Successional patterns in bitterbrush habitat types in north-central Washington

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Abstract

Twenty-five plant communities were classified within 3 bitterbrush *(Purshia tridentata)* habitat types along the Columbia River in north-central Washington. Topography, indicator species, and soils data were used to assign stands to habitat type. Ordination across 3 habitat types reflected a moisture gradient: bitterbrush/Idaho fescue *(Festuca idahoensis)* communities occupied the moist end, bitterbrush/needle-and-thread *(Stipa comata)* communities the xeric end, and bitterbrush/bluebunch wheatgrass *(Agropyron spicatum)* an intermediate position. Solar radiation index and elevation accounted for 76% of the variation in the major axis. Ordinations of communities within habitat types described the sere. High-seral communities were not present on the study area. Mid-seral communities had greater perennial grass cover and lower bitterbrush density than low-seral communities.

Key Words: bitterbrush, *Purshia tridentata*, plant successionclassification, ordination

Secondary plant succession patterns in forest habitat types are relatively well documented and ungulate use of forest seral stages has received a good deal of research attention (Miller 1968, Wallmo et al. 1972, Peek et al. 1976, Regelin and Wallmo 1978, Singer 1979, Wallmo 1969, Collins and Urness 1983, Irwin and Peek 1983). In contrast, secondary successional sequences in rangeland habitat types have received much less attention. Only recently (Huschle and Hironaka 1980, Hacker 1983) has a classification and ordination procedure for seral communities within rangeland habitat types been presented and evaluated. To date, the most detailed level of resolution in studies of ungulate use of rangelands has been at the habitat type or series level (Mackie 1970). To our knowledge ungulate selection of seral stages within rangeland habitat types has not been quantitatively addressed.

In order to evaluate mule deer preference for seral stages within rangeland habitat types, we needed to delineate the secondary successional sere within important habitat types and to determine whether a complete sere was available to mule deer on our study area. We chose to evaluate antelope bitterbrush habitat types because bitterbrush is one of the most palatable and nutritious browse species in western North America (Smith and Hubbard 1954, Kufeld et al. 1973), is known to be preferred by mule deer (Carson and Peek 1986), and because natural succession and disturbance have led to decreases in bitterbrush production and changes in understory composition throughout its range (Ferguson and Medin 1983). Although climax communities of bitterbrush habitat types have been described (Daubenmire 1970) no delineation of seral communities is available.

The purposes of this paper are: (1) to determine the relationship between topographic and edaphic site factors and bitterbrush habitat types, (2) to determine if established multivariate analysis tech-

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niques can effectively delineate the sere within bitterbrush habitat types, and (3) to provide summary descriptions of bitterbrush seral communities.

Study Area

The study area was part of the southern shore of an impounded segment of the Columbia River between Chief Joseph Dam and Grand Coulee Dam in north-central Washington. Elevations range from 300 m at the lakeshore to 900 m at the top of the canyon. The lake banks are a series of nearly level to gently sloping river terraces interspersed by long steep escarpments.

The climate is semiarid with cold winters and warm, dry summers. Most of the 240 mm mean annual precipitation falls as rain outside the growing season. Droughty summers have a great effect on the vegetation of the region (Daubenmire 1970).

Daubenmire (1970) recognized 3 bitterbrush habitat types in this area: bitterbrush/Idaho fescue *(Festuca idahoensis)*, bitterbrush/needle-and-thread *(Stipa comata)*, and bitterbrush/bluebunch wheatgrass *(Agropyron spicatum)*. All 3 habitat types are included within the big sagebrush *(Artemisia tridentata)*/bluebunch wheatgrass and threetip sagebrush *(Artemisia tripartita)*/Idaho fescue vegetation zones (Daubenmire 1970). Bitterbrush communities comprise approximately 25% of the study area.

The study area was a single pasture spring-fall range for 1,000–1,250 cattle. This grazing regime had been in effect for about 10 years prior to the study.

Methods

We selected 3 study sites of 280, 382, and 585 ha that included the range in elevation, slope, and vegetation composition of bitterbrush stands in the canyon. Bitterbrush stands were delineated on 8 inch-to-the-mile (1:660) black-and-white aerial photographs and stratified according to slope and aspect.

