-to-edge are important components of these models that managers often try to use fully to maximize landscape use by wild herbivores. In practice, managers accomplish this by dispersing episodic disturbance in small units rather than large ones. Maximizing landscape use by ruminants is counter, however, to developing refugia in which grazing-sensitive plants can reproduce (Alverson et al. 1988, Mitchell 1951, Parks et al. 1998, Reimoser and Gossow 1996). New models will have to be developed to help managers project the influences of herbivory across landscapes under varying disturbance regimes.

Herbivores can affect long-term site productivity—In mature conifer forests, most of the total N is contained in soil, whereas N sequestered in aboveground biomass (trees, understory, woody debris, and forest floor) ranges from 12 to 39 percent of the total (Brown 1977, Klemmedson 1975). About 60 to 70 percent of the aboveground N is contained in the forest floor alone. Nutrients in the aboveground biomass (including forest-floor biomass) are vulnerable to volatilization by fire. Nitrogen and S are most susceptible to volatilization (Debano and Conrad 1978, DeBell and Ralston 1970, Klemmedson 1976, Tiedemann 1987) and are often deficient in soils of the Blue Mountains (Geist 1974, Tiedemann et al. 1998).

Burning can enhance the amount of N immediately available to plants, thereby enhancing plant growth for some time after burning, but fire also can cause a net loss in the total amount of N on a site (St. John and Rundel 1976, Tiedemann et al. 2000). Nitrogen loss approximating 700 to 800 kg/ha has been documented following wildfire and broadcast burning (Grier 1975, Jurgensen et al. 1991). Compared to episodic losses of this magnitude, passive accretion of N from precipitation in the Blue Mountains is < 2 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Tiedemann et al. 1988). Thus, several hundred years can be required for passive replacement of volatilized N.

Under such circumstances, N-fixing plant taxa can be critical to recovery of the N-pool. Reported accretions of N by fixation are highly variable, ranging from 2 to 280 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Binkley et al. 1982; Boring et al. 1988; Carlson and Dawson 1985; Jurgensen et al. 1981, 1991). Nonetheless, there is general agreement that fixation is an important mechanism of N-accretion (Boring et al. 1988, Bormann et al. 1977, Griffiths et al. 1993, Sprent and Sprent 1990) and N-pool restoration on disturbed sites (Boring et al. 1988). Even if N is fixed at only 2 $kg \cdot ha^{-1} \cdot yr^{-1}$, the rate of N-replacement is double that if no N-fixing occurs, and higher rates of fixation can substantially shorten the time required for restoration of the prefire pool.

Several taxa we studied have effective rhizobium or actinomycete associations involved in N-fixing (Klemmedson 1979, Vlassak et al. 1973), including *Astragalus* spp., *Ceanothus* spp., *Lathyrus nevadensis*, *Thermopsis montana*, and *Trifolium* spp. *Trifolium* and *Lathyrus* were more developed outside the exclosures than inside them, whereas *Astragalus*, *Ceanothus*, and *Thermopsis* developed to greater extents inside the exclosures on average (fig. 12). We did not compare rates of N-fixing among treatments or plant species, but one can certainly hypothesize that herbivores influenced N-accretion at these sites by altering the composition of plant communities. More research is needed regarding how the composition of plant communities influences N-fixation and on how grazing influences the N-fixing of individual plants.

Pastor and Binkley (1998) calculated the mass balance of N in a model ecosystem, explicitly accounting for N-fixation and residence time of N in plant tissues (among several other variables). In their model, residence time is crucial to the flow of N through the ecosystem. Residence time is relatively high for N bound in woody tissues; this N is lost via leaching and denitrification at relatively low rates compared to N bound in herbage (Harmon et al. 1986, Pastor and Binkley 1998, Pastor et al. 1993).

Suppressing shrubs thus can enhance tree growth early in stand development by reducing competition for nutrients, but doing so may reduce N-availability later in stand development. Weigand and others (1993) projected timber-volume yield based on tree growth they observed at exclosures. Timber yield was usually greater in grazed areas than in ungrazed areas, apparently because herbivores suppressed competing vegetation early in stand development (e.g., Monfore 1983). However, one of the stands studied was 50 years old, and its projected timber yield was 30 percent greater *inside* the exclosure than outside it. At that site, *Ceanothus velutinus*, a fire-adapted, shade-intolerant, N-fixing shrub (Binkley et al. 1982, Tiedemann and Klock

1977, Youngberg and Wollum 1976), completed its life cycle within the exclosure, but it was virtually eliminated outside the exclosure early in succession (Tiedemann and Berndt 1972). *Ceanothus* bound and retained N in its tissues early in the succession; the N then was released as the forest canopy developed and eventually suppressed *Ceanothus* later in the succession. Deciduous shrubs or trees can enhance nutrient availability in southwestern pine forests as well (Klemmedson 1991).

Several investigators have observed that herbivores enhance the N-pool where they deposit urine and feces (Floate 1981, Hilder 1964, Petersen et al. 1956, Watson and Lapins 1969). This enhancement is certainly real and is often cited as evidence that herbivores positively influence site productivity. Nevertheless, it is crucial to bear in mind that in performing this function herbivores are only redistributing a part of the extant N-pool around the landscape. In contrast, N-fixing plants actively add new N to landscapes. Consequently, herbivory focused on N-fixing plants may profoundly influence the rates of replenishment of N-pools after episodic depletion. This effect could be particularly significant to site productivity in landscapes subjected to frequent fire. In commercial timberlands, it could exert substantial control on the amount of supplemental N required to maintain wood production over extended period. Thus, herbivore management is relevant to the sustainability of production and to management costs.

Conclusions

Wild and domestic herbivores should be considered agents of chronic disturbance, capable of influencing succession, nutrient cycles, forest productivity, and habitat characteristics, to extents equal to those of episodic fire or timber harvest. Dominant management paradigms for upland forests in the Blue Mountains ecoregion have largely assumed succession to be rather unresponsive to herbivory, however, and have focused instead on fire and logging as the primary determinants of forest attributes. Fire and logging certainly influence forest attributes by initiating secondary succession. Nevertheless, the consequences of episodic disturbance are strongly dependent on the herbivory regimes that follow. If ecosystem management depends on being able to predict the consequences of stand management, then ruminant herbivory must be given standing equal to that of episodic agents in management and planning paradigms. Focusing on episodic disturbance agents ignores the keystone role of ruminant herbivory in ecosystem processes.

