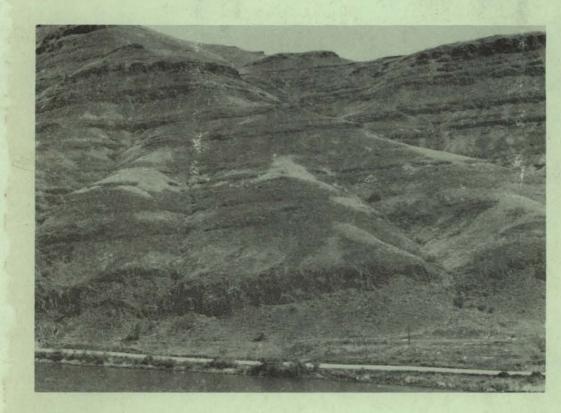
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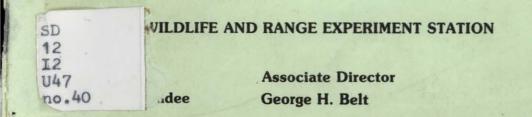


College of Forestry, Wildlife and Range Sciences

Canyon Grasslands and Associated Shrublands of West-central Idaho and Adjacent Areas



By E. W. Tisdale





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The author is indebted to many people and several institutions for support and encouragement in this post-retirement project. Thanks are due to the Forest, Wildlife and Range Experiment Station of the University of Idaho for travel funds and this publication, to the U.S. Forest Service for river transportation and accommodations in the Hells Canyon area, and the Soil Conservation Service for soils information.

People who helped include especially my wife, Norah, who assisted with virtually all of the field work and aided in many other ways; Mary Bramble-Brodahl, who did the computer analyses and co-authored an earlier paper on vegetation-site relationships; several University of Idaho faculty members including Maynard Fosberg for help in soil classification, Douglass Henderson and Steve Brunsfeld for plant identification, and Minoru Hironaka, Fred Johnson, and Steve Bunting for general support and manuscript review.

AVAILABILITY OF DATA

Much of the information from this study has been entered in a computer data base that can be accessed through the Department of Range Resources at the University of Idaho College of Forestry, Wildlife and Range Sciences. Data including all individual site data sheets will be available for research and retrieval purposes.

ABSTRACT

Grasslands dominated by perennial bunchgrasses occupy the canyon-like valleys of the Snake and Salmon Rivers and their tributaries in west-central Idaho. The grassland areas differ in elevation from 215 to 2400 m. (710-7800 ft.) with slopes commonly of 45 to 70 percent and ranging to over 100 percent. Soils, mainly Xerolls, derived from volcanic materials are permeable and relatively stable. Vertical zonation of climate, vegetation and soils prevails, modified mainly by differences in aspect. Plant communities (series) characterized by *Agropyron spicatum*, *Festuca idahoensis* and *Carex hoodii* respectively, occupy most of the grassland area and form five habitat types. Minor types of less certain seral status occur at low elevations and are dominated by *Sporobolus cryptandrus* and *Aristida longiseta*. Small inclusions of shrubgrass types are dominated by *Artemisia rigida*, *Symphoricarpos albus*, *Rhus glabra*, *Cercocarpus ledifolius* and *Celtis reticulata*. Vegetation altered by the effects of livestock grazing in the century of white settlement shows extensive loss of native species and replacement by aliens, mainly of Mediterranean origin. Principal invaders were *Bromus tectorum* and other annual bromes, but others, including several species of *Centaurea*, are increasing on depleted sites.

KEY WORDS: Idaho, Canyons, Grassland, Agropyron spicatum, Festuca idahoensis

Cover Photo-The long, steep slopes of the Snake River Canyon near its junction with the Grande Ronde River. Numerous layers of basalt underlie the canyon grasslands.



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Canyon Grasslands and Associated Shrublands of West-central Idaho and Adjacent Areas

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INTRODUCTION

The grasslands and shrublands of the middle Snake and lower Salmon River Valleys and their tributaries constitute a relatively small, but distinctive vegetation region of the Pacific Northwest. Located in northwestern Idaho and adjacent northeastern Oregon and southeastern Washington, these grasslands occur in the form of relatively narrow bands which vary from approximately 2 to 25 km (1.2 to 15.5 miles) in width along the slopes and bottoms of the deeply cut valleys that form the Snake and Salmon River systems. The area is characterized by steep topography and great differences in elevation within short distances.

Due to its rugged topography and relatively dry climate, most of this grassland region has remained uncultivated. The mild winter climate and presence of high quality native forage makes these lands highly valuable for wildlife and domestic livestock. The native grasslands provide stability for steep slopes where accelerated erosion would seriously damage water quality in the rivers. Recreational values are also high, as indicated by the recent designation of a sizeable portion of the area as the Hell's Canyon National Recreational Area.

Tributaries of the Snake and Salmon Rivers, including the Imnaha and Grande Ronde on the west and Clearwater on the northeast provide major additions to the canyon grassland habitat. The counties involved include portions of Nez Perce, Lewis, Clearwater, Idaho, Adams and Washington in Idaho; Whitman and Asotin in Washington; and Wallowa and Baker in Oregon (Figure 1).

OBJECTIVES

- To determine the climax botanical composition of the grasslands and shrublands, to classify them, and relate them to vegetation types previously described in the Pacific Northwest Bunchgrass Region.
- To investigate the relationships of these vegetation types to climatic, topographic, edaphic, and biotic factors.

The study area included all of the canyon grassland system in Idaho plus adjacent areas in Washington along the Snake and Grande Ronde Valleys (Fig. 1). Investigations on the Oregon side of the Snake River and in the Imnaha River Valley were confined to reconnaisance and detailed sampling of a few sites sufficient to confirm the presence of the types described in the study area.

THE PHYSICAL SETTING

Geology and Physiography

The dominant surface rock formation over much of the study area is Columbia River basalt, mainly Miocene in age. This was formed in a series of thick, extrusive flows in relatively flat lying beds, which are prominently displayed on the canyon walls.

Older formations, exposed in the lower canyons or in areas of recent uplift, include metamorphic rocks of both igneous and sedimentary origin. One of the most widespread is the Seven Devils Volcanics of Triassic-Permian age. These are metamorphosed flows consisting mainly of andesites and rhyolites, with some intercalated sediments.

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Other pre-Miocene formations include schists and other crystalline and sedimentary materials. Isolated outcrops of limestone occur, particularly in the Salmon River portion of the study area (Ross and Forrester 1958, Richmond et al. 1965).

More recent surficial materials include deposits of volcanic ash, loess and alluvium. The ash resulted from volcanic activity in the Cascade range of western Washington and Oregon. The thickest deposit in the study area is from the eruption of Mount Mazama about 6600 years ago. The process continues, as shown by the eruption of Mount St. Helens in 1980, although ashfall from this event affected only the north end of the study area.

The area was not glaciated during the recent Wisconsin advance, but indirect effects are seen in extensive loess deposits blown from glacial outwash deposits in southcentral Washington. Post-glacial alluvium from various sources has been deposited in the valley bottoms, but covers only a small portion, probably less than 5 percent of the study area.

Two other geological influences on the topography of the area are the rapid cutting of the main valleys following regional uplift and vigorous stream flow; and the particular weathering characteristics of the Columbia basalt (White 1974). Rapid cutting of valleys below the prevailing plateau levels has resulted in over-steepening of the canyon sides, so that slopes of 45 to 70 percent predominate, and gradients exceeding 100 percent are not uncommon. The weathering of Columbia basalt flows follows a vertical cleavage pattern which produces a series of vertical cliffs, each with a steep and often long talus slope at its base (See cover photo).

The region traversed by the Snake River canyon ranges from approximately 750 to 1070 m (2460-3500 ft) in elevation in the plateau portion, but rises to 1420 m (4625 ft) near the northern end of the area, and 2863 m (9393 ft) in the Seven Devils Mountains in the southern portion. Marked differences in aspect, produced by the erosional patterns of the main drainages and their numerous tributaries, are another major feature. These aspect differences, coupled with steepness of slope and differences in elevation, produced a highly variable environment within the canyon system.

Soils

The soils of the area reflect great variability in impact of the soil-forming factors, especially differences in climate, relief and vegetation.

Published data on the soils of much of the study area are contained in survey reports for Idaho and Nez Perce counties in Idaho (USDA 1982, 1976) and Whitman county in Washington (USDA 1980). While these reports provide much information, they do not provide sufficient detail on the variability of soils found in the rugged areas of the canyon grasslands. Furthermore, the mapping units often are too broad to pinpoint the soils of specific areas.

While the regional climate of the area imposes certain limitations, microclimate is the critical influence on soil formation. Microclimate is influenced primarily by the factor of relief, operating through differences in elevation and aspect. The pattern of both soils and vegetation is dominated by this climatic-topographic interaction.

Differences in parent material are less influential, since the majority of the soil-forming materials (basalt and many metamorphics) produce fairly similar soils. Loams are the most common textural class although coarser textures occur in limited areas. Most of the soils have developed from a mixture of residual and colluvial materials, and contain a high proportion (20 to 50%) of gravel and stone.

On first consideration, the time factor might not appear to be limiting, since the bulk of the area has undergone no major geological change in the Quaternary, and only the alluvial deposits of the valley bottoms are post-Pleistocene. The steepness of the valley slopes, however, favors surface movement and colluvial deposition, factors which have prevented soils from developing to the extent that their geologic age might warrant.

Taxonomically, most of the soils belong to the order Mollisols, suborder Xerolls (USDA 1975). At Great Group level, Argixerolls and Haploxerolls predominate although Calcixerolls also occur. Entisols, represented by Xerorthents and Xeropsamments, occur sparingly in the valley bottoms. Inceptisols, in the form of Cryumbrepts, occur only at the highest elevations in the grasslands.

Many of these soils are classed as loamy-skeletal, reflecting the influence of colluvial material and surface creep. Profile depth varies greatly, with many soils of southerly slopes rating as lithosols, while those on steep northerly slopes are much deeper and usually contain considerable loess. A high proportion of the soils show only limited development of the "B" horizons.

Soil stability is high, despite steepness of terrain and sparseness of vegetal cover on the drier slopes. Soil slips occur when a saturated top layer slides over frozen subsoils, but these are usually small, isolated events, and appear to stabilize within a few years.

Climate

Climatic data for the study area are sparse, and derived almost entirely from weather stations located in or near the bottoms of the major valleys. Data from these stations and others in the vicinity were put on a computer storage and retrieval program (HISAR) at the University of Idaho. This program provided the data used in the present study, including calculations of biotemperatures according

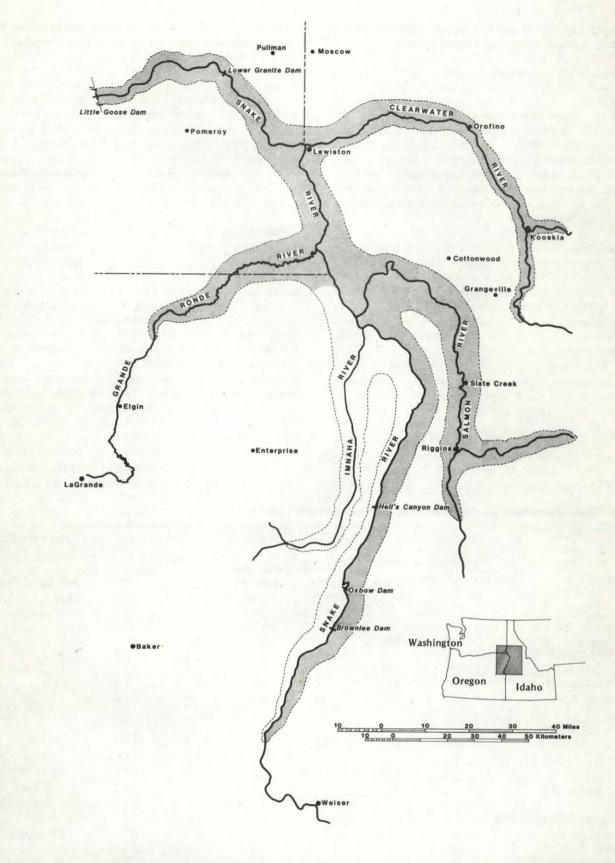


Fig. 1. Sketch map of area occupied by the canyon grasslands. Study area is shown as the stippled portion. The portion of the study area that borders the Snake River from the vicinity of Hell's Canyon Dam to its junction with the Imnaha River is located in the Hell's Canyon National Recreation Area.

to Holdridge (1967). A summary of data from the canyon locations and adjacent areas is presented in Table 1.

Records for the canyon stations indicate a semi-arid climate with hot summers and mild winters. Differences in both total precipitation and its seasonal distribution are also evident. Brownlee, at the southern end of the study area, has approximately the same total precipitation as the two central stations (Riggins and Slate Creek), but receives less than half of its moisture in the April to October period, while the latter stations receive well over half in this time. Farther north and west, Lewiston and Little Goose Dam have lower precipitation and belong in the summer-low, winter-high moisture group.

Similar differences in pattern show for plateau sites situated close to the canyon system. All have higher total precipitation than the canyon sites although the increase over the central and southern canyon area averages only 27 percent. The two stations closest to the central canyon area, Grangeville and Cottonwood, show the same high proportion of precipitation in the April-October period, while the two northern stations, Moscow and Pullman, show a winter-high moisture regime. Precipitation is very low at all stations in July through August, and the main difference between the two patterns lies in the proportion of moisture falling in May and June.

This difference could be a significant factor in the development of soils and vegetation. For soils, increased organic matter content for profiles developed under the higher May-June moisture pattern has been reported (USDA 1982). The effects on vegetation have not been documented, but may include a greater abundance of perennial forbs in communities of the moist May-June region.

Air temperatures differ less among the canyon stations than precipitation does. In all cases the winters are mild, with only limited and ephemeral snow in the valley bottoms. July temperatures and mean biotemperatures (Holdridge 1967) are relatively high at all stations. Both winter and summer temperatures are noticeably lower in the Plateau stations, and there is little difference among stations within this group.