Five strata were identified. The first consisted of relatively flat stands with slope >4 degrees. Stands with >4 degrees slope on northern, southern, eastern, and western aspects comprised the remaining 4 strata. Sample stands were randomly chosen within strata.

We located a 20 × 20-m macroplot in each sample stand in an area of relatively uniform vegetation. Species presence, frequency of occurrence, and forb and grass canopy cover estimates were recorded from forty 20-by-50-cm microplots located at 2-m intervals along four 20-m-long transects placed parallel to the slope. Shrub cover was estimated using the line intercept method (Canfield 1941). Starting points for each transect were randomly located within successive 5-m intervals. Bitterbrush density was estimated from twelve 5-m^2 circular plots (Oldemeyer 1980) systematically located along the line intercept transects in each macroplot.

Elevation, slope, and aspect were recorded for each macroplot. Solar radiation index (SRI) was calculated from latitude, aspect, and slope (Frank and Lee 1966).

A soil pit was excavated to the C horizon in each macroplot. Soil was collected from each horizon. Soils were classified to family and series levels (USDA Soil Conservation Service 1975, USDA Soil Conservation Service 1981).

Sampled stands were assigned to habitat types based on topography, indicator plant species, and soil classification. Vegetative data were utilized to classify communities within habitat types using two-way species indicator analysis (TWINSPAN, Hill et al. 1975, Hill 1979a). Since this method is sensitive to rare species (Gauch and Singer 1982), forb and grass species present in <10% of the microplots per stand were eliminated from the analysis. Shrubs with canopy coverage of <3% were also deleted. Classification was based on presence or absence of species.

Plant communities identified by TWINSPAN were ordinated on the basis of canopy coverage within and among habitat types using detrended correspondence analysis (DECORANA, Hill 1979b, Hill and Gauch 1980). This ordination technique is based on reciprocal averaging and has been successful in community analysis (Gauch 1982; but see Wartenberg et al. 1987).

Ordination of communities can effectively identify seral relationships provided that all analyzed communities come from the same habitat type and a logical endpoint for succession is incorporated in the analysis (Huschle and Hironaka 1980, Tueller and Blackburn 1974). Climax communities sampled by Daubenmire (1970) in the vicinity were incorporated in the ordinations as reference stands for each of the habitat types. Hacker (1983) demonstrated the validity of reciprocal averaging methods to identify seral relationships in both simulated and real communities. DECORANA is an improved form of reciprocal averaging (Hill and Gauch 1980).

Cover estimates from sampled stands were averaged within communities. Stepwise multiple regression (Draper and Smith 1966, SAS Institute 1985) was utilized to aid in the interpretation of axes in the ordinations across all habitat types. Statistical analyses of differences ($P \leq 0.10$) in vegetation characteristics among habitat types and between seral stages were conducted with ANOVA of rank transformed data (Conover and Iman 1981). Pairwise comparisons were conducted with the Bonferroni approach (Miller 1966:67) at alpha = 0.10, experiment-wise.

Results

The 3 habitat types were located on distinctive topographic positions within the study area. Bitterbrush/needle-and-thread was found on relatively flat terrace benches (<4 degrees slope), bitterbrush/Idaho fescue was located on north facing slopes >4 degrees, bitterbrush/bluebunch wheatgrass was established on all other exposures with slope >4 degrees. Soils on all sites were derived from glaciofluvial deposits and were almost all sandy, sandy skeletal or loamy skeletal Typic or Entic Haploxerolls. "Cashmere", "Benge", "Skaha", "Pogue", and "Quincy" were the soil series encountered on the study area. Mollic epipedons were 15 to 36 cm thick over weakly developed cambric B horizons.

Soils were not as useful as topographic position in distinguishing habitat types. Needle-and-thread soils could not be visually differentiated from bluebunch wheatgrass soils. However, needle-and-thread is often found on sandier sites than bluebunch wheatgrass (Hironaka et al. 1983). Fescue soils were distinctive due to their darker color indicating a greater organic matter content.