The effects of herbivores on upland forests probably have been studied more in the Blue Mountains than anywhere else in the inland region of the Pacific Northwest (see Case and Kauffman [1997] for some data regarding lowland forests). Nonetheless, the knowledge generated to date can be considered as only rudimentary owing to the limits of extant experimental designs. If variation in herbivory regimes can modify the influence of episodic disturbances, then consideration of herbivores must be intensified in disturbance research. This will require much more than retrospective analysis of a handful of old exclosures. Scientists must be challenged to integrate herbivory into disturbance research at scales meaningful to managers. Meeting this challenge will require much larger experimental designs and modeling that can clarify how varying herbivore species and density can be expected to influence succession in a variety of circumstances. These designs should be developed and executed in interdisciplinary contexts so that research results and their application can benefit from herbivore ecologists, forest ecologists, and landscape ecologists.

Predicting the influences of alternate management strategies for ecosystem management will depend on identifying the range of successional pathways that can result from various combinations of herbivory and episodic disturbance, and the conditions under which each occurs. Ecosystem research must be adjusted accordingly, to focus less on single-agent effects and more on effects of multiagent interactions.

Acknowledgments

J.G. Smith and R.D. Nelson provided support for establishing the Mottet and Hoodoo exclosures in the 1960s. G. Strickler and J.M. Geist provided early insight on processes of forest development in the Blue Mountains. W.G. Williams was instrumental in the construction, maintenance, and collection of data at Mottet and Hoodoo through 1988. T. Smergut collected data at Mottet and Hoodoo in 1992. M. Messaros collated the Mottet and Hoodoo data sets for analysis. L. Erickson, Oregon Department of Fish and Wildlife, interpreted the census data from which we calculated cattle-equivalencies for wild herbivores. D. Verbyla advised the senior author on FORTRAN programming. J. Dick prepared the tables. The manuscript benefited from constructive reviews by C.E. Kay, J. Kie, L.J. Lyon, R. Moen, J. Pastor, T. Philippi, and D. Verbyla. K. Esterholdt and L. Starr edited the manuscript. This research was funded by Boise Cascade Corporation, USDA Forest Service, Oregon Agricultural Experiment Station, and the National Council of the Paper Industry for Air and Stream Improvement.

English Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	0.39	Inches
Meters (m)	3.28	Feet
Square meters (m^2)	1.20	Square yards
Kilograms (kg)	2.21	Pounds
Grams (g)	0.035	Ounces
Hectares (ha)	2.47	Acres
Kilograms per hectare (kg/ha)	0.89	Pounds per acre
Celsius (°C)	1.8 + 32	Fahrenheit
Square kilometers (km^2)	0.386	Square miles

References

Agee, J.K. 1996. Fire in the Blue Mountains: a history, ecology, and research agenda. In: Jaindl, R.G.; Quigley, T.M., eds. Search for a solution: sustaining the land, people, and economy of the Blue Mountains. Washington, DC: American Forests: 119-145.

Allison, T.D. 1987. The reproductive biology of Canada yew (*Taxus canadensis*) and its modification by herbivory: implications for wind pollination. Minneapolis: University of Minnesota. 145 p. Ph.D. thesis.

Alverson, W.S.; Waller, D.M.; Solheim, S.L. 1988. Forests to deer: edge effects in northern Wisconsin. Conservation Biology. 2: 348-358.

Ammer, C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management. 88: 43-53.

Anderson, R.C.; Katz, A.J. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure. Biological Conservation. 63: 203-208.

Aubry, K.B.; Amaranthus, M.P.; Halpern, C.B. [and others]. 1999. Evaluating the effects of varying levels of patterns of green-tree retention: experimental design of the DEMO study. Northwest Science. 73: 12-26.

Barnes, R.M. 1977. Review of the applications of the inductively coupled plasma. In: Barnes, R.M., ed. Applications of inductively coupled plasma to emission spectroscopy. Philadelphia: The Franklin Institute Press: 3-49.

Bartos, D.L.; Brown, J.K.; Booth, G.D. 1994. Twelve years biomass response in aspen communities following fire. Journal of Range Management. 47: 79-83.

Belsky, A.J.; Blumenthal, D.M. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology. 11: 315-327.

Binkley, D.; Cromack, K., Jr.; Fredriksen, R.C. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. Forest Science. 28: 720-724.

Binkley, D.; Husted, D.L. 1983. Nitrogen accretion, soil fertility, and Douglas-fir nutrition in association with redstem ceanothus. Canadian Journal of Forest Research. 13: 122-125.

Bobek, B.; Perzanowski, K.; Siwanowicz, J.; Zielinski, J. 1979. Deer pressure on forage in a deciduous forest. Oikos. 32: 373-380.

Boring, L.R.; Swank, W.T.; Waide, J.B.; Henderson, G.S. 1988. Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. Biogeochemistry. 6: 119-159.

Bork, E.W.; Hudson, R.J.; Bailey, A.W. 1997. Upland plant community classification in Elk Island National Park, Alberta, Canada, using disturbance history and physical site factors. Plant Ecology. 130: 171-190.

Bormann, F.H.; Likens, G.E.; Melillo, J.M. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science. 196: 981-983.

Bowers, M.A. 1997. Influence of deer and other factors on an old-field plant community. In: McShea, W.L.; Underwood, H.B.; Rappole, J.H., eds. The science of overabundance: deer ecology and population management. Washington, DC: Smithsonian Institution Press: 310-326.

Bowman, R.A. 1988. A rapid method to determine total phosphorus in soils. Soil Science Society of America Journal. 52: 1301-1304.

Bremner, J.M.; Mulvaney, C.S. 1982. Total nitrogen. In: Page, A.L., ed. Methods of soil analysis. Part 2: Chemical and microbiological properties. 2d ed. Madison, WI: American Society of Agronomy: 595-624.

Brown, T.H. 1977. Nutrient distributions of two eastern Washington forested sites. Pullman, WA: Washington State University. 111 p. M.S. thesis.

Bunnell, F.L.; Kremsater, L.L; Wells, R.W. 1997. Likely consequences of forest management on terrestrial, forest-dwelling vertebrates in Oregon. Rep. M-7. Vancouver, BC: University of British Columbia, Centre for Applied Conservation Biology. 130 p.

Canon, S.K.; Urness, P.J.; DeByle, N.V. 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. Journal of Range Management. 40: 433-438.

Carlson, P.J.; Dawson, J.O. 1985. Soil nitrogen changes, early growth, and response to internal drainage of a plantation of *Alnus jorullensis* in the Columbian Highlands. Turrialba. 35: 141-150.