The data cited in Table 1 are inadequate to describe the complex pattern of microclimates in the canyon; i.e., the question of precipitation increase at higher elevations is not answered. Precipitation on the adjacent plateaus cannot be assumed to indicate that of higher areas within the canyons. Eight years of data from rain gauges located at three different elevations in the Salmon River drainage near Riggins (Smith 1979) show average annual precipitation of 416, 497 and 617 mm. respectively at elevations of 640, 823, 1494 meters. These differences in precipitation with increasing elevation roughly parallel those indicated by the weather stations of the area (Table 1). They represent an extremely limited base, however, from which to make inferences for the remainder of the canyon system. No data are available for areas above 1500 m.

Other microclimatic factors, such as the influence of elevation and aspect on air temperatures, wind flow and

Table 1-Climatic data	from weather stations in	the study area and environs.
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		Elevation (m)		Precipitation	1	Mean Temp. (°C)		Mean Bio-Temp. ¹ (°C)	
			Total (mm)	Percentage April to October	Percentage July to August	Jan.	July	Apr. to Oct.	Nov. to March
I.	Canyon Stations	*****	W 81.7						
	Brownlee, ID	562	450	42	6.1	-0.8	25.9	17.5	4.5
	-Riggins, ID	548	429	59	9.2	1.0	24.3	17.2	5.3
	-Slate Creek, ID	518	440	62	8.0	2.4	23.7	16.6	5.9
	-Lewiston, ID	431	328	54	9.5	-0.4	23.3	16.3	4.5
	Little Goose Dam, WA	183	300	40	9.4	1.9	24.4	17.3	5.5
II.	Plateau Stations								
	Grangeville, ID	1022	585	63	8.1	-2.4	19.2	13.2	3.1
	Cottonwood, ID	1036	504	60	9.3	-3.3	18.6	12.8	2.7
	Moscow, ID	811	594	42	5.7	-2.3	19.2	13.9	3.1
	Pullman, WA	776	562	40	7.0	-2.6	18.2	13.3	2.9
III.	Sagebrush Grass Stations	3							
	Weiser, ID	641	313	36	6.4	-2.9	22.8	14.2	4.0
	Payette, ID ²	655	276	40	7.7	-1.6	23.4	16.3	4.5
	Emmett, ID ²	762	337	42	4.0	-1.2	22.8	16.0	4.5

¹Calculated according to Holdridge (1967).

²Payette is 12 km and Emmett is 33 km southeast of Weiser.

snow retention, are not covered by existing data, and their effects can be estimated only by means of edaphic and vegetational indicators.

The sagebrush-grass region just south of the study area is represented by stations at Weiser, Payette and Emmett in southwestern Idaho. They show less annual precipitation than the grassland stations, and a lower percentage occurring in the April-October period. Temperatures are slightly lower in both summer and winter than in the canyons.

Climatic differences also occur between the study area and the Palouse grasslands to the north and west. Stations within this latter type, (Moscow and Pullman), which occur close to the study area have a winter-high pattern of precipitation. At lower elevations farther west, total precipitation is less than for canyon sites while temperatures are approximately as high. These tendencies are shown in the data for Little Goose dam.

LAND USE

Use of the study area by wildlife prior to European settlement was relatively light since the region lacked major populations of large grazing herbivores such as the bison of the Great Plains region (Buechner 1953). The only alteration to this pattern came with the acquisition of the horse by the Nez Perce and other local Indian tribes in the mid-1700s. These horses grazed on the grasslands of the plateau areas during the summers, but were wintered in the canyons. By the late 1800s, this use was probably heavy in certain localities, but there is no evidence of widespread, heavy use or damage to the canyon grasslands during this period.

White settlement started with discovery of gold in the Snake and Salmon valleys in the 1860s. Ranching developed rapidly in the 1880s, and initiated a period of largely unrestricted grazing. Cattle predominated at first until large losses of animals occurred during the unfavorable years 1884 to 1886. Then sheep were introduced in large numbers and remained important until the 1940s when cattle once more became the principal domestic livestock of the area.

Range use during the period 1890 through 1940 was heavy, with rates of stocking many times greater than would be considered sustainable now. Cattle tended to utilize the bottom lands and gentler slopes most heavily, but sheep, better adapted to rough topography, were herded onto the steeper slope as well. As a result of this excessive use, most of the more accessible portions of the lower Snake and lower Salmon river valleys were overgrazed and their vegetation greatly altered.

The grazing pattern was not uniform, however, and many areas escaped overuse due to various combinations of inaccessibility, steepness of slope, and distance from stock water. In the Hells Canyon portion of the Snake River, particularly, settlement and grazing use were less intense, and large areas of grassland have remained in relatively undisturbed condition to the present time.

Cultivation for crop production has been a minor factor of land use in the area. It is restricted largely to gentler slopes and benches which can support dryland crops, and to irrigated areas of small extent in the valley bottoms.

The situation is quite different on adjoining plateau areas, where climate, soils and topography are more favorable for cultivated crops. Here the great majority of the land is under cultivation, with winter wheat the principal crop. Stands of native Palouse grasslands in the mesic eastern portion which borders the study area are scarce, and largely confined to localized areas of stony soils and/or rough topography.

ECOLOGICAL CONSIDERATIONS

The highly varied environment of the study area has allowed the development of a mosaic of forest, grassland and shrubland vegetation. The first objective of the present study was to determine whether a rational pattern could be found in the composition and distribution of the grassland and shrub-dominated vegetation.

The approach used was the habitat type concept of environmental classification, proposed by Daubenmire (1952) and used to classify many kinds of vegetation (Daubenmire 1970, Mueggler and Stewart 1980, Steele et al. 1981, Hironaka et al. 1983). The concept is based on use of the entire plant community as an integrated indicator of environment. The composition of relatively uniform stands of undisturbed vegetation serves to indicate specific ecosystems. All areas with the potential of supporting one specific kind of vegetation are considered to belong to a particular habitat type, regardless of the current successional stage of the vegetation. The habitat type is considered the basic ecosystem unit, although "phases" may be recognized, which differ in minor ways. Habitat types related by the dominance of one or more identical species are classed as "series," communities possessing a common climax species which corresponds to the term "vegetation zone" used by many workers.

TAXONOMIC CONSIDERATIONS

Studies based on the composition of the whole plant community require accurate identification and a reasonably complete list of vascular species present on each stand. In the current study, sampling was done when the major species were fully grown. Identification of very early or late maturing species often required additional visits. Identification to subspecies rank was confined to cases where ecological differences at this level were evident. Some species of *Astragalus, Castilleja, Lomatium, Crepis, Lupinus, Erigeron* and *Carex* proved difficult to identify unless complete material, often including both flowers and fruits, could be obtained. Even a few of the most common species presented problems. *Poa sandbergii (P. secunda* according to Arnow 1971) is a highly variable species composed of populations which differ considerably in phenology, stature and probably other characters of ecological importance (Daubenmire 1970, Heidel et al. 1982). The introduced annual *Bromus* species, *B. japonicus* and *B. mollis* could be distinguished with certainty only after the inflorescence was mature. Most collections were identified as *B. japonicus*, but *B. mollis* probably occurred on some sites. The nomenclature used follows Hitchcock and Cronquist (1973) unless otherwise stated.

The nomenclature of Agropyron spicatum is currently in a state of flux as a result of suggested major revisions in the tribe Triticeae. According to Dewey (1983) and others, this species does not belong in the genus Agropyron as defined in recent studies, and is more properly termed Elytrigia spicata (Pursh) D.R. Dewey or Pseudoroegneria spicata (Pursh) A. Löve. Since uncertainty concerning the designation for this species still exists, I have used the old name.

PREVIOUS STUDIES

Published data on the canyon grasslands and shrublands are in short supply despite an increase in recent years. Most information on the vegetation is found in reports from the University of Idaho. Campbell (1962) studied grasslands at the higher elevations in the northern part of the study area. On a basis of limited sampling (12 sites) he described two climax communities, the Festuca idahoensis/ Koeleria cristata in more mesic areas and Agropyron spicatum/Festuca idahoensis on drier sites. Evans and Tisdale (1972) reported on the lower elevation grasslands, mainly in the Salmon River drainage. This study was concerned primarily with the ecology of Aristida longiseta and Agropyron spicatum. The seral role of A. longiseta in much of the area was established, as well as its high temperature requirements for germination. Two communities were recognized, one on alluvial fans and terraces, dominated strongly by A. longiseta. The other type occurred on colluvial slopes and had A. spicatum co-dominant with A. longiseta on most sites.

Horton (1972), in an ecological reconnaissance of the lower Salmon River, recognized the grasslands occupying the valley bottom and lower slopes from a point some 19 km (12 mi) above Riggins to the junction with the Snake River. The vegetation of this area was described as greatly altered by livestock grazing, and currently dominated by exotic species, especially annual bromes. Agropyron spicatum, Festuca idahoensis and to a lesser extent Sporobolus cryptandrus and Aristida longiseta were classed as potential climax species on various habitats. The scarcity of Poa sandbergii in many communities was noted.

Huschle (1975) studied the vegetation of a 400-mile, narrow strip of land bordering the Snake River from the vicinity of Weiser, Idaho, to McNary Dam, Washington. Most of the communities he recognized were seral, but one, the Agropyron spicatum/Poa sandbergii was regarded as climax. This habitat type appeared more mesic than the one of the same name described by Daubenmire (1970) in eastern Washington. Smith (1979) studied the grazing relationships of cattle, elk and mule deer on high elevation ranges in the Salmon River drainage. The vegetation was all somewhat disturbed and dominated by varying proportions of A. spicatum and annual Bromus species.

A preliminary report on the current investigation (Tisdale 1979) was confined to sites in the western (Snake River) portion of the study area. This publication documented the status of the canyon grasslands as a distinct section of the Pacific Northwest Bunchgrass Region, Two vegetation series and five habitat types dominated by Agropyron spicatum and Festuca idahoensis were described. General relationships to site factors were also indicated. Vegetation of the highest elevations, and of fans and terraces in the valley bottoms, was not described in this report. Tisdale and Bramble-Brodahl (1983) investigated the relationship of site characteristics of the five major grassland habitat types described in the current study. Relations with soil taxa proved relatively weak, and several soil families were found to be associated with each of four of the five habitat types. Strong relationships were revealed, however, between the vegetation units and 13 soil and site factors when the data were analyzed by stepwise discriminant analysis. Site factors showing the strongest relationship to vegetation units included elevation, radiation index; color (value) and organic matter of the "A" horizon; and lime in the profile.

The vegetation of other portions of the Pacific Northwest Bunchgrass Region has been studied by a number of workers, including Daubenmire (1942, 1970) in Washington; Poulton (1955) and Johnson (1981) in parts of Oregon; Tisdale (1947) and McLean (1970) in British Columbia; Mueggler and Stewart (1980) in Montana. Tisdale (1983) reviewed the data available for the Pacific Northwest Bunchgrass and indicated its importance as one of the major grassland formations of this continent, embracing parts of four states and two Canadian Provinces. The existence of regional differences within this type was pointed out, along with associated problems of community identification and nomenclature.

Of those portions of the Pacific Bunchgrass region closely associated with the current study area, that of eastern Washington has been most comprehensively studied (Daubenmire 1942, 1970). This author described eight grassland habitat types, five of which are dominated by one or both of the two main grasses of the region, Agropyron spicatum and Festuca idahoensis. Three edaphic communities of lesser extent, dominated by Aristida longiseta, Sporobolus cryptandrus and Stipa comata respectively, were also recognized, as well as several associated shrub communities.

The most recent addition to the literature, received just before this paper went to press, consists of two draft reports by Johnson and Simon (1985, 1985a). These contain descriptions of vegetation and site characteristics of the Oregon portion of the canyon grasslands plus a sizeable area on the Idaho side of the Snake River in the Hells Canvon National Recreation Area. The vegetation units described by these authors are differentiated by a combination of vegetational and environmental characteristics. This approach has lead to recognition of local variations, many of which resemble "range sites" or "ecological sites" (R.I.S.C. 1983, S.C.S. 1976) more than habitat types as generally recognized. The relation of several of the types recognized by Johnson and Simon to those described in the current publication are discussed in the Section entitled "Variability of communities". The sites sampled by these authors include a high proportion in various stages of disturbance, and thus contribute to knowledge of the reaction of species and communities to grazing and other disturbance.

METHODS

I made reconnaissance notes on about 30 stands during the 1960s. In addition, detailed studies of portions of the area were made by two graduate students (Campbell 1962 and Evans 1967). These data sources established a background for the present study.

For this investigation, it was evident that the great variability of habitats and vegetation required relatively large numbers of sample plots for reliable results. Sampling equipment had to be light and compact since many sites could be reached only by extensive foot travel. Limited manpower for the project reinforced the need for a rapid sampling method with easily portable equipment.

The sampling approach involved laying out a macroplot 30 x 15m (100 x 50 feet) in size for recording site characteristics and species lists. Microplots of 50×20 cms (20 x 8 inches) were used to measure vegetational composition. Presence, frequency, and estimates of foliage cover were recorded for all vascular species. Percentage of ground surface occupied by cryptogams, litter, gravel or rock, and bare ground was also estimated.

The rating of foliage cover was made on the basis of actual amount of leafage present (RISC 1983), rather than on the canopy-coverage method of Daubenmire (1959) in which a presumed zone of influence is assigned to each plant. The former method usually gives lower ratings but probably comes closer to measuring actual photosynthetic surface. Only twenty microplots per site were used in order to maximize the number of sites sampled. Preliminary tests indicated that the information so obtained was highly comparable to that from larger numbers of plots for all but the rarer species, and the latter were included in the species list made for the macroplot. The microplot size was chosen as suitable for the majority of species encountered and because of its extensive previous use in Pacific Northwest grasslands. Microplots were located at 2m (6.5 feet) intervals along two randomly selected transects in each macroplot. Sites were located in relation to natural features and their positions marked on maps and/or aerial photographs.

Physiograhic data were recorded and notes made on the amount of erosion, evidence of grazing use, and signs of fire or other disturbance. A soil pit was dug at a representative spot at each site. Parent material, amount of profile development, stoniness, solum depth, presence of restrictive layers and occurrence of lime were recorded. During the second and subsequent years of the project, soil temperatures at 50 cms (20 ins) were measured at the time of sampling.