The classification yielded 11 communities from the 41 stands sampled in the bitterbrush/bluebunch wheatgrass habitat type, 6 communities from 16 stands sampled in the bitterbrush/needle-and-thread habitat type, and 8 communities from the 22 stands sampled in the bitterbrush/Idaho fescue habitat type. These classifications were based primarily on the presence or absence of perennial forbs. Presence of bitterbrush and perennial grasses had little influence on community classification. Stands that had been burned in a 1981 wildfire were not separated from unburned stands in the classification. Communities therefore included both burned and unburned stands. Communities were named for the species with the greatest percent canopy coverage in the shrub, grass, and forb layer (Table 1).

The ordination across habitat types utilizing 28 communities represented an environmental gradient of all bitterbrush types on the study area (Fig. 1). SRI plus elevation accounted for 76% of the variation in axis 1. More mesic fescue sites were cooler, higher elevation communities located at one end of the ordination. Needle-and-thead sites were the warmest and driest communities at the opposite end. The bluebunch wheatgrass sites were intermediate between the other two. Bitterbrush cover and perennial grass cover accounted for 40% of the variation in axis 2.

Perennial grass cover in all communities in all habitat types sampled was much less than in reference climax stands (Table 1). Perennial forb cover in bitterbrush/bluebunch wheatgrass and bitterbrush/Idaho fescue habitat types was also much less than in

Table 1. Percent canopy coverage of perennial grasses, annual grasses, perennial forbs, annual forbs, and bitterbrush, and bitterbrush density for 28 bitterbrush communities in 3 habitat types, northcentral Washington, 1985.

Habitat type									
Community							Bitterbrush		
Number	Name	Seral stage	Burned[a]	Perennial grass cover (%)	Perennial forb cover (%)	Annual grass cover (%)	Annual forb cover (%)	cover (%)	Density (plants/ha)
	Putr/Agsp[b]								
1	Agsp/Basa	Mid	+	23.2	4.5	20.6	0.8	0.9	3250
2	Putr/Agsp/Basa	Mid	+	23.9	11.9	4.6	3.2	3.3	4500
3	Putr/Agsp/Basa	Mid	+	20.2	11.8	13.2	0.9	7.9	8625
4	Putr/Agsp/Basa	Mid	+	18.9	10.6	34.5	0.7	3.0	3000
	Mid-seral Average			21.6	9.7	18.2	1.4	3.8	4844
5	Putr/Agsp/Basa	Low		4.9	10.3	35.4	2.7	12.2	9429
6	Sado/Spcr	Low	+	14.5[c]	2.6	10.5	1.5	0.0	6000
7	Putr/Brte/Ardr	Low	+	2.2	7.7	24.1	0.5	8.0	6667
8	Putr/Brte/Erst	Low	+	1.5	5.6	25.6	1.3	9.7	11500
9	Putr/Brte/Libu	Low		6.0	12.6	26.6	1.6	7.0	45000
10	Putr/Brte/Basa	Low		6.2	6.7	29.2	14.7	12.2	12333
11	Putr/Brte/Loam	Low		2.5	6.7	34.6	3.6	7.9	7000
	Low-seral Average			5.4	7.5	26.6	3.7	8.1	13990
	Putr/Agsp Average			11.3	8.3	23.5	2.9	6.6	10664
	Putr/Stco								
12	Putr-Chna/Stco/Lepu	Low		9.6	3.9	27.7	1.4	5.6	12500
13	Putr/Stco-Spcr/Basa	Low	+	13.1	5.5	49.2	0.6	8.7	16667
14	Putr/Stco/Phha	Low		19.7[d]	1.9	22.8	2.3	22.0	26545
15	Putr/Stco/Libu	Low	+	9.1	7.0	20.5	9.7	11.3	11500
16	Putr/Stco/Acmi	Low	+	4.8	2.5	25.4	0.6	12.7	20000
17	Putr/Stco/Lule	Low		23.8	8.4	18.8	0.8	6.3	6000
	Putr/Stco Average			13.4	4.9	27.4	2.6	11.1	15535
	Putr/Feid								
19[e]	Feid-Agsp/Erhe	Mid	+	31.9	21.1	11.1	1.8	0.5	3333
20	Prvi/Feid-Agsp/Pogl	Mid	+	32.8	23.8	18.5	0.9	0.0	1000
21	Putr/Feid-Agsp/Erhe	Mid	+	18.5	24.9	23.2	5.4	9.6	8500
22	Putr/Feid-Agsp/Basa	Mid		17.7	16.3	7.2	3.0	12.9	11000
23	Putr/Feid-Agsp/Basa	Mid		22.8	20.3	12.0	0.5	8.1	5667
24	Putr/Feid-Agsp/Basa	Mid		27.1	20.2	4.1	0.2	9.4	8600
25	Putr/Feid-Agsp/Basa	Mid		27.5	18.7	1.2	0.0	6.2	4000
26	Putr/Feid-Agsp/Basa	Mid		39.4	23.4	1.0	0.2	4.6	4000
	Putr/Feid Average			27.2	21.1	9.8	1.5	6.4	5762
	Climax Reference[f]								
27	Putr/Agsp	High		88.0	32.0	1.0	9.0	11.0	—
28	Putr/Stco	High		78.0	3.0	5.0	15.0	12.0	—
29	Putr/Feid	High		98.0	91.0	2.0	12.0	25.0	—