Case, R.L.; Kauffman, J.B. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. Northwest Science. 71: 115-126.

Caughley, G. 1979. What is this thing called carrying capacity? In: Boyce, M.S.; Hayden-Wing, L.D., eds. North American elk: ecology, behavior, and management. Laramie, WY: University of Wyoming: 2-8.

Chadde, S.W.; Kay, C.E. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. In: Keiter, R.B.; Boyce, M.S., eds. The Greater Yellowstone ecosystem: redefining America's wilderness heritage. New Haven, CT: Yale University Press: 231-262.

Chapman, H.D.; Pratt, P.F. 1961. Methods of analysis for soils, plants, and waters. Davis, CA: University of California: 161-172.

Chesson, J. 1978. Measuring preference in selective predation. Ecology. 59: 211-215.

Chytrý, M.; Danihelka, J. 1993. Long-term changes in the field layer of oak and oak-hornbeam forests under the impact of deer and mouflon. Folia Geobotanica et Phytotaxonomica. 28: 225-246.

Collins, W.B.; Urness, P.J.; Austin, D.D. 1978. Elk diets and activities on different lodgepole pine habitat segments. Journal of Wildlife Management. 42: 799-810.

Cook, J.G. [In press]. Nutrition and food habits. In: Toweill, D.E.; Thomas, J.W., eds. Elk of North America: ecology and management. 2d ed. Harrisburg, PA: Stackpole Books.

Cook, J.G.; Quinlan, L.J; Irwin, L.L. [and others]. 1996a. Nutrition-growth relations of elk calves during late summer and fall. Journal of Wildlife Management. 60: 528-541.

Cook, J.G.; Riggs, R.A.; Tiedemann, A.R. [and others]. 1996b. Large herbivore-vegetation feedback relations in the Blue Mountains ecoregion. In: Edge, W.D.; Olson-Edge, S.L., eds. Proceedings of the symposium: sustaining rangeland ecosystems; 1994 August 29-31; La Grande, OR. SR953. Corvallis, OR: Oregon State University: 155-159.

Cook, J.G.; Stutzman, T.W.; Bowers, C.W. [and others]. 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildlife Society Bulletin. 23: 711-717.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science. 33: 43-64.

Daubenmire, R.; Daubenmire, J.B. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agricultural Experiment Station, Washington State University.

DeBano, L.F.; Conrad, C.W. 1978. Effects of fire on nutrients in a chaparral ecosystem. Ecology. 59: 489-497.

DeBell, D.S.; Ralston, C.S. 1970. Release of nitrogen by burning in light forest fuels. Soil Science Society of America Proceedings. 34: 936-938.

DeByle, N.V. 1979. Potential effects of stable versus fluctuating elk populations in the aspen ecosystem. In: Boyce, M.S.; Hayden-Wing, L.D., eds. North American elk: ecology, behavior, and management. Laramie, WY: University of Wyoming: 13-19.

deCalesta, D.S. 1994. Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management. 58: 711-718.

deCalesta, D.S.; Stout, S.L. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin. 25: 252-258.

DellaSala, D.A.; Strittholt, K.R.; Noss, R.F.; Olson, D.M. 1996. A critical role for core reserves in managing inland Northwest landscapes for natural resources and biodiversity. Wildlife Society Bulletin. 24: 209-221.

Dick, W.A.; Tabatabai, M.A. 1979. Ion chromatographic determination of sulfate and nitrate in soils. Soil Science Society of America Journal. 43: 899-904.

Dyer, M.I.; Turner, C.L.; Seastedt, T.R. 1993. Herbivory and its consequences. Ecological Applications. 3: 10-16.

Dzieciolowski, R. 1980. Impact of deer browsing upon forest regeneration and undergrowth. Ekologia Polska. 28: 583-599.

Eberhardt, L.L.; Thomas, J.M. 1991. Designing environmental field studies. Ecological Monographs. 61(1): 53-73.

Edgerton, P.J. 1966. A study of plant succession and animal use following logging in the mixed-conifer type of the Blue Mountains, Oregon. Unpublished study plan FS-PNW-1701-W-20. 29 p. On file with: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850.

Edgerton, P.J. 1971. The effect of cattle and big game grazing on a ponderosa pine plantation. Res. Note PNW-172. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 p.

Edgerton, P.J. 1972. Big game use and habitat changes in a recently logged mixed conifer forest in northeastern Oregon. In: Proceedings of the 52d annual conference of Western Association of State Game and Fish Commissioners and Western Division, American Fisheries Society; 1972 July 16-19; Portland, Oregon. [Place of publication unknown]: [publisher unknown]: 1-8.

Edgerton, P.J. 1987. Influence of ungulates on the development of the shrub understory of an upper slope mixed conifer forest. In: Provenza, F.D.; Flinders, J.T.; McArthur, E.D., comps. Proceedings: symposium on plant-herbivore interactions; 1985 August 7-9; Snowbird, UT. Gen. Tech. Rep. INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 162-167.

Edgerton, P.J.; McConnell, B.R. 1976. Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. Res. Note PNW-277. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 6 p.

Erickson, L.R. 1974. Livestock utilization of a clear-cut burn in northeastern Oregon. Corvallis, OR: Oregon State University. 53 p. M.S. thesis.

Everett, R.L.; Lehmkuhl, J.F. 1996. An emphasis-use approach to conserving biodiversity. Wildlife Society Bulletin. 24: 192-199.

Floate, M.J.S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In: Clark, F.E.; Rosswall, T., eds. Terrestrial nitrogen cycles. Ecological Bulletin (Stockholm). 33: 485-601.

Fowler, W.B.; Helvey, J.D.; Johnson, C. 1979. Baseline climatic and hydrologic relationships for the High Ridge Evaluation Area. Gen. Tech. Rep. PNW-91. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 17 p.

Frank, D.A.; Evans, R.D. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology. 78: 2238-2248.

Frank, D.A.; Inouye, R.S.; Huntly, N. [and others]. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry. 10: 163-180.

Franklin, J.F.; Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Fulé, P.Z.; Covington, W.W.; Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications. 7: 895-908.

Geist, J.M. 1974. Chemical characteristics of some forest and grassland soils of northeastern Oregon. Res. Note PNW-217. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 15 p.

Gill, R.M.A. 1992a. A review of damage by mammals in North Temperate forests. 1: Deer. Forestry. 65: 145-169.

Gill, R.M.A. 1992b. A review of damage by mammals in North Temperate forests. 3: Impact on trees and forests. Forestry. 65: 363-388.