Samples for laboratory analysis were taken from each horizon recognized. Emphasis was placed on major divisions of the profile, listing only horizons that were readily apparent. Subsequent analyses of these samples were made for color (dry), texture, PH, organic matter and, in some cases, total exchangeable cations.

Sampling was confined to stands of relatively undisturbed and uniform vegetation chosen to represent major topographic situations and soil types of the study area. Altogether, 125 stands were sampled in the manner described. Reconnaissance notes were also made on a number of sites where circumstances did not permit intensive sampling, or where the stand contained features of interest, but did not meet the criteria for full-scale study.

The question of what constitutes undisturbed vegetation arose in selecting stands for intensive study. In the study area as elsewhere in grasslands, no stand can be assumed pristine if domestic livestock have been in the area. Also, concentrations of wild ungulates, accentuated by settlement of much of their former range, can cause disturbance. Criteria for site selection included presence of a well-developed and vigorous stand of the principal climax species and their common associates along with a minimum of exotics, or of native species known to be increasers under grazing. A complete lack of exotic species could not be used as a criterion for some of these, especially annual species of *Bromus* and the biennial *Tragopogon dubius*, occurred on a majority of the sites sampled.

Data analysis for classification of the vegetation included preparation of association tables and statistical analysis based on clusters defined by the Monit Program (Lambert et al. 1973). The first order sorting by cluster analysis was based on species presence or absence, followed by measures of frequency and cover. Classification was based on the vegetation, but soils and physographic data were correlated with vegetation and incorporated into the description of each community.

	Carex Series	Festuca Series		Agropyro	on Series	Community Types	
Species	Carex/ Festuca ht	Festuca/ Koeleria ht	Festuca/ Agropyron ht	Agropyron/Poa Balsamorhiza ht	Agropyron/ Opuntia ht	Aristida/ Poa ct	Sporobolu: Poa ct
PERENNIAL GRAMINO	OIDS:		1				
Bromus carinatus	50	6	-	-	-	-	-
Carex hoodii	67		-	-	- 1	-	-
Carex geyeri	67	5		-	-		-
Carex multicostata	50	-	-			-	-
Carex rossii	67	-	-			- 1	-
Poa nervosa var. wheeler	ri 67	-	-		-	-	-
Danthonia intermedia	67	-	-	1.00 _ hits	1.11	-	-
Stipa occidentalis var. occidentalis	78	20		_	-	_	-
Festuca idahoensis	100	100	100	19	÷.,	mo	-
Koeleria cristata	78	100	21	19	-		-
Poa sandbergii	22	80	78	100	75	100	75
Agropyron spicatum	-	100	100	100	100	66	25
Aristida longiseta		-	-	25	19	100	75
Sporobolus cryptandrus		-	-	19	25	50	100
Stipa comata var. comat	ta –	-	-		-	50	50
*Poa pratensis	-	5	-	6	- 1	100	-
PERENNIAL FORBS A	ND HALF SH	RUBS					
Antennaria anaphaloide	s 66	-	-		-	-	-
Antennaria microphylla	75	5	-		A		- 12.00
Arenaria congesta var. congesta	58	10	-	-	1	-	-
Aster foliaceus	50	20	-			-	-
Eriogonum flavum	58	-	-	-		-	-
Potentilla glandulosa	50	15	-	-		-	-
Calochortus elegans	22	52	7		-	-	-
Castilleja hispida	33	90	57	19	-	-	-
Eriogonum heracleoides	41	52	50	6	6	•-	-
Geum triflorum	50	52	35	_	-	-	-
Hieracium albertinum	66	81	7	-	_	0_	
Lupinus laxiflorus	91	62	14	-		- •	
Balsamorhiza sagittata	-	76	85	75	44	-	
Lithophragma parviflord	<i>z</i> –	62	64	43	6	-	-
Lithospermum ruderale		52	28	19	6	_	-

Table 2-Constancy (%) of common species¹ in canyon grassland communities.

Table 2 - (continued)

Life Form and	Carex Series	Festua	a Series	Agropyro	n Series	Community Types	
Species	Carex/ Festuca ht	Festuca/ Koeleria ht	Festuca/ Agropyron ht	Agropyron/Poa Balsamorhiza ht	Agropyron/ Opuntia ht	Aristida/ Poa ct	Sporobolus Poa ct
Lomatium triternatum	ı –	52	78	62	19	1.1.1	-
Lupinus sericeus	-	25	50	68	31	- S.	
Phlox colubrina + longifolia	-	40	28	56	50	_	-
Astragalus arthuri	-	5	14	56	25	16	-
Cirsium undulatum	-	10	7	50	69	50	25
Erigeron pumilis	-	24	29	37	50	66	75
*Hypericum perforatu	<i>m</i> –	30	7	31	12	66	50
Lomatium macrocarpu	um –	-	-	31	50	33	- 12
Opuntia polyacantha		-	-	19	69	16	100
Phacelia heterophylla	-		-	6	56	16	-
Scutellaria angustifolia	ı –	-	-	6	62	-	-
Astragalus inflexus	-	-	-	25	12	84	50
Chrysopsis villosa	-	-	-	6	19	50	50
Calochortus macrocar	pus –	-	-	_	-	-	50
Achillea millefolium v lanulosa	ar. 100	95	100	94	94	84	25
Brodiaea douglasii	-	62	78	56	25	33	50
*Tragopogon dubius	1997-20	52	50	37	19	100	75
ANNUALS							
*Bromus brizaeformis	-	52	78	56	44	33	50
*Bromus japonicus	-	38	71	62	56	66	75
*Bromus tectorum	-	29	43	75	94	84	100
Festuca megalura	- 1 m	14	36	67	25	-	-
*Alyssum alyssoides	-	20	7	56	50	16	-
Epilobium paniculatur	n 16	29	36	25	6	50	50
*Erodium cicutarium	-	-		50	31	50	75
*Lactuca serriola	-	20	57	37	25	84	75
*Myosostis micrantha	-	34	43	50	12	33	50
Plantago patagonica	-	_	1997	25	12	84	75
Stellaria nitens	-	52	50	69	37	66	25

¹Confined to species occurring with a constancy of 50% or more in at least one community.

*Exotic species

KEY TO GRASSLAND AND SHRUBLAND COMMUNITIES

- 1. Shrubs rare or absent, graminoids dominant.
 - 2. Upland Carex spp. abundant and usually dominant. Carex series Carex hoodii/Festuca idahoensis ht Carex hoodii and other Carex spp. co-dominant with Festuca idahoensis 2. Carex spp. rare or absent Festuca idahoensis series 3. Festuca idahoensis abundant and usually dominant Festuca idahoensis/Koeleria cristata ht 4. Koeleria cristata present and usually abundant 4. Koeleria cristata infrequent or absent, Agropyron spicatum abundant and often co-dominant. Festuca idahoensis/Agropyron spicatum ht 3. Festuca idahoensis infrequent, usually absent. 5. Agropyron spicatum dominant Agropyron spicatum series 6. Poa sandbergii abundant; B. sagittata, Lomatium triternatum and Lupinus sericeus common. Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata ht 6. Poa sandbergii sparse and sometimes absent; Opuntia polyacantha, Scutellaria angustifolia and Phacelia heterophylla common. Agropyron spicatum/Opuntia polyacantha ht 5. Agropyron sparse or absent 7. Sporobolus cryptandrus dominant, soils usually calcareous Sporobolus cryptandrus/Poa sandbergii ct 7. Aristida longiseta dominant, soils not usually calcareous Aristida longiseta/Poa sandbergii ct

1. Shrubs abundant and usually dominant

- 8. Overstory shrubs low, usually <2 m tall
 - 9. Soils <20 cm deep over basalt, Artemisia rigida dominant Artemisia rigida series
 - Poa sandbergii abundant Artemisia rigida/Poa sandbergii ht
 - 9. Soils various but >20 cm deep, A. rigida absent
 - 10. Rhus glabra dominant Rhus glabra series
 - 10. Symphoricarpos albus dominant Symphoricarpos albus series
- 8. Overstory shrubs usually >2 m tall, sometimes tree-like
 - 11. Cercocarpus ledifolius dominant Cercocarpus ledifolius series
 - A. spicatum dominant in the understory
 - 11. Celtis reticulata dominant

Agropyron spicatum dominant in the understory

Celtis reticulata/Agropyron spicatum ht

C. ledifolius/A. spicatum ht

Celtis reticulata series

RESULTS

Grassland Ecosystems

The vegetation of the grasslands of the study area was classified into three series, five habitat types, and two community types. The composition of these communities based on species presence is summarized in Table 2. The data are arranged to show differences in species occurrence among the vegetation types. Notable features of the data include:

- (a) the large number of perennial grasses and sedges in the Carex/Festuca ht and the restriction of most of these species to that type;
- (b) the complete ubiquity of two perennial species: Poa sandbergii and Achillea millefolium var. lanulosa, and only slightly less broad range of Agropyron spicatum, Brodiaea douglasii, Erigeron pumilis, Cirsium undulatum and two exotics, Hypericum perforatum and Tragopogon dubius. Annuals are commonly wide-ranging ecologically, and most of the common species occur in all of the communities except the Carex/ Festuca.

The pattern is one of elevational zonation, strongly modified by aspect. The influence of the latter factor is particularly evident at the middle and upper elevations, where southerly slopes are occupied by climax grassland, while adjacent north slopes may be covered by coniferous forest.

The major vegetation types recognized are as follows:

AGROPYRON SPICATUM SERIES

Vegetation dominated by Agropyron spicatum and lacking Festuca idahoensis occupies over half of the canyon grassland area, extending from the valley bottoms to middle elevations. The vegetation is characterized by the abundance of A. spicatum, mainly of the non-rhizomatous type. Annual grasses, especially introduced species of Bromus occur commonly, but with low cover. Perennnial forbs are fairly numerous, but few species exhibit high constancy or cover. Shrubs are sparse, with Chrysothamnus nauseosus the most common.

Habitat types of the Agropyron spicatum series

This complex was classified into two habitat types, Agropyron spicatum/Opuntia polyacantha and A. spicatum/Poa sandbergii/Balsamorhiza sagittata. This division is supported by the environmental data (Tisdale and Bramble-Brodahl 1983).

Agropyron spicatum/Opuntia polyacantha ht

This type was recognized early in the study (Tisdale 1979) as distinct from the *A. spicatum/Poa sandbergii* ht (See Fig. 2, page 12).

The vegetation (Table 3) is characterized by dominance of widely spaced plants of *A. spicatum*, all of them caespitose. *P. sandbergii* occurs on a majority of sites, but usually with scanty cover. Perennial forbs are not abundant, but six species occurred on 50 percent or more of the sites. *Opuntia polyancantha* and two forbs, *Phacelia heterophylla*, and *Scutellaria angustifolia* are important in characterizing the type. Each occurred in over half of the sites, and is rare or lacking in other major ht's. *Opuntia polyacantha* was chosen in naming the ht since it has the highest constancy and cover of the three. Among the annuals, *Bromus tectorum* is the most widespread and abundant, although *B. japonicus* is common.

The ground cover in this ht is distinctive, with total gravel, rock and bare ground averaging 50 percent. The cryptogam and litter cover is lower than in any of the other major hts in the canyon grasslands.

Foliage cover and frequencies for all species, and for each of the four life-form groups, are all lower than in other habitat types.

This ht occupies large areas on the lower and middle slopes of the valleys. It extends from elevations of 240 m to 1000 m (787 to 3280 ft), but is confined to southerly slopes and exposed ridge tops at all but the lowest elevations.

Physiographic and soils data are shown in Table 4. This is the most xeric of the grassland habitat types in the study area. Climatically, it occurs in the zone indicated for the valley bottoms in Table 1. Any increase in precipitation at higher elevations is apparently offset by the microclimate of the southerly slopes to which this type is confined. Soil temperatures at 50 cm are higher than in the other major types.

The soils are lighter colored, lower in organic matter, stonier, higher in pH, and shallower than those of the *Agropyron/Poa/Balsamhoriza* ht. Entisols, in the form of Xerorthents occur along with the more common Mollisols. Loamy skeletal mixed mesic Lithic Haploxerolls are the most common of the nine soil families. Lithic profiles occur in 56 percent of the sites.

The combination of environmental factors described results in a vegetation that begins growth very early in the spring, develops rapidly, and becomes dormant early in the summer. Fall regrowth of perennials is less frequent than in the other major grassland types, although it does occur some years in *A. spicatum* and *P. sandbergii*.

This habitat type seems to be unique to the canyon grasslands. The only type which resembles it to any extent



Fig. 2. Agropyron spicatum/Opuntia polycantha habitat type with sparse vegetation cover and an abundance of surface gravel and rock.

is the Agropyron spicatum/Poa secunda of eastern Washington (Daubenmire 1970), but the latter lacks the characteristic species of the Agropyron/Opuntia, and has a much higher frequency and cover of *P. sandbergii*.

Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata ht

This is the community described as the A. spicatum/ Poa sandbergii ht in earlier reports on this project (Tisdale 1979, Tisdale and Bramble-Brodahl 1983). The change was made to distinguish it from different communities which have been described by the term Agropyron/Poa in other parts of the Pacific Northwest. Although P. sandbergii occurs commonly in the ht described here, its ubiquitous presence throughout the grasslands of the Pacific Northwest make it a poor indicator species.

The best solution to this problem appeared to be the use of trinomial nomenclature, as recommended in a recent study by Crawford and Johnson (1985). These authors point out that use of binomials in certain situations can conceal information on community structure and function. This problem can be overcome by the addition of a third diagnostic species to the name of the community. In the case presented here, *Agropyron* is the ecological dominant and *Poa* is abundant but not diagnostic due to its wide ecological amplitude. The feature which best distinguishes this community from others designated as *Agropyron/Poa* is the presence of a group of perennial forbs, of which *B. sagittata* is the most conspicuous. The name *Agropyron/Poa/Balsamorhiza* recognizes this difference, but still relates the community to others dominated by A. spicatum and Poa sandbergii.