[a] +denotes communities with at least one burned stand.

[b] Acmi=*Achillea millefolium,* Agsp=*Agropyron spicatum,* Ardr=*Artemisia dracunculoides,* Basa=*Balsamorhiza sagittata,* Brte=*Bromus tectorum,* Chna=*Chrysothamnus nauseosus,* Erhe=*Eriogonum heracleoides,* Erst=*Eriogonum strictum,* Feid=*Festuca idahoensis,* Lepu=*Leptodactylon pungens,* Libu=*Lithophragma bulbifera,* Loam=*Lomatium ambiguum,* Lule=*Lupinus leucophyllus,* Pogl=*Potentilla glandulosa,* Putr=*Purshia tridentata,* Prvi=*Prunus virginiana,* Phha=*Phacelia hastata,* Sado=*Salvia dorrii,* Spcr=*Sporobolus cryptandrus,* Stco=*Stipa comata.*

[c] Sand dropseed *(Sporobolus cryptandrus)* accounted for 97% of perennial grass cover.

[d] Needle-and-thread grass *(Stipa comata)* only accounted to 21% of perennial grass cover.

[e] Community Number 18 could not be assigned to a habitat type and was deleted from the analysis.

[f] Daubenmire (1970) communities #79,22,77.

respective reference climax stands. Mean bitterbrush density in Idaho fescue was lower (P=0.003) than in the needle-and-thread habitat type. In the Idaho fescue type mean perennial grass cover was higher ($P = 0.002$, $P = 0.012$) and mean annual grass cover was lower ($P = 0.002$, $P = 0.005$) than in bluebunch wheatgrass and needle-and-thread habitat types, respectively. Perennial forb cover differed ($P \leq 0.026$) among all habitat types. There was no significant variation among habitat types in annual forb ($P = 0.404$) or bitterbrush ($P = 0.324$) cover.

The first 2 axes of the community ordinations within habitat types accounted for 41 to 63% of community variation. Eigenvalues for axes 3 and 4 were quite small. In the bitterbrush/bluebunch wheatgrass habitat type axis 1 encompassed more than 3 standard deviations in species turnover. Axis 1 represented a secondary successional sere because the reference community (Daubenmire 1970) appeared at one end of the ordination. Com-

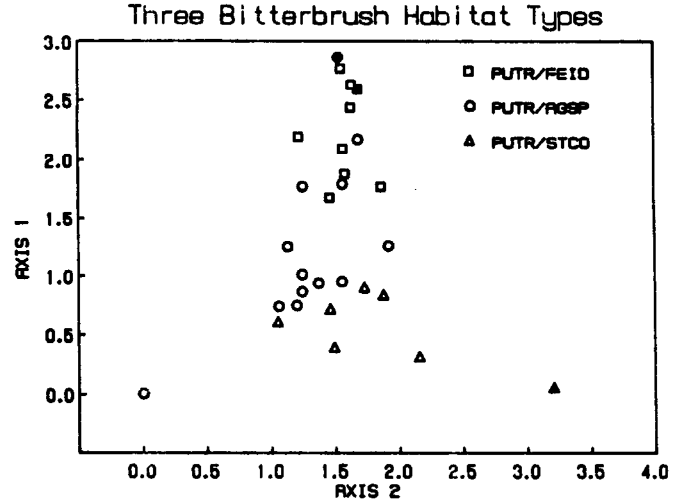

Fig. 1. *DECORANA ordination of 28 bitterbrush communities across 3 habitat types; PUTR/AGSP=bitterbrush/bluebunch wheatgrass, PUTR/FEID=bitterbrush/Idaho fescue and PUTR/STCO=bitterbrush/needle-and-thread. Solid symbols represent reference communities (Daubenmire 1970).*