Gillen, R.L.; Krueger, W.C.; Miller, R.F. 1984. Cattle distribution on mountain rangeland in northeastern Oregon. Journal of Range Management. 37: 549-553.

Grier, C.C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Canadian Journal of Forest Research. 5: 599-607.

Griffiths, R.P.; Harmon, M.E.; Caldwell, B.A.; Carpenter, S.E. 1993. Acetylene reduction in conifer logs during early stages of decomposition. Plant and Soil. 148: 53-61.

Hall, F.C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. Region 6 Area Guide 3-1. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 62 p.

Harmon, M E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research. 15: 133-302.

Harris, R.W. 1954. Fluctuations in forage utilization on ponderosa pine ranges in eastern Oregon. Journal of Range Management 7: 250-255.

Haufler, J.B. 1994. An ecological framework for forest planning for forest health. Journal of Sustainable Forestry. 2: 307-316.

Haufler, J.B.; Irwin, L.L. 1993. An ecological basis for forest planning for biodiversity and resource use. Proceedings of the International Union of Game Biologists. 21: 73-81.

Haufler, J.B.; C.A. Mehl; Roloff, G.J. 1996. Using a coarse filter approach with a species assessment for ecosystem management. Wildlife Society Bulletin. 24: 200-208.

Hedrick, D.W.; Young, J.A.; McArthur, J.A.B.; Keniston, R.F. 1968. Effects of forest and grazing practices on mixed coniferous forests of northeastern Oregon. Tech. Bull. 103. Corvallis, OR: Oregon State University, Agricultural Experiment Station. 24 p.

Heinselman, M.L. 1978. Fire in wilderness ecosystems. In: Hendee, J.C.; Stankey, G.H.; Lucas, R.C., eds. Wilderness management. Misc. Publ. 1365. Washington, DC: U.S. Department of Agriculture, Forest Service: 248-278.

Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In: Mooney, H.A.; Bonnicksen, T.M.; Christensen, N.L. [and others], tech. coords. Fire regimes and ecosystem properties. Gen. Tech. Rep. WO-26. Washington, DC: U.S. Department of Agriculture, Forest Service: 7-57.

Hernandez, M.P.G.; Silva-Pando, F.J. 1996. Grazing effects of ungulates in a Galician oak forest (northwest Spain). Forest Ecology and Management. 88: 65-70.

Hett, J.; Taber, R.; Long, J.; Schoen, J. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabilis* forest, western Washington. Environmental Management. 2: 561-566.

Hilbert, D.W.; Swift, D.M.; Detling, J.K.; Dyer, M.I. 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia. 51: 14-18.

Hilder, E.J. 1964. The distribution of plant nutrients by sheep at pasture. Proceedings, Australian Society of Animal Producers. 5: 241-248.

Hitchcock, C.L.; Cronquist, A. 1981. Flora of the Pacific Northwest. Seattle: University of Washington Press. 730 p.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management. 60: 695-713.

Hobbs, N.T.; Schimel, D.S.; Owensby, C.E.; Ojima, D.S. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology. 72: 1374-1382.

Hobbs, N.T.; Swift, D.M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management. 49: 814-822.

Holechek, J.L.; Berry, T.J.; Vavra, M. 1987. Grazing system influences on cattle performance on mountain range. Journal of Range Management. 40: 55-59.

Holechek, J.L.; Vavra, M.; Skovlin, J.; Krueger, W.C. 1982. Cattle diets in the Blue Mountains of Oregon. 2: Forests. Journal of Range Management. 35: 29-242.

Holland, E.A.; Parton, W.J.; Detling, J.K.; Coppock, D.L. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. American Naturalist. 140: 685-706.

Hudson, R.J.; Watkins, W.G. 1986. Foraging rates of wapiti on green and cured pastures. Canadian Journal of Zoology. 64: 1705-1708.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54: 187-211.

Irwin, L.L.; Cook, J.G.; Riggs, R.A.; Skovlin, J.M. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystems. Gen. Tech. Rep. PNW-GTR-325. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 49 p.

Irwin, L.L.; Peek, J.M. 1983a. Elk, *Cervus elaphus*, foraging related to forest management and succession in Idaho. Canadian Field-Naturalist. 97: 443-447.

Irwin, L.L.; Peek, J.M. 1983b. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management. 47: 664-672.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. New Haven, CT: Yale University Press. 302 p.

Jenkins, K.; Starkey, E. 1996. Simulating secondary succession of elk forage values in a managed forest landscape, western Washington. Environmental Management. 20: 715-724.

Johnson, C.G., Jr.; Clausnitzer, R.R. 1992. Plant associations of the Blue and Ochoco Mountains. R6-EDW-TP-036-92. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 164 p.

Johnson, C.G., Jr.; Simon, S.A. 1987. Plant associations of the Wallowa-Snake Province. R6-ECOL-TP-255A-86. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 399 p.

Jurgensen, M.F.; Harvey, A.E.; Larsen, M.J. 1981. Effects of prescribed fire on soil nitrogen levels in a cutover Douglas-fir/western larch forest. Res. Pap. INT-275. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 6 p.

Jurgensen, M.F.; Tonn, J.R.; Graham, R.T. [and others]. 1991. Nitrogen fixation in forest soils of the inland Northwest. In: Harvey, A.E.; Neuenschwander, L.F., comps. Proceedings: management and productivity of western-montane forest soils; [dates of meeting unknown]; [location unknown]. Gen. Tech. Rep. INT-280. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 101-109.

Kaufmann, M.R.; Graham, R.T.; Boyce, D.A., Jr. [and others]. 1994. An ecological basis for ecosystem management. Gen. Tech. Rep. RM-246. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 22 p.

Kay, C.E. 1995. Browsing by native ungulates: effects on shrub and seed production in the Greater Yellowstone Ecosystem. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., comps. Proceedings: wildland shrub and arid land restoration symposium; [dates of meeting unknown]; [location unknown]. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 310-320.

Kay, C.E. 1997. The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: implications for ecological integrity. Canadian Field Naturalist. 111: 607-616.

Kay, C.E.; Chadde, S. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. In: Clary, W.P.; McArthur, E.D.; Bedunah, D.; Wambolt, C.L., comps. Proceedings: symposium on ecology and management of riparian shrub communities; [dates of meeting unknown]; [location unknown]. Gen. Tech. Rep. INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 92-99.

Keeney, D.R.; Nelson, D.W. 1982. Nitrogen-inorganic forms. In: Page, A.L., ed. Methods of soil analysis. Part 2: Chemical and microbiological properties. 2d ed. Madison, Wisconsin: American Society of Agronomy: 643-698.