The botanical composition of the Agropyron/Poa/ Balsamorhiza ht is summarized in Table 5. It is characterized by dominance of A. spicatum, most of it the caespitose form. P. sandbergii is the only other perennial grass of significance in the type. Balsamorhiza sagittata is the most frequently occurring and conspicuous perennial forb. found in 75 percent of the sites sampled. Seven other perennial forbs, each occurred on 50 percent or more of the sites, and constitute an important segment of the community. Annuals are common, with eight species occurring on half or more of the sites. Most of these are exotics, but include the native Festuca megalura and Stellaria nitens. Annual bromes, B. tectorum, B. japonicus and B. brizaeformis are all common but do not dominate the annual cover to the same extent as they do in the Agropyron/ Opuntia ht.

The ground surface is occupied mainly by cryptogams and litter. The combination of these with standing vegetation provides a high degree of cover.

The high constancy and cover of *B. sagittata*, greater cover of *Agropyron* and *Poa* along with the common occurrence of the other perennial forbs listed, and of *Festuca megalura*, are key characters which separate this ht from the *Agropyron/Opuntia*.

The general aspect of this type is characterized by the dominance of well-defined clumps of *A. spicatum*. Because of the greater cover of both live vegetation and litter, and smaller amount of surface gravel, the Agropyron/ Poa/Balsamorhiza ht gives a general impression of relatively well-vegetated ground. Areas occupied by the Agropyron/Opuntia, in comparison, appear as poorly vegetated and rather barren.

The Agropyron/Poa/Balsamhoriza ht occurs widely throughout the lower and middle elevations of the study area, from about 300 to 1370 m (985 to 4500 ft). Generally, it occupies the more favored aspects and deeper soils within the Agropyron-dominated zone, but a lithic phase occurs in a portion of the type at higher elevations.

The climate for the type is presumably more mesic than that of the canyon bottoms. Increased moisture at the higher elevations is offset by the restriction of the type to southerly aspects or shallow soils.

Most soils are of mixed residual and colluvial origin, from volcanic materials. Textures range from sandy loam to clay loam, with loams and silt loams most common; and all are relatively stony. The soils are all Xerolls, with Argixerolls and Haploxerolls equally represented. Loamy sketetal mixed mesic Ultic Haploxerolls are the most common of the nine soil families represented. Overall, these soils are deep and permeable enough to provide adequate soil moisture for the peak growing season of April-June in this type. Compared to those of the Agropyron/Opuntia ht, the soils show darker color and greater organic matter, greater depth of profile, less stoniness and less surface gravel and rock.

This ht is closely related to several communities designated as A. spicatum/P. sandbergii by other investigators. The closest of these geographically, the A. spicatum/P. sandbergii described by Daubenmire (1970) is a more xeric type, with less species diversity, and fewer perennial forbs. Marked differences in annual grasses also exist, with F. megalura, Bromus brizaeformis and B. japonicus all rare or lacking in the Washington community. Agropyron/Poa communities described for eastern Oregon (Poulton 1955, Johnson 1981) western Montana (Mueggler and Stewart 1980) and southern British Columbia (Tisdale 1947) also appear to be more mesic than the Washington type, but differ considerably in botanical composition from the Agropyron/Poa/Balsamorhiza described here.

Table 3. Frequency and cover of major species¹ of the Agropyron/Opuntia ht (16 sites). (AGSP/OPPO)

	Freque	ncy (%)	Foliage cover (%)		
Species	Mean	S.D.	Mean	S.D.	
Agropyron spicatum	73.0	20.3	15.5	6.15	
Poa sandbergii	25.8	25.5	0.6	0.33	
Achillea millefolium	26.2	25.3	0.7	0.83	
Cirsium undulatum	10.0	5.0	0.5	0.28	
Eriogeron pumilis	25.0	30.8	0.6	0.64	
Lomatium macrocarpum	13.0	16.5	0.6	0.70	
Opuntia polyacantha	16.0	10.7	1.7	1.97	
Phlox (colubrina and longifolia)	25.0	17.8	0.6	0.29	
Phacelia heterophylla	30.0	35.0	0.9	1.06	
Scutellaria angustifolia	20.6	16.3	0.6	0.67	
*Bromus japonicus	38.0	32.2	0.5	0.44	
*Bromus tectorum	60.0	33.4	1.1	0.95	
*Alssum alyssoides	46.6	24.2	0.4	0.18	

¹ Species occurring in 50% or more of sites.

* Exotic species.

Table 4. Site characteristics for habitat types of the Agropyron series.

	Agropyron/ (AGSP/OP		Agropyron/ Poa/Balsamorhiza (AGSP/POSA/BASA)		
Character	Mean	S.D.	Mean	S.D.	
Elevation (m)	726	160	840	285	
Slope (%)	49	12.6	51	17.0	
Radiation index ¹	530	40	447	91	
Depth of solum (cms)	50	38	60	18	
Depth of "A" horizon (cms)	19.5	5.7	23.0	6.9	
Solum stoniness (%)	58	-	42	-	
Lime layer present (%)	18.7		37.5	- 10.00	
Texture "A" horiz	sdy 1loam		loam	-	
Texture "B" horiz	loam-clay 1.	-	clay 1.	-	
Color (value) "A"	4.4	-	3.8	-	
Organic matter "A" (%)	2.2	0.7	3.3	1.3	
Organic matter "B" (%)	1.6	0.4	2.1	1.0	
Organic matter (total gms)	114	-	176	-	
pH "A" horiz	6.8	0.47	6.5	0.64	
pH "B" horiz	6.7	0.45	6.7	0.70	
GROUND COVER (%)					
Cryptogams	12.0	15.0	18.5	10.6	
Litter	28.0	13.7	47.4	9.4	
Gravel and rock	42.0	14.0	14.8	12.2	
Bare	8.0	8.1	5.5	2.1	

¹Calculated according to Frank and Lee (1966).

'n

Agropyron spicatum





Table 5. Frequency and cover of major species of the Agropyron/Poa/Balsamorhiza ht (16 sites).

	Freque	ncy (%)	Foliage	Cover (%)
Species	Mean	S.D.	Mean	S.D.
Agropyron spicatum	90.3	14.9	20.3	8.9
Poa sandbergii	71.3	19.5	2.6	1.55
Achillea millefolium	38.3	21.6	1.5	1.07
Astragalus arthuri	15.7	10.6	1.0	0.73
Balsamorhiza sagittata	23.7	18.7	3.1	2.55
Brodiaea douglasii	21.2	11.8	0.4	0.12
Cirsium undulatum	7.0	2.9	0.3	0.28
Lomatium triternatum	32.8	31.9	1.3	1.54
Lupinus sericeus	19.6	14.5	1.6	1.88
Phlox (colubrina and longifolia)	19.4	17.0	0.6	0.40
*Bromus brizaeformis	4 2.7	28.9	0.6	0.41
*Bromus japonicus	41.1	38.2	0.8	0.79
*Bromus tectorum	61.2	27.8	1.5	1.69
Festuca megalura	55.0	32.1	0.9	0.79
*Alyssum alyssoides	12.5	15.0	0.2	0.17
*Erodium cicutarium	43.5	37.7	0.9	1.05
*Myosotis micrantha	40.0	32.2	0.8	0.98
Stellaria nitens	76.5	30.0	3.1	3.98

*Exotic species.

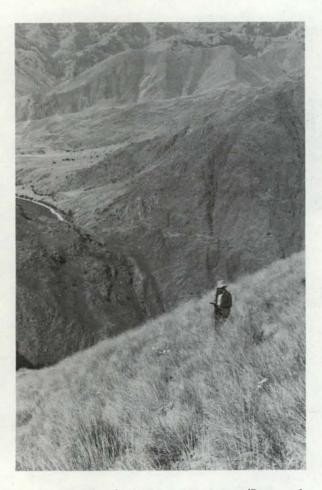


Fig. 3. Stand of Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata on a typical steep slope of canyon grassland in the Hells Canyon region of the Snake River. This area provides great variety in environmental factors caused by great differences in elevation and aspect.

FESTUCA IDAHOENSIS SERIES

Vegetation in which *Festuca idahoensis* is always present and usually dominant constitutes the other major series of the canyon grasslands. The elevational range is great, since the type descends to the 400 m (1310 ft) level on steep north slopes, and reaches 2000 m (6560 ft) on southerly slopes.

The vegetation is characterized by dominance of F. idahoensis, and to a lesser extent, A. spicatum. Plants of the latter species are generally of the rhizomatic type characteristic of relatively mesic sites (Daubenmire 1960, Dobrowolski 1979). Native forbs are more abundant than in the Agropyron series, while introduced annuals, including the bromes are less common. Total species diversity, frequency and foliage cover are greater than in the Agropyron series.

Habitat types of the Festuca series

In the first report on this study (Tisdale 1979), three habitat types were described: the Festuca idahoensis/Agropyron spicatum, the F. idahoensis/Koeleria cristata and the F. idahoensis/Symphoricarpos albus. The first two have proved to be communities of major extent in the canyon grasslands. The third, characterized by an abundance of dwarfed plants of S. albus, has proved on further study to be a marginal type of very limited extent, essentially no more than an ecotone of the S. albus thickets that are a characteristic feature of the study area. For this reason, the Festuca/Symphoricarpos has been removed from the list of major habitat types and Symphoricarpos-dominated vegetation is discussed in a later section dealing with shrub communities.

Data for vegetation and site characteristics of the two major *Festuca* habitat types are presented in Tables 6, 7, and 8.

Festuca idahoensis/Agropyron spicatum ht

This type is characterized by the presence of A. spicatum as a co-dominant, often equaling or even exceeding F. idahoensis in foliage cover and frequency. Poa sandbergii is common, but other perennial grasses are scarce. Total grass cover exceeds that of other hts in either the Festuca or Agropyron series. Perennial forbs are fairly well represented, and 8 native species occur on 50 percent or more of the sites. Native annuals are moderately abundant, with Stellaria nitens, Galium aparine and Clarkia pulchella most common. Exotic annuals, including all three annual Bromus species and Lactuca serriola are common. The ground cover is high in litter, with lesser amounts of cryptogams and rock or gravel and little bare ground. Shrubs are virtually lacking in this type.

The co-dominance of *A. spicatum*, scarcity of *K. cristata* and lower total frequency and cover of perennial forbs, separate this community from the *Festuca/Koeleria* ht.

The Festuca/Agropyron ht occupies large areas of the lower and middle valley slopes, from 400 m (1310 ft) to an upper limit of approximately 1500 m (4920 ft). Stands below 1000 m are restricted to northern slopes, but occur with increasing frequency on southerly slopes at higher elevations. The marked elevational overlap with the Festuca/Koeleria ht suggests that higher temperatures due to aspect, rather than differences in precipitation, may be the most critical factor involved.

Soils are moderately deep, loamy in texture, and have a considerable loess content. Stoniness is low compared to that in the *Agropyron* series but slightly higher than in the *Festuca/Koeleria* ht. Six soil families are represented: the most common are fine loamy mixed mesic Pachic Haploxerolls. Compared to soils of the *Festuca/Koeleria* ht these are similar in depth and texture, but lighter in color of the "A" horizon, higher in pH and lower in organic matter.

Communities of the same name have been described in Washington (Daubenmire 1970), Oregon (Poulton 1955, Johnson 1981), and Montana (Mueggler and Stewart 1980). The Montana type differs most; its grass component includes an abundance of Koeleria cristata and Stipa comata, while the perennial forbs are almost all different. The Washington community is closer, but apparently more xeric. It lacks some of the key forbs of the Idaho type, shows a greater occurrence of Chrysothamnus nauseosus, and a higher proportion of Bromus tectorum compared to B. brizaeformis and B. japonicus. The Oregon community described by Johnson (1981) has K. cristata occurring commonly, and poor representation of species such as Castilleja hispida, Lomatium triternatum, and Phlox longifolia. Further confusion regarding the Festuca/Agropyron complex arises from the positioning of these species names. Daubenmire (1970) used the term Agropyron/Festuca for his community, relating it to the Agropyron/Poa in physiognomy, rather than to the "meadow-steppe" represented by the Festuca/Symphoricarpos ht. In the series concept, the key relationship is considered to be the presence of the series dominant, and the ht is named accordingly, i.e. Festuca/Agropyron. The Festuca/Agropyron ht resembles other communities of the F. Idahoensis series more closely in both vegetation and habitat characteristics than those of the A. spicatum series.

Festuca idahoensis/Koeleria cristata ht FEID/KOCR

This community is distinguished by dominance of F. idahoensis and constant presence of K. cristata. Agropyron spicatum and Poa sandbergii are both common; but other perennial grasses are rare. Perennial forbs are abundant, and 12 native species occur on half or more of the sites. Many of these species are also common in the Festuca/Agropyron ht, but Calochortus elegans and Hieracium albertinum are rare in that type. Lupinus is abundant in both habitat types, but is represented mainly by L. laxiflorus in the Festuca/Koeleria and by L. sericeus in the Festuca/Agropyron. Many native annuals occur, but only one, Stellaria nitens was recorded on more than half the sites. Exotics are relatively scarce, with only the biennial Tragopogon dubius and the annual Bromus brizaeformis and B. japonicus rated as abundant. Three shrubs, Spiraea betulifolia, Rosa woodsii and Symphoricarpos albus occur, but with low constancy (25 percent or less) and low frequency and cover.

This habitat type is the most mesic in the F, idahoensis series, with greatest species diversity, average number of perennial forbs per stand, total frequency and foliage cover of perennial forbs (Table 8).

The range in elevation for the type is from 530 m to 2000 m (1740-6560 ft). The climate appears to be moister and cooler than that of the grassland types described so far

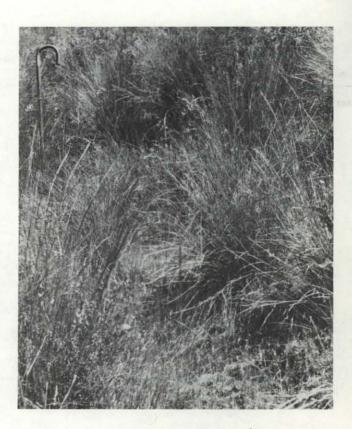


Fig. 4. Festuca idahoensis/Koeleria cristata habitat type showing the abundant cover of many grasses and perennial forbs.

in this report. An eight-year record of precipitation in the Salmon River drainage (Smith 1979) indicates an increase from 416 mm annually at 640 m to 497 mm at 823 m and 617 mm at 1493 m. Most of the sites in this ht lie above 800 m and those which occur below this level are on slopes compensated in temperature by steep northern aspects.