munities with highest perennial grass cover appeared near the reference stands. Communities with least perennial grass cover were located far from the reference communities on axis 1. Communities were assigned to mid- or low-seral status (Table 1) based on a difference ($P<0.001$) in perennial grass cover because this was a readily observable criterion which has management utility. Low-seral communities had greater ($P = 0.086$) bitterbrush density than mid-seral communities (Table 1). Axis 2 accounted for only a small amount of variation.

In bitterbrush/needle-and-thread and bitterbrush/Idaho fescue a secondary successional gradient was not obvious. Ordinations in these 2 habitat types encompassed less than 2 standard deviations in species turnover, and a clear dichotomy in percent perennial grass cover within habitat type was not evident (Table 1). Because bitterbrush/Idaho fescue communities had consistently high perennial grass cover and bitterbrush/needle-and-thread communities had variable but generally low perennial grass cover, all communities in each of these habitat types were classed as mid-seral and low-seral respectively.

Discussion

Our ordination across habitat types identified an environmental gradient that can be used to evaluate wildlife habitat selection in rangelands. The habitat types occurred along an increasingly cooler and moister gradient from bitterbrush/needle-and-thread through bitterbrush/bluebunch wheatgrass to bitterbrush/Idaho fescue. This gradient of bitterbrush habitat types is consistent with Daubenmire's (1970) descriptions. By determining SRI and elevation from topographic maps and identifying bitterbrush stands from aerial photos or ground reconnaissance, land managers can map bitterbrush habitat types when the herbaceous layer is too disturbed to allow accurate habitat type assignment. Topographic data and soil properties can also be valuable in predicting habitat type of other grass or shrub communities (Anderson 1956, Tisdale and Bramble-Brodahl 1983).

In none of the habitat types on the study area did we observe communities approaching the pristine condition of reference climax communities; therefore a complete sere was not available in any habitat type. A similar situation would be expected on most low precipitation and low elevation rangelands with a history of grazing by non-native herbivores. Community variation in bitterbrush/Idaho fescue and bitterbrush/needle-and-thread habitat types was low and no seral separation would be made in these habitat types. The bitterbrush/Idaho fescue communities were located on steep north slopes not often utilized by livestock (Ganskopp and Vavra 1987). These sites either escaped prolonged grazing or were able to recover quickly from such disturbance due to a more favorable moisture regime; they were classed as mid-seral due to relatively high perennial grass cover. The bitterbrush/needle-and-thread communities were found on low elevation flat terrace benches that were close to water and historically received the greatest grazing pressure. Needle-and-thread grass cover in these communities was generally low, the grass layer was dominated by cheatgrass *(Bromus tectorum)*, and all communities in this habitat type were classed as low-seral.

Only in the bitterbrush/bluebunch wheatgrass habitat type did we observe 2 relatively distinct seral levels. Communities in this habitat type occurred on a variety of slopes, aspects, and elevations and had variable perennial grass cover. Most of the communities classed as mid-seral were found in areas with only moderate summer and fall cattle grazing; low seral communities were located predominantly in areas with heavy spring livestock grazing.

Within habitat type ordinations of communities were effective in objectively identifying the presence or absence of seres available for selection by mule deer. Delineation of seres provided an ecological framework which enhances our ability to predict long term changes in plant communities and to evaluate mule deer habitat selection relative to vegetation dynamics in rangelands. A similar approach could be used with other wildlife species in other rangeland types.

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Correction on Murray Article

A second Table 2 was erroneously included in "Response of three shrub communities in southeastern Idaho to spring-applied tebuthiuron" by Robert Murray on page 17 of the January issue. My apologies to the author.—The Editor