Kilgore, B.M. 1981. Fire in ecosystem distribution and structure: Western forests and scrublands. In: Mooney, H.A.; Bonnicksen, T.M.; Christensen, N.L. [and others], tech. coords. Fire regimes and ecosystem properties. Gen. Tech. Rep. WO-26. Washington, DC: U.S. Department of Agriculture, Forest Service: 58-59.

Klemmedson, J.O. 1975. Nitrogen and carbon regimes in an ecosystem of young, dense ponderosa pine in Arizona. Forest Science. 22: 163-168.

Klemmedson, J.O. 1976. Effect of thinning and slash burning on nitrogen and carbon in ecosystems of young, dense ponderosa pine. Forest Science. 22: 45-53.

Klemmedson, J.O. 1979. Ecological importance of Actinomycete nodulated plants in the Western United States. Supplement to Botanical Gazette. 140: S91-S96.

Klemmedson, J.O. 1991. Oak influence on nutrient availability in pine forests of central Arizona. Soil Science Society of America Journal. 55: 248-253.

Kroll, J.C.; Goodrum, W.D.; Behrman, P.J. 1986. Twenty-seven years of over-browsing: implications to white-tailed deer management on wilderness areas. In: Kulhavy, D.L.; Conner, R.N., eds. Wilderness and natural areas in the Eastern United States: a management challenge. Nacogdoches, TX: Stephen F. Austin University, School of Forestry, Center for Applied Studies: 294-303.

Krueger, W.C. 1983. Cattle grazing in managed forests. In: Roche, B.F.; Baumgartner, D.M., eds. Proceedings: forestland grazing symposium; 1983 February 23-25; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service: 29-41.

Krueger, W.C.; Winward, A.H. 1974. Influence of cattle and big game grazing on understory structure of a Douglas fir-ponderosa pine/Kentucky bluegrass community. Journal of Range Management. 27: 450-453.

Krueger, W.C.; Winward, A.H. 1976. Effects of grazing and selective logging on a mixed coniferous forest. In: Proceedings of the Oregon Academy of Science. [Vol. unknown]: 27-35.

Langston, N. 1995. Forest dreams, forest nightmares: the paradox of old growth in the inland West. Seattle: University of Washington Press. 368 p.

Leege, T.A. 1968. Prescribed burning for elk in northern Idaho. Tall Timbers Fire Ecology Conference. 8: 235-253.

Manley, B.; McDonald, L.; Thomas, D. 1993. Resource selection by animals: statistical design and analysis for field studies. London: Chapman & Hall. 177 p.

McCullough, D.R. 1979. The George Reserve deer herd. Ann Arbor: The University of Michigan Press. 271 p.

McCullough, D.R. 1992. Concepts of large herbivore population dynamics. In: McCullough, D.R.; Barrett, R.H., eds. Wildlife 2001: populations. New York: Elsevier Applied Science: 967-984.

McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science. 191: 92-94.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist. 128: 765-770.

McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist. 124: 863-886.

McNaughton, S.J. 1992. The propagation of disturbance in savannas through food webs. Journal of Vegetation Science. 3: 301-314.

McShea, W.J.; Rappole, J.H. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology. 14: 1161-1170.

Milchunas, D.G.; Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs. 63: 327-366.

Miller, R.F.; Krueger, W.C.; Vavra, M. 1981. Deer and elk use on foothill rangelands in northeastern Oregon. Journal of Range Management. 34: 201-204.

Mills, L.S.; Soule, M.; Doak, D.F. 1993. The keystone species concept in ecology and conservation. Bioscience. 43: 219-224.

Minson, D.J.; Wilson, J.R. 1994. Prediction of intake as an element of forage quality. In: Fahey, G.C., ed. Forage quality, evaluation, and utilization. Madison, WI: American Society of Agronomy: 533-563.

Mitchell, G.E. 1951. Status of browse on ranges of eastern Oregon and eastern Washington. Journal of Range Management. 4: 249-253.

Molvar, E.M.; Bowyer, R.T.; Van Ballenberghe, V. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia. 94: 472-470.

Monfore, J.D. 1983. Livestock: a useful tool for vegetation control in ponderosa pine and lodgepole pine plantations. In: Roche, B.F.; Baumgartner, D.M., eds. Proceedings: forestland grazing symposium; 1983 February 23-25; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service: 105-107.

Morgan, P.; Aplet, G.H.; Haufler, J.B. [and others]. 1994. Historical range of variability: a useful tool for evaluating ecological change. Journal of Sustainable Forestry. 2: 87-111.

Nelson, W.W.; Sommers, L.E. 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L., ed. Methods of soil analysis. Part 2: Chemical and microbiological properties. 2d ed. Madison, WI: American Society of Agronomy: 539-579.

Neu, C.W.; Byers, C.R.; Peek, J.M. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.

Olsen, S.R.; Sommers, L.E. 1982. Phosphorus. In: Page, A.L., ed. Methods of soil analysis. Part 2: Chemical and microbiological properties. 2d ed. Madison, WI: American Society of Agronomy: 403-430.

Oregon Department of Fish and Wildlife. 1990. Mule deer plan. Portland, OR. 49 p.

Oregon Department of Fish and Wildlife. 1992. Oregon's elk management plan. Portland, OR. 63 p.

Parks, C.G.; Bednar, L.; Tiedemann, A.R. 1998. Browsing ungulates—an important consideration in dieback and mortality of Pacifc yew (*Taxus brevifolia*) in a northwestern Oregon stand. Northwest Science. 72(3): 190-197.

Pastor, J.; Binkley, D. 1998. Nitrogen fixation and the mass balance of carbon and nitrogen in ecosystems. Biogeochemistry. 43: 63-78.

Pastor, J.; Cohen, Y. 1997. Herbivores, the functional diversity of plant species, and the cycling of nutrients in ecosystems. Theoretical Population Biology. 51: 165-179.

Pastor, J.; Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist. 139: 691-705.

Pastor, J.; Naiman, R.J.; Dewey, B.; McInnes, P. 1988. Moose, microbes, and the boreal forest. Bioscience. 38: 770-777.

Pastor, J.; Naiman, R.J.; Dewey, B. [and others]. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology. 74: 467-480.

Peek, J.M.; Johnson, F.D.; Pence, N.N. 1978. Successional trends in a ponderosa pine/bitterbrush community related to grazing by livestock, wildlife, and to fire. Journal of Range Management. 31: 49-53.

Pengelly, W.L. 1963. Timberlands and deer in the northern Rockies. Journal of Forestry. 61: 734-738.