Soils in this type are relatively deep, loamy in texture, often high in loess with deep "A" horizons. Color of the "A" horizon is darker and its organic matter content higher than in the *Festuca/Agropyron* ht. Taxonomically the soils are mostly Mollisols, divided about equally between Argixerolls and Haploxerolls. Many of the sites have pachic profiles, reflecting deep mollic epipedons. A few sites belong in the frigid temperature category, reflecting the cooler climate at higher elevation. The temperature influence is shown most strongly in two sites at 1950 m elevation, where the soils are Inceptisols, classed as loamy skeletal mixed Cryumbrepts. Soil temperatures at 50 cm are definitely lower than for sites in the *Agropyron* series.

Daubenmire (1970) makes no mention of this community in Washington, but I have identified it in the Snake and Grand Ronde River Valleys in the eastern part of that state. There is no report of such a community in Montana or British Columbia. A *Festuca idahoensis/Koeleria cristata*

	Frequen	cy (%)	Foliage con	ver (%)
Species	Mean	S.D.	Mean	S.D.
Agropyron spicatum	82	19.4	18.5	8.7
Festuca idahoensis	83	19.8	15.0	8.2
Poa sandbergii	56	25.0	2.3	1.2
Achillea millefolium	30	18.3	1.6	1.2
Balsamorhiza sagittata	28	13.6	5.3	3.6
Brodiaea douglasii	20	10.7	0.5	0.2
Castilleja hispida	13	5.8	0.8	0.3
Eriogonum heracleoides	20	14.0	1.8	0.9
Lithophragma parviflora	48	21.0	0.8	0.3
Lomatium triternatum	16	22.8	0.4	0.8
Lupinus sericeus	21	11.4	1.1	0.7
*Tragopogon dubius	17	10.0	1.2	0.7
*Bromus brizaeformis	48	17.5	0.7	0.3
*Bromus japonicus	28	32.7	0.4	0.6
*Bromus tectorum	38	25.9	0.5	0.4
Clarkia pulchella	24	17.0	0.5	0.3
Galium aparine	49	43.0	0.6	0.4
*Lactuca serriola	17	5.1	0.3	0.1
Stellaria nitens	59	21.0	1.0	0.3

Table 6. Frequency and cover of major species of the Festuca/Agropyron habitat type (14 sites).

*Exotic species.

	Festuca/Ag	gropyron	Festuca/Ko	eleria	
Character	Mean	S.D.	Mean	S.D.	
Elevation (m)	930	345	1162	424	
Slope (%)	52	10	51	6	
Radiation index	346	89	375	116	
Depth of solum (cm)	77	29	75	11	
Depth of "A" horizon (cm)	28	6.1	30	6.6	
Stoniness solum (%)	34		26	_	
Lime present (%)	0		5	-	
Texture "A" horiz	loam-silt 1.		loam-silt 1.	1	
Texture "B" horiz	silt 1clay 1.		silt 1.		
Color (value) "A"	3.5	-	2.9		
Organic matter "A" (%)	5.8	2.5	6.7	2.6	
Organic matter "B" (%)	2.9	0.7	4.1	1.8	
Organic matter (total gms)	345	-	410	-	
pH of "A" horiz	6.5	2.3	6.2	0.5	
pH of "B" horiz	6.4	1.1	6.1	0.4	
GROUND COVER (%)					
Cryptogam	17.5	14.9	19.5	14.1	
Litter	46.0	9.9	54.0	9.4	
Gravel and rock	14.0	15.0	7.1	11.0	
Bare	3.7	3.2	3.5	2.8	

Table 7. Site characteristics for habitat types of the Festuca idahoensis series.

	Frequenc	y (%)	Foliage cover (%)	
Species	Mean	S.D.	Mean	S.D
Agropyron spicatum	62	23.4	5.8	4.6
Festuca idahoensis	93	10.8	21.0	6.6
Koeleria cristata	41.5	18.5	2.0	1.4
Poa sandbergii	34	31.5	1.2	1.5
Achillea millefolium	33.6	15.6	1.6	0.8
Balsamorhiza sagittata	13.2	8.1	1.7	1.2
Brodiaea douglasii	18.6	10.3	0.5	0.2
Calachortus elegans	27.8	23.7	0.4	0.2
Castilleja hispida	12.0	9.0	0.6	0.4
Eriogonum heracleoides	37.0	30	5.1	4.0
Geum triflorum	33.0	29.5	2.3	1.6
Hieracium albertinum	13.0	9.3	0.7	0.3
Lithophragma parviflora	28.0	19.0	0.4	0.3
Lithospermum ruderale	11.2	2.5	1.0	1.1
Lomatium triternatum	13.4	10.0	0.4	0.3
Lupinus laxiflorus	33.1	21.1	2.3	2.3
*Tragopogon dubius	19.0	12.2	0.5	0.3
*Bromus brizaeformis	26	18.5	0.5	0.3
Stellaria nitens	59	30.0	1.0	0.5

Table 8. Frequency and cover of major species of the Festuca/Koeleria habitat type (21 sites).

*Exotic species.

association was described by Poulton (1955) in eastern Oregon. Poulton describes this type as the most mesic grassland in his study area, occurring just below the forest line in an elevational zonation pattern. His description includes many elements of the *Festuca/Koeleria* ht as described here. The perennial forb cover, however, is less varied and abundant. A community which invites comparison is the *Festuca idahoensis/Symphoricarpos albus* (Daubenmire 1970) that occupies the most mesic habitat of the Palouse grasslands of the Columbia plateau. This type resembles the *Festuca/Koeleria* in the dominance of *F. idahoensis* and presence of many perennial forbs, but differs in the importance of shrubs (*S. albus* and *Rosa* spp.), and in the greater abundance of forbs.

CAREX SERIES

Vegetation in which one or more species of upland *Carex* are abundant constitutes a relatively small but distinctive element of the canyon grasslands. *Festuca idahoensis* and other perennial grasses are often co-dominant with the *Carex*. Perennial forbs are well represented, but shrubs are virtually absent.

This is a high elevation series, confined to the moistcool end of the canyon grassland climatic gradient. All of the vegetation recognized in this series was assigned to the following habitat type:

Carex hoodii/Festuca idahoensis ht

This type is characterized by co-dominance of Carex spp., (C. hoodii, C. geyeri, C. multicostata and C. rossii) along with F. idahoensis (Table 9). C. hoodii was chosen in naming the type, since it has the highest constancy (75 percent) of the sedges. The other dominant, F. idahoensis, occurs on all sites. The perennial grass component includes several other species, five of which occur with constancies of 50 percent or more. This feature is in strong contrast to the grassland types at lower elevations where only two or three perennial grasses occur in abundance. Furthermore, with the exception of K. cristata, these species are rare or lacking in other communities of the canyon grasslands. Perennial forbs are abundant also, with 12 species occurring on 50 percent or more of the sites. Six of these species are also abundant in the most closely related community, the Festuca/Koeleria ht. The others, Antennaria anaphaloides, A. microphylla, Arenaria congesta, Aster foliaceus, Eriogonom flavum and Potentilla glandulosa are largely or totally confined to the Carex/Festuca ht.

Annuals are sparse in the *Carex/Festuca* ht, with grasses virtually absent, and a few annual forbs that are native.

Due to its relatively gentle topography and attractiveness as a source of forage in summer, this type has been grazed rather uniformly. As a result, the stands sampled, although the least disturbed that could be found, probably represent a greater departure from climax condition than was available at sites in the *Agropyron* and *Festuca* series. The influence of past grazing may be reflected in the relative abundance of forbs such as species of *Antennaria*, *Arenaria* and *Eriogonum*, which are low in palatability to livestock. The continued abundance of species including *Festuca idahoensis*, *Carex hoodii*, *Bromus carinatus* and



Fig. 5. Carex hoodii/Festuca idahoensis ht with dense cover of sedges, grasses, and perennial forbs.

Danthonia intermedia which are much higher in palatability (Bryan and Madden, personal correspondence) suggests that these changes have not been fundamental. This view is supported by the absence of exotic species, including the aggressive *Poa pratensis*, from these stands.

Another community, dominated by *Festuca viridula* and *Carex geyeri*, was found in a small portion of the southern end of the study area. This type occurs on immature sandy loam soils derived from granitic parent material. The vegetation differs from that of the *Carex/Festuca* ht mainly in the substitution of *F. viridula* for *F. idahoensis* as a dominant, and by a sparser perennial forb component. This is the only spot in the study area where *F. viridula* was found, although it is common on mountain "balds" farther north in the state.

The Carex/Festuca habitat type is confined to the highest elevations occupied by the canyon grasslands, between 1950 and 2400 m (6400-7870 ft). It occurs commonly in the form of openings, wholly or partially surrounded by forests (Fig. 5). In parts of the area, however, on south and west slopes of the Snake River Canyon, the type is contiguous with other grassland communities below. Here the whole grassland complex from the Agropyron spicatum series through the Festuca idahoensis series to Carex-dominated communities occurs without interruption.

Geographically, the *Carex/Festuca* type was found only on the high ridge separating the Snake and Salmon River systems in Idaho and similar ridgetops in adjacent Oregon. The 12 sites I sampled are all in Idaho.

This type is limited to the moister and cooler portion of the study area. Meterological data are lacking, but it is a reasonable assumption that the increase in precipitation mentioned earlier in connection with the *Festuca/Koeleria* ht continues to higher elevations. Vegetationally this is indicated by the presence of forests dominated by *Abies* grandis and *A. lasiocarpa* in the same general area as the grasslands.

The soils are distinctive (Table 10). They are shallow and stony, and have the highest organic matter content, lowest pH and lowest temperature at 50 cm of any of the canyon grassland soils. Only one soil family, loamy skeletal mixed Cryumbrepts was found. Restriction of this habitat type to sites with droughty soil and maximum wind exposure within a macroclimate suited to mesic forest communities establishes it as a topo-edaphic climax.

Adjacent forest communities generally occupy deeper and less stony soils. Forests also occur on relatively shallow soils where the underlying basalt is weathered and permeable to plant roots. Soils of similar depth which overlie dense, unweathered basalt support grassland (Olson and Crockett 1965).

The *Festuca viridula* grasslands of the Wallowa mountains west of the study area are close geographically, but quite different in composition. In climax condition, these are described as much lower in species diversity, and marked by sole dominance of *F. viridula* (Pickford and Reid 1942, Reid et al. 1980).

Grasslands containing a substantial portion of upland *Carex* spp. have been observed in the mountains of central Idaho, but data for these types are minimal. Schlatterer (1972) described vegetation dominated by *Festuca idahoensis* along with lesser amounts of *Carex geyeri* and other

unspecified species of *Carex*. This type was found at elevations around 2400 m (7870 ft). A similar type I observed at 2700 m (8860 ft) in the Pioneer Mountains is dominated by *F. idahoensis* and *C. hoodii. Carex geyeri, Poa nervosa, Stipa* spp. (*S. occidentalis* and *S. lettermannii*) and *Sitanion hystrix* occur abundantly. Neither of the two high elevation grassland types described by Mueggler and Harris (1969) in central Idaho resemble the *Carex* series. Two of their unclassified stands, however, located at an elevation of 2300 m (7545 ft) are dominated by *F. idahoensis*, with *C. geyeri* and an unidentified species of *Carex* present in abundance.

Table 9. Frequency and cover of major species of the Carex/Festuca habitat type (9 sites).

	Freque	ncy (%)	Foliage cover (%)		
Species	Mean	S.D.	Mean	S.D	
Bromus carinatus	51.6	32.1	2.03	1.05	
Carex geyeri	55.2	44.1	10.4	9.5	
Carex hoodii	53.0	41.7	8.0	8.4	
Carex multicostata	23.3	12.6	1.3	0.62	
Carex rossii	20.8	16.5	1.0	0.90	
Danthonia intermedia	47.0	39.5	3.1	3.2	
Festuca idahoensis	82.7	28.1	16.0	10.6	
Koeleria cristata	36.8	28.8	1.5	1.50	
Poa nervosa	14.4	9.0	0.6	0.44	
Stipa occidentalis	55.4	34.7	2.7	2.10	
Achillea millefolium	58.4	21.2	3.5	1.6	
Antennaria anaphaloides	27.7	26.3	1.62	1.84	
Antennaria microphylla	30.0	23.2	1.70	1.49	
Arenaria congesta	49.5	22.0	2.02	1.40	
Aster foliaceus	41.0	42.6	3.72	4.46	
Eriogonum flavum	35.4	27.9	2.74	2.53	
Geum triflorum	36.0	27.6	3.17	2.86	
Hieracium albertinum	43.0	26.7	3.28	2.96	
Lupinus laxiflorus	69.7	16.2	6.75	2.80	
Potentilla glandulosa	16.0	11.4	1.02	1.20	

Table 10. Site Characteristics of the Carex/Festuca habitat type.

Character .	Mean	S.D.
Elevation (m)	2178	127
Slope (%)	6.0	1.3
Radiation index	450	48
Depth solum	56	9.5
Depth "A" Horiz	28	9.3
Stoniness solum (%)	56	-
Lime present (%)	0	-
Texture "A" horiz	loam	-
Texture "B" horiz	sandy loam	
Color (value) "A"	2.8	-
Organic matter "A" (%)	11.1	2.9
Organic matter "B" (%)	7.0	2.7
Organic matter (total gms)	626	
pH "A" horiz	5.0	0.3
pH "B" horiz	5.0	0.3
GROUND COVER (%)	and the second se	
Cryptogam	8.1	10.5
Litter	61.0	12.0
Gravel and rock	10.4	4.0
Bare	2.4	1.3

Carex spp. play no major role in the Palouse grasslands (Daubenmire 1970), although C. rossii and C. geyeri occur in 20 and 27 percent respectively of sites in the Symphoricarpos albus/Festuca idahoensis ht. Aller et al. (1981) described a type dominated by C. geyeri on steep north slopes at the eastern edge of the Palouse region, but apart from the dominance of this sedge there is little resemblance to the vegetation described in the present study. Aristida-dominated sites contain a higher percentage of exotic species than the Agropyron-dominated hts (Table 11). Furthermore, Aristida is a species of low livestock preference, and even Sporobolus, because of its low growth habit and late phenology is more tolerant of the common pattern of spring-fall grazing than is A. spicatum. The latter species occurs in most of the Artistida-dominated and at least one-third of the Sporobolus sites. A. spicatum also

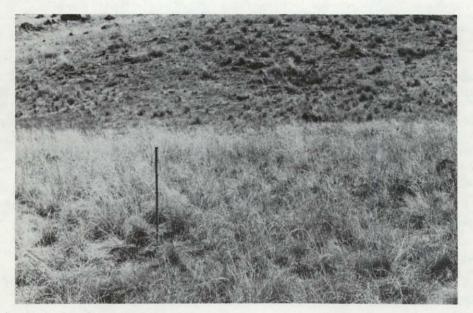


Fig. 6. Sporobolus cryptandrus/Poa sandbergii stand on river terrace with sandy loam soil. Agropyron spicatum is the dominant perennial on the finer soils of the slope in background.

OTHER GRASSLAND COMMUNITIES

The five habitat types just described occupy the greater part of the canyon grasslands. Much of the remaining area is occupied by grassland communities that are not only less extensive, but have virtually no stands that have not been exposed to heavy use by livestock.

These communities of doubtful successional status have a number of characteristics in common. All are located at low elevations in or near valley bottoms, and occupy the warm-dry end of the grassland climatic spectrum. Physiographically these vegetation types occur mainly on fans, terraces and benches. The soils are formed from alluvial or mixed alluvial and colluvial materials, and most are fairly deep, but immature.

COMMUNITY TYPES

The term community type (ct) is used here to describe these kinds of vegetation, which are distinctive, but whose climax status is uncertain. Two communities were recognized, one dominated by *Sporobolus cryptandrus*, the other by *Aristida longiseta*. These *Sporobolus* and occurs as a dominant on sandy soil sites judged to be only slightly less xeric than those dominated by *Sporobolus* and *Aristida*.

In most of these comparisons, the *Aristida*-dominated sites show less difference from the *Agropyron* communities than does the *Sporobolus* type.

Sporobolus cryptandrus/Poa sandbergii ct

The vegetation (Table 12) is characterized by strong dominance of S. cryptandrus. Poa sandbergii is a common associate, but it varies greatly in amount in different stands. Aristida longiseta and Stipa comata are common, Agropyron spicatum is sparse or lacking. Annual grasses include three species of Bromus (B. brizaeformis, B. japonicus and B. tectorum) with the latter most abundant. Perennial forb cover is sparse, but 8 species occur on 50 percent or more of the sites. Annual forbs are common, and 4 species have constancies of 50 percent or more. The component of exotic species is high (Table 11). The ground cover contains a high proportion of litter. Characteristic native species of this type include three perennials: Astragalus inflexus, Calochortus macrocarpa and Chrysopsis villosa; and one annual, Plantago patagonica which are uncommon or lack-

Community	No. of species ¹			Foliage cover (%)		
	Exotic	Total	Percent Exotic	Exotic	Total	Percent Exotic
Sporobolus/Poa ct	7	15	47	6.4	29.7	21
Aristida/Poa ct	8	20	40	8.8	34.5	25.5
Agropyron/Opuntia ht	3	12	25	2.0	23.7	9
Agropyron/Poa/ Balsamorhiza ht	6	18	33	4.8	41.3	11

Table 11-Percentage of common exotic species in canyon grassland communities.

¹ Species occurring on 50% or more of sites.

ing in the grassland types described earlier. All of these species except *C. macrocarpa* are also found commonly in the *Aristida longiseta/Poa sandbergii* ct.

The Sporobolus/Poa type is confined to elevations of 240 to 525 m (790 to 1725 ft) approximately, in the lower parts of the main river valleys. Topography is mostly level or gently sloping, and aspect is minimal as a site factor (Fig. 6).

The macroclimate is the driest and warmest in the canyon grassland sysem. The microclimate, however, is probably no more severe than that of southerly slopes at slightly higher elevations, occupied by *Agropyron*-dominated types. Soil temperatures at 50 cm averaged 16.5° C. from mid-May to early June, compared to 17° C. on *Agropyron/Opuntia* sites during the same period.

The soils are primarily alluvial in origin, with colluvial materials included at some sites. Most are coarse, loamy Calcic Haploxerolls, but Typic Xeropsamments also occur. The key features in relation to vegetation appear to be coarse texture, very low organic matter content and light color of the "A" horizon (Table 13).

This type is much like the Sporobolus cryptandrus/ Poa secunda (sandbergii) ht described by Daubenmire (1970) in eastern Washington. The two types are close in botanical composition, with S. cryptandrus and P. sandbergii the principal grasses, B. tectorum the most abundant annual, and few perennial forbs. The principal differences are the lack of Bromus brizaeformis and Chrysopsis villosa and a greater occurrence of Chrysothamnus nauseosus in the Washington type. The habitats appear similar, although the soils described by Daubenmire are slightly finer in texture. The Sporobolus cryptandrus/Poa sandbergii community described by Huschle (1975) on the Snake River is similar to that described above, but has a higher content of A. spicatum.

Aristida longiseta/Poa sandbergii ct

This type is clearly dominated by *A. longiseta*, while *P. sandbergii* occurs commonly, but in amounts varying greatly from site to site (Table 14). Unlike other lower elevation grassland communities, this one also contains four other perennial grasses, three of which are relatively abundant. *Agropyron spicatum*, although low in amount, occurs on two-thirds of the sites. The presence of the alien *P. pratensis* is noteworthy, since the other types in which it occurs belong in the *Festuca idahoensis* series.

The perennial forb cover includes seven species which appear on 50 percent or more of the sites, but only *Achillea millefolium* occurs in abundance. Annuals are relatively abundant, with *Bromus tectorum* and *B. japonicus* most common. The percentage of exotic species is high (Table 11).

This community, like the Sporobolus/Poa ct, is located in the lower parts of the major valleys, on alluvial fans, benches and the crests of low ridges. The elevational range is from about 300 to 600 m (915 to 1830 ft) although A. longiseta was found up to 1300 m as a seral species on sites in the Agropyron spicatum series. The slopes occupied are usually gentle, and southerly aspects predominate.

Climatic conditions are much as for the *Sporobolus/ Poa* ct, namely at the warm-dry end of the climatic spectrum for the canyon grasslands.

The soils (Table 13) are relatively deep, and formed mainly from alluvial materials. They range from sandy loam to silt loam in texture, and are light in color, low in organic matter and stony, with little profile development. Compared to the soils of the *Sporobolus/Poa* ct, these are deeper, slightly darker and higher in organic matter, finer in texture, lower in pH and less likely to be calcareous. In most of these respects they are more like the soils of communities in the *Agropyron* series.

	Freque	ncy (%)	Foliage	Foliage cover (%)		
Species	Mean	S.D.	Mean	S.D.		
Aristida longiseta	21.7	16.1	2.3	1.7		
Poa sandbergii	36.0	30.0	2.3	1.6		
Sporobolus cryptandrus	98.0	13.0	16.2	5.9		
Astragalus inflexus	1.5	_	0.2	-		
Chrysopsis villosa	1.0		0.1	-		
Erigeron pumilis	1.0	-	0.2	-		
*Hypericum perforatum	6.1	5.0	0.2	-		
Opuntia polyacantha	11.0	3.0	1.5	1.8		
*Tragopogon dubius	8.0	5.2	0.2	-		
*Bromus japonicus	33.0	18.0	0.6	0.3		
*Bromus tectorum	95.0	33.2	3.9	1.5		
*Erodium cicutarium	56.6	45.0	0.7	0.52		
*Lactuca serriola	16.6	11.5	0.3	0.22		
*Myosotis micrantha	31.6	17.2	0.4	0.3		
Plantago patagonica	32.5	16.0	0.58	0.4		

Table 12-Frequency and cover of the Sporobolus/Poa com	munity type (6 sites).
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*Exotic species.

Daubenmire (1970) described an Aristida longiseta/ Poa sandbergii ht occurring in the Snake River Valley in Washington. This community resembles that described in this report, but comparison is tentative since his description is based on only two sites. Soils of the two communities may be fairly similar, although the one profile described by Daubenmire is calcic, whereas 5 of 6 sites I sampled are non-calcic.

Daubenmire regards this vegetation type as climax, probably differing from the adjacent Agropyron/Poa ht by subtle soil characteristics. At the same time, he mentions the capability of A. longiseta to increase with disturbance and his data indicate a large component of exotic species.

These Sporobolus and Aristida-dominated communities obviously present a problem so far as their successional status is concerned. They seem relatively stable under existing conditions, but too much affected by past grazing use to present a clear picture of their climax composition. They show relatively discrete patterns of occurrence, often adjacent to Agropyron-dominated vegetation that has presumably experienced similar grazing use. Habitat differences occur also between the Sporobolus and Aristida sites and those dominated by A. spicatum (Tables 5 and 13). Differences in soil texture, presence of lime, total organic matter and pH, and soil classification exist, but their significance is hard to evaluate from existing data.

Another feature in which S. cryptandrús and A. longiseta differ from A. spicatum and other major grasses of the area is in their C 4 pattern of photosynthesis (Waller and Lewis 1979). This feature would seem to offer an advantage for growth during the hot, dry summer of the canyon bottomlands (Sosebee 1977), but this has not been demonstrated to date.

A third species of this low elevation group, *Stipa* comata also occurs on coarse-textured soils in the canyon bottoms and lower slopes. Stands in which this species is dominant or abundant are of very limited extent. On sev-

	Sporobo	Aristida/Poa			
Character	Mean	S.D.	Mean	S.D.	
Elevation (m)	480	170	475	46	
Slope (%)	4.0	2.8	3.2	0.9	
Radiation index	471	58	446	33	
Depth solum (cms)	68	10	80	21	
Depth "A" horizon (cms)	19	4	19	4	
Stoniness solum (%)	7.0	-	6.0		
Lime present (%)	100		16	-	
Texture "A" horiz	sdy 1.	-	fine sdy 1.	-	
Texture "B" horiz	sand-sdy 1.	-	fine sdy 1.	-	
			-loam		
Color (value) "A" (dry)	4.3		4.1		
Organic matter "A" (%)	2.0	0.9	2.2	0.4	
Organic matter "B" (%)	1.1	0.8	1.4	0.4	
Organic matter (total gms)	66		145		
pH "A" horiz	7.3	0.9	6.4	0.3	
pH "B" horiz	7.9	1.1	6.5	0.2	
GROUND COVER (%)					
Cryptogam	28.0	23.2	22.0	7.6	
Litter	49.6	22.4	52.0	16.3	
Gravel and rock	6.8	14.0	8.4	8.5	
Bare	5.6	6.0	6.6	5.7	

Table 13. Site characteristics for community types of the Sporobolus/Aristida complex.

Table 14. Frequency and cover of major species of the Aristida/Poa community type (6 sites).

	F	Frequency (%)	Foliage cover (%)		
Species	Mean	Standard Deviation	Mean	Standard Deviation	
Agropyron spicatum	7.2	8.6	1.0	1.1	
Aristida longiseta	95.2	9.02	22.2	5.7	
*Poa pratensis	22.8	22.8	1.1	0.3	
Poa sandbergii	43.3	40.1	2.6	1.5	
Sporobolus cryptandrus	32.3	24.2	1.6		
Stipa comata	28.0	42.5	1.3	-	
Achillea millefolium	61.6	35.1	2.1	0.86	
Astragalus inflexus	15.0	13.2	0.2	_	
Chrysopsis villosa	2.0		0.1		
Cirsium undulatum	11.0	1.4	0.3		
Erigeron pumilis	13.3	7.6	0.1	-	
*Hypericum perforatum	10.2	14.6	0.1		
*Tragopogon dubius	11.7	10.1	0.2	-	
*Bromus japonicus	73.7	46.1	2.7	1.1	
*Bromus tectorum	62.0	43.7	2.3	1.0	
*Epilobium paniculatum	10.0	8.6	0.2	0.1	
*Erodium cicutarium	63.0	46.2	1.7	1.3	
*Lactuca serriola	25.0	22.1	0.5	0.4	
Plantago patagonica	16.6	2.9	0.3	0.1	
Stellaria nitens	80.0	34.6	2.7	2.0	

*Exotic species.

eral sites, *Stipa comata* appears to be seral in stands where the climax dominant is *Agropyron spicatum*. In other stands, it is associated with *Sporobolus cryptandrus* and/or *Aristida longiseta*, and here its successional status is as doubtful as is that of these two species. In all cases, the soils are on the coarse-textured side, mostly fine sandy loams.

The only relatively undisturbed stand in which *S. comata* was found as a dominant is on a low elevation south slope in the Salmon River Valley. The profile is poorly developed, fine sand in texture, with extremely low organic matter (0.4% in the "A" horizon).

Daubenmire (1970) reports a *Stipa comata/Poa sandbergii* ht on dry, sandy soil sites in the Columbia Basin. Tisdale (1947) and Parson et al. (1971) found *S. comata* dominant on coarse-textured soils in southern Interior British Columbia. In both areas, *A. spicatum* dominated on adjacent areas of finer-textured soils.

SHRUB-DOMINATED COMMUNITIES

A small, but conspicuous portion of the study area is occupied by vegetation dominated by shrubs. These range from low-growing species such as *Artemisia rigida* to much taller forms, *Cercocarpus ledifolius* and *Celtis reticulata*. Unlike the adjacent coniferous forests, which occupy large blocks of the landscape, these shrub communities occur in relatively small stands, scattered throughout the grasslands. The forest communities have received considerable investigation (Steele et al. 1976, 1981), but the shrub types have been studied little.

Because of the dearth of information and the intimate association of shrub types with the grasslands, they were included in the present study even though time did not permit sampling as intensive as that for the grasslands. Sampling of 60 percent of the shrub stands was done by a modified reconnaissance method that included a full species listing on a standard ($30 \times 15 \text{ m}$) macroplot with relative abundance ratings for all vascular species and measurement of density, height, and foliage cover for the shrub component. The latter was accomplished on subplots, ranging in size from 1 m² for low shrubs, to 5 x 10 m² for the tallest species. The standard intensity of sampling was used on the remaining 40 percent of sites.