Petersen, R.B.; Woodhouse, W.W.; Lucas, H.J. 1956. The distribution of excreta by freely grazing cattle and its effect on pasture fertility. 1: Excretal distribution. Agronomy Journal. 48: 440-444.

Pettit, R.D. 1968. Effects of seeding and grazing on a clearcut-burn in a mixed-coniferous forest stand of the Wallowa Mountain[s] foothills. Corvallis, OR: Oregon State University. 133 p. Ph.D. diss.

Pickford, G.D.; Reid, E.H. 1948. Forage utilization on summer cattle ranges in eastern Oregon. Circ. 796. Washington, DC: U.S. Department of Agriculture. 27 p.

Pielou, E.C. 1966a. Shannon's formula as a measure of specific diversity: its use and disuse. American Naturalist. 100: 463-465.

Pielou, E.C. 1966b. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology. 13: 131-144.

Pierce, J.D.; Peek, J.M. 1984. Moose habitat use and selection patterns in north-central Idaho. Journal of Wildlife Management. 48: 1335-1343.

Quigley, T.M.; Arbelbide, S.J., tech. eds. 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 4 vol. (Quigley, T.M., tech ed.; The Interior Columbia Basin Ecosystem Management Project: scientific assessment).

Regelin, W.L.; Wallmo, O.C.; Nagy, J.; Dietz, D.R. 1974. Effect of logging on forage values for deer in Colorado. Journal of Forestry. 72: 282-285.

Reimoser, F.; Gossow, H. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. Forest Ecology and Management. 88: 107-119.

Renecker, L.A.; Hudson, R.J. 1988. Seasonal quality of forages used by moose in the aspen-dominated boreal forest, central Alberta. Holarctic Ecology. 11: 111-118.

Rhodes, B.D.; Sharrow, S.H. 1990. Effect of grazing by sheep on the quantity and quality of forage available to big game in Oregon's Coast Range. Journal of Range Management. 43: 235-237.

Roath, L.R.; Krueger, W.C. 1982. Cattle grazing and behavior on a forested range. Journal of Range Management. 35: 332-338.

Robbins, C.T.; Podbielancik-Norman, R.S.; Wilson, D.L.; Mould, E.D. 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. Journal of Wildlife Management. 45: 172-186.

Roloff, G.J.; Carroll, B.; Scharosch, S. 1999. A decision support system for incorporating wildlife habitat quality into forest planning. Western Journal of Applied Forestry. 14: 91-99.

Romesburg, H.C. 1984. Cluster analysis for researchers. Malabar, FL: Krieger Publishing Company. 334 p.

Roscoe, J.T.; Byars, J.A. 1971. An investigation of the restraints with respect to the sample size commonly imposed on the use of the chi-square statistic. Journal of the American Statistical Association. 66: 755-759.

Ruess, R.W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. In: Walker, B.H., ed. Determinants of tropical savannas. Paris, France: International Union of Biological Scientists: 93-141.

Ruess, R.W.; McNaughton, S.J. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos. 49: 101-110.

Sallabanks, R; Riggs, R.A. 1998. Bird-habitat relationships in *Abies grandis* forests of the Blue Mountains, Oregon. Manuscript in preparation. On file with: Boise Cascade Corporation, 1917 Jackson Avenue, La Grande, OR 97850.

SAS Institute, Inc. 1988. SAS/STAT user's guide. Release 6.03. Cary, NC. 1028 p.

Schimmel, J.; Granstrom, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology. 77: 1436-1450.

Schreiner, E.G.; Krueger, K.A.; Happe, P.J.; Houston, D.B. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Canadian Journal of Forest Research. 26: 255-265.

Schwartz, C.C.; Hobbs, N.T. 1985. Forage and range evaluation. In: Hudson, R.J.; White, R.G., eds. Bioenergetics of wild herbivores. Boca Raton, FL: CRC Press: 25-52.

Scott, M.J.; Davis, F.; Csuti, B. [and others]. 1993. GAP analysis: a geographic approach to protection of biological diversity. Wildlife Monographs. No. 123. 41 p.

Seagle, S.W.; McNaughton, S.J.; Ruess, R.W. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. Ecology. 73: 1105-1123.

Shannon, C.E.; Weaver, W. 1963. The mathematical theory of communication. Urbana, IL: University of Illinois Press. 117 p.

Shipley, L.A. 1999. Grazers and browsers: how digestive morphology affects diet selection. In: Launchbaugh, K.L.; Sanders, K.D.; Mosley, J.C., eds. Grazing behavior of livestock and wildlife. Bull. 70. Moscow, ID: Idaho Forest, Wildlife and Range Experiment Station: 20-27.

Smith, A.D. 1965. Determining common use grazing capacities by application of the key species concept. Journal of Range Management. 18: 196-201.

Sprent, J.I.; Sprent, P. 1990. Nitrogen fixing organisms: pure and applied aspects. London, United Kingdom: Chapman and Hall. 256 p.

Statsoft. 1994. Statistica for windows. Tulsa, OK.

Steel, G.G.D.; Torrie, J.H. 1960. Principles and procedures of statistics. New York: McGraw-Hill Book Co. 481 p.

St. John, T.V.; Rundel, P.W. 1976. The role of fire as a mineralizing agent in a Sierran coniferous forest. Oecologia. 25: 35-45.

Stohlgren, T.J.; Schell, L.D.; Vanden Heuvel, B. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications. 9: 45-64.

Strickler, G.S.; Edgerton, P.J. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology. 57: 801-807.

Swanson, F.J.; Jones, J.A.; Wallin, D.A.; Cissel, J.H. 1994. Natural variability-implications for ecosystem management. In: Jensen, M.E; Bourgeron, P.S., eds. Vol. 2: Ecosystem management–principles and applications. Gen. Tech. Rep. PNW-GTR-318. Portland, OR: Department of Agriculture, Forest Service, Pacific Northwest Research Station: 80-95. (Everett, Richard L., assessment team leader; Eastside forest ecosystem health assessment).

Thomas, J.W.; Leckenby, D.A.; Henjum, M. [and others]. 1988. Habitat-effectiveness index for elk on Blue Mountain winter ranges. Gen. Tech. Rep. PNW-GTR-218. Portland, OR: U.S. Department of Agriculture, Forest Service. 28 p.

Tiedemann, A.R. 1987. Combustion losses of sulfur from forest foliage and litter. Forest Science. 33: 216-223.