The level of study described made it possible to describe and classify a number of shrub communities. In order of the stature of the dominant shrub, these are the *Artemisia rigida, Symphoricarpos albus, Rhus glabra, Cercocarpus ledifolius* and *Celtis reticulata* series. A sixth type, dominated by *Crataegus douglasii* was so sparsely represented and the stands so disturbed that sampling was not attempted.

Another type, dominated by *Physocarpus malvaceus* and *Symphoricarpos albus*, was found in a few spots in northerly aspects of middle elevations in the canyons. *P. malvaceus* is a common understory member of the coniferous forests of the area, in the *Pinus ponderosa* and *Pseudotsuga menziesii* series, and also occurs in seral stages of these types. The stands mentioned above do not appear to be seral to forest. The understory is sparse, and resembles that of moister stands of *Symphoricarpos albus*. Johnson and Simon (1985) have described this type in the western part of the canyon grassland area.

The five communities sampled share certain common characteristics: the shrub layer of each is dominated by a single species, the understory is composed almost entirely of herbaceous species found also in the adjacent grasslands, and each type occurs in relatively discrete patches, which form a characteristic pattern within the canyon grassland landscape. Sagebrush vegetation other than that dominated by *Artemisja rigida* was not included in this study since it lies essentially outside the canyon grassland area and has already been described (Hironaka et al. 1983).

A description of these types is presented as follows:

Artemisia rigida Series.

Vegetation dominated by *A. rigida* is poorly represented in the study area. The largest stands, extending over several km², are on the plateau east of Brownlee Reservoir. Smaller stands occur in the Snake River valley near Brownlee Reservoir, on the Whitebird grade near Grangeville, and on slopes of the Clearwater River Valley near Lewiston. Stands in the two higher elevation areas, east of Brownlee and on Whitebird Grade, were found in reasonably undisturbed condition, but vegetation and soil had been much disturbed by grazing and trampling in the other two areas. The high elevation community was recognized as a variant of the habitat type, described as follows:

Artemisia rigida/Poa sandbergii (High Elevation)

At the sites sampled, *A. rigida* forms an open stand with a foliage cover averaging 12 percent, density of 1.8 plants per m^2 , and average height of 37 cm. A few young plants (density averaging $0.1/m^2$ were found at each site, and a similar number of dead plants. No other shrub species occurred on these sites.

The herbaceous cover is dominated by *P. sandbergii* with *Sitanion hystrix* present in small amounts. Eleven species of perennial forbs, all native, occur on more than half the sites. The most abundant of these are *Balsamorhiza hookeri, Lomatium* spp. (*L. cous, L. leptophyllum* and *L. macrocarpum*), Sedum stenopetalum, Trifolium macrocephalum, Sisyrinchium inflatum and Allium tolmiei.

Annuals occurring commonly are Bromus brizaeformis, Draba verna, Epilobium paniculatum, Microsteris gracilis and Stellaria nitens, but their cover is slight. The ground cover is characterized by a small amount of litter (28%), much bare ground (13%), and rock (27%).

These sites occur on upper slopes of the canyons and on adjacent plateaus. Here the climate is presumably cooler and moister than that recorded for the canyon stations (Table 1). The soils are distinctive, consisting of extremely shallow (16 to 18 cm), weakly developed profiles over a dense substrate of basalt. These are classified as Lithic Ultic Haploxerolls, with textures of silt loam to silty clay loam, and high stoniness (50%). The surface layer is relatively light-colored (10 YR 3.5/2.6), low in organic matter (2.5%), and in pH (5.9). This type of soil is the specific habitat for *A. rigida* (Daubenmire 1982) and the scarcity of this species in the study area reflects the small amount of this habitat present.

The vegetation of this community differs from the *Artemisia rigida/Poa sandbergii* ht described by Daubenmire (1970) principally in the much greater abundance of perennial forbs. These average 16 species per site, 13 of them occurring with a consistency of over 50 percent; while in the habitat type described by Daubenmire the average is 12 species, of which only 3 occur on more than half of the sites. Elevation is a major difference in habitat, for the sites described here occur between 1200 and 1250 m, while the *Artemisia/Poa* of Daubenmire ranges from 190 to 830 m in altitude.

The vegetation type just described is sufficiently distinct from the *A. rigida/P. sandbergii* ht described by Daubenmire (1970) to warrant recognition as a separate phase, or perhaps a different habitat type. Further study is needed to clarify this situation.

Two closely associated types of vegetation also occur on the shallow soils of the Brownlee plateau. One consists of a sparse shrub cover of *Eriogonum sphaerocephalum* and dwarfed *Artemisia rigida*, with a thin understory of grasses, half-shrubs and forbs, including *Poa sandbergii*, *Danthonia unispicata*, *Haplopappus nudicaulis*, *Lewisia rediviva*, *Balsamorhiza hookeri* and *Erigeron linearis*. This type occurs on soils only 7-10 cm deep.

The other type is a grass/forb community dominated by *Poa sandbergii* and *Balsamorhiza hookeri*, and containing several other perennial forbs, of which *Trifolium macrocephalum*, *Lomatium leptocarpum* and *Sisyrinchium inflatum* are most abundant. *A. rigida* is rare or lacking. This type occurs in shallow depressions which form a mosaic with sites occupied by the *Artemisia/Poa* ht. The soils are a little deeper (20 cm), less stony, and slightly higher in organic matter than those of the latter type. The absence of *A. rigida* could be due to excessive moisture and consequent poor aeration in these depressional sites during the spring.

The lower elevation areas in the study area dominated by *A. rigida* occur at elevations of 450 to 600 m. Small stands of this type on the slopes of the Clearwater River near Lewiston and near Brownlee Reservoir are poor in forbs and appear to fit the pattern of the typical Artemisia rigida/Poa sandbergii ht.

Symphoricarpos albus Series

Vegetation dominated by *S. albus* in the study area occurs mainly as dense thickets, with a sparse herbaceous understory. In the four stands sampled, the shrub layer consists mainly of *S. albus*, but *Rosa woodsii* is common and two taller shrubs, *Prunus virginiana* var. *melanocarpa* and *Crataegus douglasii*, occur on the more mesic sites.

Herbaceous understory species average 11 per site, but occur sparsely and irregularly. Balsamorhiza sagittata, Brodaea douglasii, Cirsium brevifolium, Lithophragma parviflora, Lomatium dissectum and Hypericum perforatum are the only perennials occurring in appreciable amounts. Annuals are represented mainly by Bromus spp. (B. brizaeformis, B. japonicus and B. tectorum) and two forbs, Plectritis macrocera and Galium aparine. Total understory foliage cover is 6 percent or less. Ground cover consists mainly of litter (65%), and rock (17%). Most of the understory species are those common in the adjacent grasslands, but the grassland dominants, A. spicatum and F. idahoensis, are sparse or lacking in Symphoricarpos stands.

Shrub foliage cover is typically dense, ranging from 50 to 80 percent in the stands sampled. Numbers of live shoots of *S. albus* vary from 48 to 70 per m^2 , with few dead shoots (1 - 3 per m^2). Stem heights range from 30 to 75 cm, averaging 50 cm at the driest sites and 60 cm at the other two. Shrub stems are generally shorter at the edge of the thickets. Inclusions of *Rosa woodsii*, *Prunus virginiana* and *Crataegus douglasii* usually occur inside these patches, along with the tallest growth of *S. albus*. This species is strongly rhizomatic, and propagation is mainly vegetative. Many patches may represent single clones (Pelton 1953).

Symphoricarpos thickets occur throughout the middle and upper canyon slopes, associated with grasslands of the Festuca series and the more mesic portions of the Agropyron series. The stands vary greatly in size, from patches as small as 10 m in diameter, to strips extending for several kilometers along slopes.

The microclimate is favorable in moisture with S. *albus* stands restricted to northerly aspects in the lower part of their elevational range (700 - 900 m) and more common on these aspects even at higher elevations.

The soils are of mixed residual and colluvial origin, derived from basalt or other fine igneous substrate, with a considerable addition of loess. Textures are loam or silt loam, and the "A" horizons moderately deep (20 - 22 cm), dark-colored (10 YR 2.6/2.0), high in organic matter (5 to 6%), with a pH of about 6.5. There is little to distinguish



Fig. 7. Rhus glabra/Aristida longiseta stand on an upper river terrace. The climax status of this vegetation type is questionable. The stake shown in the photo is 1 m. tall.

these soils from those of the adjacent grasslands, particularly those belonging to the *Festuca* series.

Local topo-edaphic features may account for the presence of these shrub stands. Some are situated on northerly slopes and confined to shallow depressions that hold extra snow in winter. Other sites are situated near the bottom of steep, easterly slopes on extremely rocky soils. In the latter case, adjacent grassland (Agropyron series) occupies finer-textured, shallower soils.

Recognition of habitat types in the S. albus series is not feasible from the data available at present. Although stands of this type occur within zones dominated by both F. idahoensis and A. spicatum, there is no clear evidence of associated differences in understory vegetation.

Similar vegetation is reported by Daubenmire (1970) in the Palouse grasslands of eastern Washington. He recognized the Symphoricarpos thicket community, but regarded it as a phase of the Festuca idahoensis/Symphoricarpos albus ht, a community virtually absent from the canyon grasslands. The thickets described by Daubenmire are basically similar to those described in the present study, but also extend into more mesic situations where Prunus virginiana dominates in a tall shrub overstory. Johnson and Simon (1985) recognize a similar community under the name of the S. albus/Rosa spp. association and affirm the dense cover of the shrub layer and sparse nature of the understory.

Rhus glabra Series

Vegetation dominated by *Rhus glabra* occurs as patches of varied size in the valley bottoms and lower slopes of the canyon grassland region. The shrub layer consists almost entirely of *R. glabra*, which varies greatly in density, height, and foliage cover on different sites. On the four sites sampled, average heights range from 60 to 105 cm, but much taller stems, up to 250 cm, were observed in favored spots. Density varies from 2 to 4 live stems/m² and foliage cover ranges from 20 to 50 percent. The stands are marked by the presence of many dead stems, approximating 35 percent of the total. New growth regularly arises from the base of dead stems. Reproduction appears to be almost entirely vegetative.

The herbaceous understory is well-developed, especially on sites with sparse stands of *Rhus glabra*, but all of the stands sampled had been disturbed by livestock grazing. The dominant species is *Aristida longiseta*, with *Agropyron spicatum* occurring in small amounts on most sites. *Poa sandbergii* is sparse or lacking. Perennial forbs are few in number, and only six species, *Achillea millefolium, Astragalus inflexus, Erigeron pumilis, Lomatium macrocarpum, Opuntia polyacantha*, and *Eriogonum* spp. (*E. niveum* and *E. strictum*) occur on more than half the sites. Annuals are numerous, with *Bromus tectorum*, *B. japonicus* and *Stellaria nitens* most abundant. The ground cover is composed mainly of litter (65%) and rock (15%).

Stands of Rhus are situated at relatively low elevations, from approximately 250 to 800 m, and usually on southerly slopes. They occur in the warmest, driest portion of the canyon complex. Soils occupied by this shrub are highly variable, ranging from silt loams to sandy loams, and from shallow, rocky types to deep, nearly stone-free profiles. Most are weakly developed and all are low in organic matter (average 1.7% in "A" horizon), relatively light-colored (10 YR 3.5/3.0), neutral in pH and lack a lime layer. The stand which differs most occurs on a steep, rocky slope with soil derived from basaltic residual and colluvial materials. The profile is shallower, and the soil finer textured and stonier than at the other three sites. These latter occurred on gentle slopes, with soils formed from more recently deposited alluvial and colluvial materials.

The disturbed condition of these *Rhus*-dominated sites makes classification difficult. The strong component of *A. spicatum* in the stony site suggests that it represents a *Rhus/Agropyron* habitat type, despite the current dominance of *Aristida longiseta* in the understory. The herbaceous vegetation of the other three sites, except for their scarcity of *Poa sandbergii*, resembles the *Aristida/Poa* community type described earlier. The successional status of these *Rhus* stands falls in the same questionable category as the *Aristida*-dominated grasslands which occur adjacent to them.

Daubenmire (1970) described vegetation dominated by *Rhus glabra*, and suggested three potential habitat types associated with *A. spicatum*, *A. longiseta* and *Sporobolus cryptandrus*, respectively. The stands he observed had been so disturbed by livestock that he recognized only a *Rhus glabra/Bromus tectorum* "zootic climax." Daubenmire associated *Rhus*-dominated sites in his area with "colluvial and sandy alluvial soils in canyons." Johnson and Simon (1985) describe a *R. glabra/A. spicatum* type, which occurs mainly on gravelly or rocky soils. They found no sites in good condition.

Cercocarpus ledifolius Series

This species, which reaches its northern limit in the study area, occurs in a shrubby growth form with branches close to the ground (30 cm or less), and in relatively open stands (see Fig. 8). The four sites sampled were classified in the following type:

Cercocarpus ledifolius/Agropyron spicatum ht

Heights of *Cercocarpus* range from 1.5 to 5 m, with an average of about 3 m. Density is 6 to 9 plants per 100 m^2 , and foliage cover 25 to 35 percent. Basal diameters range from 2.5 to 26 cm and average 14.5 cm. Seedlings and young plants are scarce (av. $1/100 \text{ m}^2$), but were found on all sites. Two shrubs of lower stature, *Chrysothamnus nauseosus* and *Glossopetalon nevadense* occur with high constancy, but sparse cover.

The understory, although obviously affected by livestock use, is well-developed considering the shallow, rocky nature of the soils. Agropyron spicatum is dominant, although with low cover (8 to 10%). Poa sandbergii and Sporobolus cryptandrus both occur in small amounts, and Stipa comata is common on the sites with coarsest soil texture. Native perennial forbs occurring on more than half the sites include Achillea millefolium, Chaenactis douglasii, Eriogonum spp. (E. niveum and E. strictum), Penstemon eriantherus, Phacelia heterophylla, Phlox colubrina and Zigadenus venenosus. Other species of high constancy are Opuntia polyacantha and Tragopogon dubius. Annuals are common, but Bromus tectorum and Stellaria nitens are the only species contributing foliage cover of 1 percent or over. The ground cover is high in percentage of surface rock (44%) and bare ground (12%), with only 26 percent litter.