Tiedemann, A.R.; Anderson, T.D. 1971. Rapid analysis of total sulphur in soils and plant material. Plant and Soil. 35: 197-200.

Tiedemann, A.R.; Berndt, H.W. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science. 46: 59-66.

Tiedemann, A.R.; Klemmedson, J.O.; Bull, E.L. 2000. Solution of forest health problems with prescribed fire: Are forest productivity and wildlife at risk? Forest Ecology and Management 127(1-3): 1-18.

Tiedemann, A.R.; Klock, G.O. 1977. Development of vegetation after fire, seeding, and fertilization on the Entiat Experimental Forest. In: Proceedings of the 15th annual Tall Timbers fire ecology conference; 1974 October 16-17; Portland, OR. Tallahassee, FL: Tall Timbers Research Station: 171-192.

Tiedemann, A.R.; Mason, R.R.; Wickman, B.E. 1998. Forest floor and soil nutrients 5 years after urea fertilization in a grand fir forest. Northwest Science. 72: 88-95.

Tiedemann, A.R.; Quigley, T.M.; Anderson, T.D. 1988. Effects of timber harvest on stream chemistry and dissolved nutrient losses in northeast Oregon. Forest Science. 34: 344-358.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management. 53: 524-533.

Trumbull, V.L.; Zielinski, E.J.; Aharrah, E.C. 1989. The impact of deer browsing on the Allegheny forest type. Northern Journal of Applied Forestry. 6: 162-165.

Turner, M.G.; Romme, W.H.; Gardner, R.H.; Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. 67: 411-433.

Urness, P.J. 1990. Livestock as manipulators of mule deer winter habitats in northern Utah. In: Severson, K.E., ed. Can livestock be used as a tool to enhance wildlife habitat? Gen. Tech. Rep. RM-194. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 25-38.

U.S. Department of Agriculture, Forest Service. 1996. Status of the interior Columbia basin: summary of scientific findings. Gen. Tech. Rep. PNW-GTR-385. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; U.S. Department of the Interior, Bureau of Land Management. 144 p.

Vavra, M. 1983. Managing grazing animal response to forestland vegetation. In: Roche, B.F.; Baumgartner, D.M., eds. Proceedings of the forestland grazing symposium; 1983 February 23-25; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension Service: 43-51.

Vavra, M. 1986. Manipulative grazing of plant communities. In: Gundmundsson, O., ed. Grazing research at northern latitudes. New York: Plenum Press: 167-178.

Vavra, M.; McInnis, M.; Sheehy, D. 1989. Implications of dietary overlap to management of free-ranging large herbivores. Proceedings, Western Section, American Society Animal Science. 40: 489-495.

Verkaar, H.J. 1987. Population dynamics: the influence of herbivory. Supplement to New Phytologist. 106: 49-60.

Vlassak, K.; Paul, E.A.; Harris, R.F. 1973. Nitrogen fixation in grasslands and associated sites. Plant and Soil. 38: 637-649.

Watson, E.R.; Lapins, R. 1969. Losses of nitrogen from urine on soils from southwestern Australia. Australian Journal of Experimental Agriculture and Animal Husbandry. 9: 85-91.

Weigand, J.F.; Haynes, R.; Tiedemann, A.R. [and others]. 1993. Ecological and economic impacts of ungulate herbivory on commercial stand development in forests of eastern Oregon and Washington. Forest Ecology and Management. 61: 137-155.

Wickstrom, M.L.; Robbins, C.T.; Hanley, T.A. [and others]. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management. 48: 1285-1301.

Williamson, S.C.; Detling, J.K.; Dodd, J.K.; Dyer, M.I. 1989. Experimental evaluation of the grazing optimization hypothesis. Journal of Range Management. 24: 149-152.

Wisdom, M.J.; Bright, L.R.; Carey, C.G. [and others]. 1986. A model to evaluate elk habitat in western Oregon. R6-F&WL-216-1986. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 35 p.

Woodward, A.; Schreiner, E.G.; Houston, D.B.; Moorhead, B.B. 1994. Ungulate-forest relationships in Olympic National Park: retrospective exclosure studies. Northwest Science. 68: 97-110.

Young, J.A.; Hedrick, D.W.; Keniston, R.F. 1967a. Forest cover and logging-herbage and browse production in the mixed coniferous forest of northeastern Oregon. Journal of Forestry. 65: 807-813.

Young, J.A.; McArthur, B.; Hedrick, D.W. 1967b. Forage utilization in a mixed-coniferous forest of northeastern Oregon. Journal of Forestry. 65: 391-393.

Youngberg, C.T.; Wollum, A.G., II. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. Soil Science Society of America Journal. 40: 109-112.

Appendix

Figure 14—Clearcut study site at Mottet in the Blue Mountains of northeastern Oregon, 1995 30 years after establishment of the exclosure: (**A**) not burned, protected; (**B**) not burned, grazed; (**C**) burned, protected; and (**D**) burned, grazed. Currently, the early successional understories are in decline as conifer canopies have begun to close. Grazed understories (B and D) are dominated by forbs, the most conspicuous being coneflower (*Rudbeckia occidentalis*). Protected understories are codominated by shrubs and forbs. The more conspicuous shrubs in (A) are thimbleberry (*Rubus parviflorus*, at center in front of meter pole), snowbush (*Ceanothus velutinus*, in foreground), and willow (*Salix* sp., tall shrub in background). The more conspicuous shrubs in (B) are mountain lover (*Pachistima myrsinites*, in foreground) and willow (in background); black cottonwood (*Populus trichocarpa*) is the tree at right in background. The flowering forb in (A) is fireweed (*Epilobium* sp.). The flowering forb in (B) is paintbrush (*Castilleja* sp.). (Photos by Art Tiedemann.)

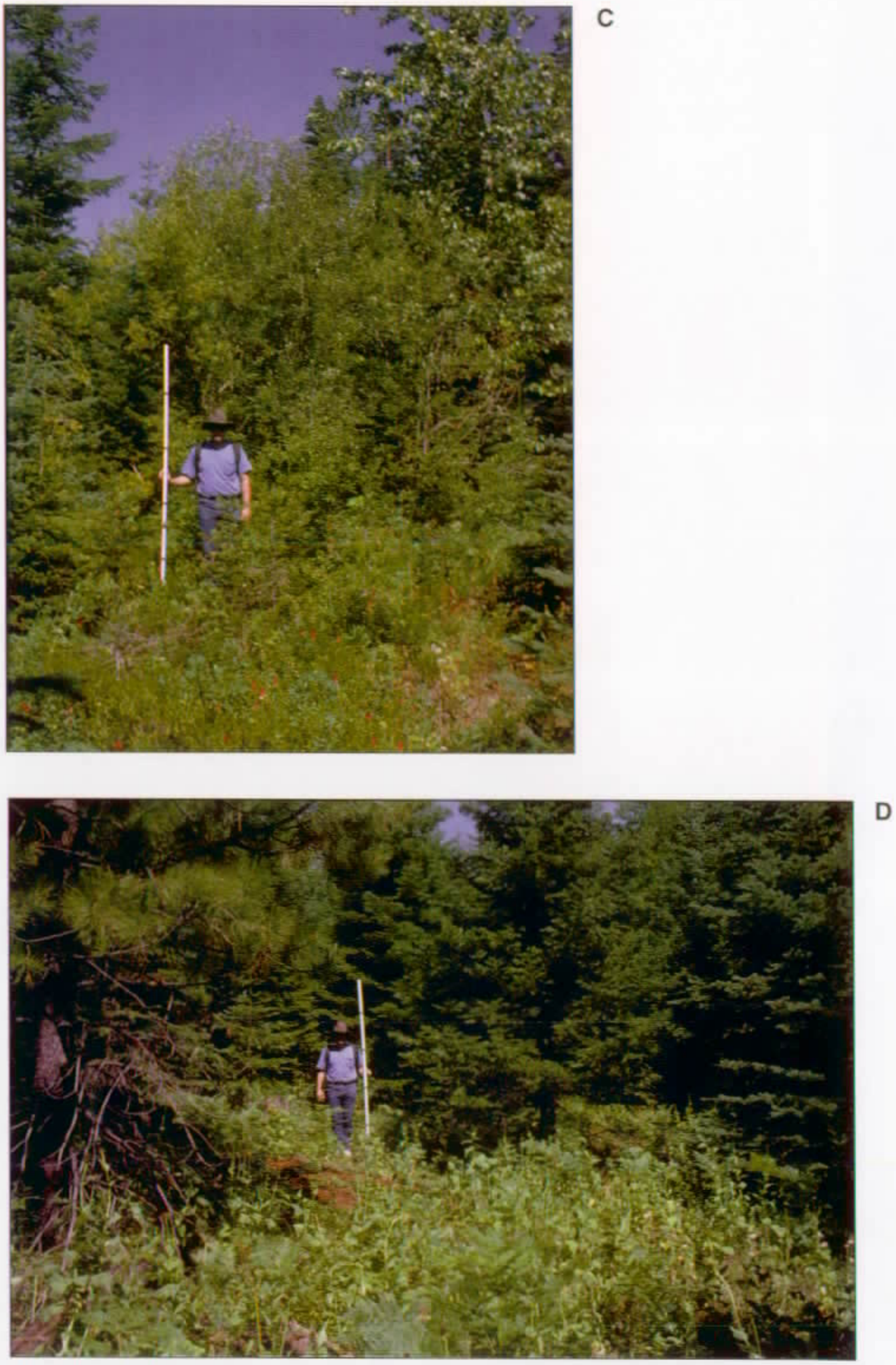

Figure 14—continued

Figure 15—Clearcut forest at Hoodoo in the Blue Mountains of northeastern Oregon, 1995: (**A**) protected, and (**B**) grazed. (Photos by Art Tiedemann.)

Figure 16—Selective cut at Hoodoo in the Blue Mountains of northeastern Oregon, 1995: (**A**) protected, and (**B**) grazed. (Photos by Art Tiedemann.)

Figure 17—Uncut forest at Hoodoo in the Blue Mountains of northeastern Oregon, 1995: (**A**) protected, and (**B**) grazed. The grazed understory was keyed to a *Clintonia uniflora* association. However the protected understory was keyed to a *Taxus brevifolia/Linnaea borealis* association based on the presence of *Taxus brevifolia* (Pacific yew, which was absent outside the exclosure). In the protected understory, Rocky Mountain maple (*Acer glabrum*, sapling at center) constitutes an intermediate deciduous layer that is apparently increasing over time. (Photos by Art Tiedemann.)


A

B


C

Figure 18—Clearcut forest at Hall Ranch in the Wallowa Mountains of northeastern Oregon, June 5, 2000. At these microsites in both the dual use (**A**) and game only (**B**) areas, understory vegetation is dominated by herbaceous taxa (*Bromus* spp., *Carex* spp., *Dactylis glomerata, Elymus glauca, Arnica cordifolia*) with scattered shrubs (predominantly *Physocarpus malvaceus* and *Symphoricarpos albus*). In the livestock only area (**C**) understory vegetation is composed of more shrubs, among which *Physocarpos malvaceus* (foreground), *Symphoricarpos albus, Ceanothus* spp., *Rosa* spp., and *Salix* spp. (tall shrub at right) were well represented. (Photos by Bob Riggs.)

A

B

C

Figure 19—Selective cut 1 on a *Pseudotsuga menziesii* forest site at the Hall Ranch in the Wallowa Mountains of northeastern Oregon, June 5, 2000. Herbivores apparently suppressed shrubs at this site. Shrub cover is lowest in the dual use area (**A**), somewhat greater in the area grazed by big game only (**B**), and greatest in the protected area (**C**). Conspicuous tall shrubs in the protected area included *Acer glabrum* (tall shrub at left), *Ceanothus sanguineus* (center background), and *Ceanothus velutinus* (at right); all these palatable tall shrubs are absent from the two grazed areas. Dominant shrubs in the game only (B) and protected areas (C) were *Physocarpus malvaceus* and *Symphoricarpos albus*. (Photos by Bob Riggs.)

A

B

C

Figure 20—Selective cut 2 on an *Abies grandis* forest site, at the Hall Ranch in the Wallowa Mountains of northeastern Oregon, June 5, 2000. Scattered shrubs (*Holodiscus discolor*, *Symphoricarpos albus*, *Vaccinium* spp.), grasses, and forbs codominate understory vegetation in the dual use area (**A**). Understory in the game only area (**B**) is dominated by the shrubs *Holodiscus discolor*, *Physocarpus malvaceus*, and *Symphoricarpos malvaceus*, but with some inconspicuous *Salix* sp. and *Vaccinium* sp. Understory in the protected area (**C**) is dominated by shrubs, including the aforementioned taxa in (B), but also with conspicuous plants of *Salix* sp. (tall shrub in background), and *Amelanchier alnifolia* (left front, and at right center). (Photos by Bob Riggs.)

Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, Oregon 97208-3890

U.S. Department of Agriculture
Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, Oregon 97208-3890