The understory vegetation resembles most closely that of the *Agropyron/Opuntia* ht and this community frequently occurs adjacent to *Cercocarpus* stands.

The distribution of the Cercocarpus/Agropyron ht within the grassland area is limited both by climate and substrate. The type is confined to low elevations (300 to 1000 m) and predominantly southerly aspects. Soil is also a restrictive influence, as virtually all of the Cercocarpus stands occur on outcrops of sedimentary rock, often limestone, rather than on the volcanics that are the principal bedrock of the area. The soils formed from these sedimentary rocks are shallow with weakly developed profiles. They are classified as coarse, loamy Entic or Lithic Haploxerolls characterized by a high degree of stoniness (50 -70%), abundant lime (often to the surface) and fine sandy loam texture. The "A" horizon is shallow (15 cm), lightcolored (10 YR 4.0/3.0), with 1. oderate organic matter content (2.9 to 3.4%) and neutral pH. Some stands on rocky outcrops are so thin as to create the impression of a savanna. These sites have minimal soil development, and sparse understory vegetation.

Cercocarpus also occurs at higher elevations (1600 - 1800 m), surrounded by conifer forest, mostly of the *Pseudotsuga menziesii* series. *Festuca idahoensis* is common in the understory of this type.

Vegetation dominated by *C. ledifolius* in the canyon area and other parts of Idaho has been described by Scheldt and Tisdale (1970), but their study was concerned mainly with the autecology of this shrub. Gruell et al. (1985) include four stands of *Cercocarpus*-dominated vegetation in the Riggins vicinity in their study of this species. These stands occur on the slopes of the Salmon River canyon at

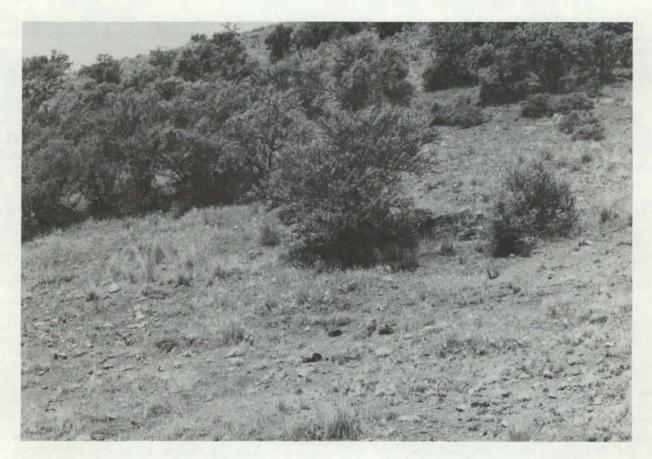


Fig. 8. Cercocarpus ledifolius/Agropyron spicatum habitat type on shallow soil derived from limestone. Adjacent Agropyron/Opuntia habitat type grassland is on slightly deeper soils formed from basalt.

elevations of 670 to 975 m (2200 to 3200 ft.). Three are on limestone substrates, the other on basaltic material. All are classified in the *Cercocarpus ledifolius/Agropyron spicatum* ht.

Johnson and Simon (1985) sampled Cercocarpusdominated vegetation at several elevations, but failed to distinguish sites whose understory is dominated by A. spicatum from those in which F. idahoensis is abundant.

Celtis reticulata Series

This shrub or small tree, depending on the site, occupies narrow strips along the river banks and forms patches on the lower slopes. It is a species of southern affinities and reaches its northern limits in the study area.

Two types of *Celtis*-dominated vegetation were found in the study area. The first occurs on the lower valley slopes, on rocky soils derived from residual and colluvial materials. The understory has been disturbed by grazing and trampling, but enough of the original herbaceous cover remains to indicate dominance by *Agropyron spicatum*. The second type occurs on alluvial terraces on deep, sandy soils. The understory of these sites has been strongly disturbed by livestock grazing, trampling and sheltering under the Celtis. Currently the dominant herbaceous species are Sporobolus cryptandrus and/or annual Bromus spp.

The first type was classified as a *Celtis/Agropyron* ht. No attempt was made to classify the highly disturbed stands of the second type, but a *Celtis/Sporobolus* ht is possible.

Celtis reticulata/Agropyron spicatum ht

Four sites were sampled in this type. The overstory consists of open stands of Celtis which differ greatly in height, crown canopy and basal diameter, depending on site quality. Heights of plants past the sapling stage average 4.5 m in the tallest stand sampled, and 2.5 m in the shortest. Not enough age data were obtained to determine how much of this height difference is due to site quality and how much to age of the stands. Differences in growth form suggest that site quality is probably the greater factor, for Celtis is shrubbier in form on the less favorable sites. Density ranges from 6 to 15 mature plants and 2 to 5 seedlings per 100 m². Canopy cover of Celtis was estimated at 20 to 40 percent. Basal diameters differ with site, averaging only 5.5 cm for shrubby, multiple stems on upland sites compared to 15 cm for tree-like individuals on sites with deeper soils.

The understory is dominated by A. spicatum. Poa sandbergii occurs sparingly, as does Aristida longiseta. Perennial forbs are represented by 8 native species and one exotic (Hypericum perforatum) occurring on half or more of the sites, but perennial forb cover is low. Three annual

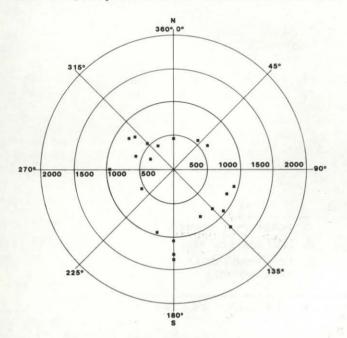


Fig. 9. Graph showing the relation of aspect (in degrees) to elevation in meters) for 21 sites in the Agropyron Spicatum/Poa sandbergii/Balsamorhiza sagittata habitat type.

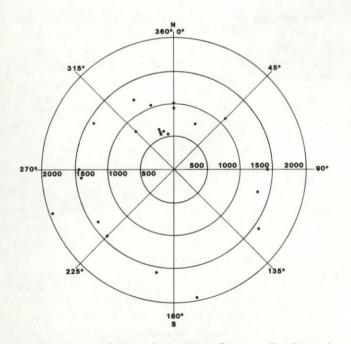


Fig. 10. Graph of the relationship of aspect (in degrees) to elevation (in meters) for 23 sites in the *Festuca idahoensis/Koeleria cristata* habitat type.

Bromus sp. (B. japonicus, B. sterilis and B. tectorum) occur on most sites, and each constitutes more cover than any of the perennial forbs. Other common species include an exotic biennial, Verbascum blattaria, and two annuals, Lotus purshiana and Stellaria nitens. The ground cover consists mainly of litter (58%) and rock (22%).

The presence of so much annual *Bromus*, along with other exotics and the unpalatable *A. longiseta* indicates a considerable degree of disturbance. A few stands in better condition occur in less accessible areas, in Hell's Canyon of the Snake River, but none of those was sampled.

The understory of the *Celtis/Agropyron* ht has many of the same herbaceous species as the *A. spicatum*-dominated types, which occur in adjacent stands. Also present are a few species, including *Bromus sterilis* and *Dipsacus sylvestris*, which are rare or lacking in these grasslands.

Climatically, the *Celtis/Agropyron* type, like the *Rhus glabra*, is restricted to the warmest parts of the canyons. Elevations are low (250 to 550 m) and aspects southerly.

The soils of this ht are weakly developed, rocky (50 to 60%), but probably deeper than the profile excavations indicated, due to the fractures in the underlying rock. Soil texture is fairly fine (silt loam) and lime is absent from the profiles. The "A" horizon is low in organic matter (2.2 to 3.0%) and light in color (10 YR 3.5), with pH slightly above neutral. In most characters, the soils resemble those of the adjacent grasslands, but high soil permeability and topographic situation of the *Celtis* sites makes them more favorable in moisture for deep-rooted species.

Vegetation of the second type of *Celtis* habitat, on alluvial terraces along the rivers, is highly disturbed by livestock use. The understory is dominated by a mixture of grasses, with *Sporobolus cryptandrus*, *Bromus japonicus* and *B. tectorum* most abundant, and *Aristida longiseta*, *Poa bulbosa* and *Poa pratensis* only a little less common. *Agropyron spicatum* occurs, but in small amounts.

Daubenmire (1970) described *Celtis*-dominated vegetation on "colluvial cones and aprons along the lower canyon walls" of the Snake and Columbia rivers in Washington. He classified this highly disturbed vegetation as the *Celtis douglasii* (*reticulata*)/*Bromus tectorum* habitat type. Designation of a climax community with an exotic annual as one of the dominants seems inappropriate, especially when stands of *Celtis*/*Agropyron* can be found on similar habitats in Washington along the Grande Ronde River.

Johnson and Simon (1985) report the occurrence of this type of vegetation, as well as its highly disturbed condition and location, on areas of subterranean moisture availability.

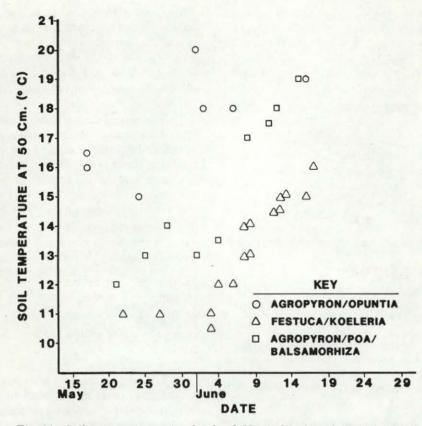


Fig. 11. Soil temperatures at a depth of 50 cm for three habitat types of the canyon grasslands.

PHYSICAL FACTOR RELATIONSHIPS

Much of the information on relationships of the major grassland communities to physical factors of the environment has already been presented (Tisdale and Bramble-Brodahl 1983).

The general pattern revealed is one of vertical zonation, strongly influenced by aspect. Of the site factors showing significant impact on vegetation types, color (value) of the "A" horizon, organic matter of both "A" and "B" horizons and pH of the "A" horizon showed the clearest pattern of vertical zonation. The first three factors increase in amount and the pH decreases from the lowest (and driest) of the grassland habitat types to the highest in the elevational sequence.

Two site factors omitted from the above analysis due to the nature and/or size of the data set are aspect and soil temperature.

Aspect and Elevation

The effects of aspect, accentuated by steepness of slope, are striking in the study area. Sharp differences in vegetation occur on different aspects at the same elevation and on similar soil parent materials. These differences reflect not only the effects of aspect on microclimate, but also the greater amount of loess deposition, with consequent deeper soils on northerly slopes (USDA 1982). The corollary is the extent to which the distribution of communities in elevation is affected by differences in aspect. The result of the interaction of the two factors on the distribution of two grassland habitat types, the *Festuca/Koeleria* and *Agropyron/Poa/Balsamorhiza* are illustrated in Figs. 9 and 10.

Data for the former type show the extent to which sites below 1000 m in elevation are confined to northerly aspects while in the 1000 to 1500 m zone the type they are found on a broad range of aspects. All sites above 1500 m are on southerly aspects; in fact, northerly aspects at these elevations are occupied often by coniferous forest. The pattern for the *Agropyron/Poa/Balsamorhiza*, a more xeric ht, shows a wide range of aspects up to about 950 m, but only southerly slopes above that elevation.

Soil Temperatures

Soil temperature data were collected at 50 cm below the surface, a depth which is relatively unaffected by shortterm fluctuations and useful as a comparative measure for soil taxa (USDA 1975). Temperatures at this depth show definite seasonal trends, however. Collection of soil temperature data was not begun until the second year of the project, and on many sites shallowness of profile did not permit sampling at the desired depth. Plotting the results for 3 of the grassland types produced the patterns shown in Fig. 11. The data show a seasonal upward trend for each type, but also indicate differences among types at any particular time during the sampling period. Soil temperatures were consistently lower in the *Festuca/Koeleria* ht than in either of the two *Agropyron*-dominated communities, and differed between the latter at most dates.

Soil temperatures for the Carex/Festuca ht, not shown in Fig. 11, also were distinct. Measured later in the season, in mid-July, these ranged from 9.5° C to 14° C, putting these soils in a cooler group than any of the other grassland hts. Overall, the data support the concept of soil temperatures at 50 cm depth as a significant site factor related to vegetation type.

BIOTIC FACTORS

Effects of Grazing

The major biotic influence operating in the canyon grasslands is herbivory. The present composition of the vegetation shows marked effects of herbivory pressure produced primarily by domestic livestock.

Since the objective of the current research was to study undisturbed vegetation, little detailed sampling of seral sites was done. The following overview is based on observations and reconnaissance samples, and does not attempt a description of the seral communities existing in the canyon grassland system. The large number of seral communities described by Huschle and Hironaka (1980) on a narrow strip of land along the Snake River shows the variety that can develop through disturbance of a few habitat types.

Prior to European settlement, herbivory on the canyon grasslands appears to have been relatively light. Although sizeable populations of mule deer (Odocoileus hemonius), elk (Cervus elaphus) and mountain sheep (Ovis canadensis) occurred, grazing pressure was far less than that placed by native herbivores on the grasslands of the Great Plains to the east. After obtaining the horse in the 1700s, the Nez Perce Indians of the canyon country made regular trips to hunt bison east of the Bitterroot Mountains. This lack of strong grazing pressure by native herbivores is probably a factor in the susceptibility of climax grasses such as Agropyron spicatum to heavy grazing use (Tisdale 1961, Mack 1984).

The situation changed in the early 1880s as white settlers entered the canyon grasslands. Large numbers of cattle were introduced, and late domestic sheep became the dominant animal. The pattern swung back to mainly cattle in the 1940s, and has remained that way to the present.

The impact of domestic livestock on the canyon grasslands has resulted from three factors operating together. First, the numbers of livestock grazed on a given area were much greater than we would now consider feasible; second, distribution of grazing was generally uneven due to the steepness of local topography, frequent shortage of water, and difficulty of access to many grazing areas. Maldistribution was particularly severe among cattle, which tended to overgraze the flats and gentler slopes, and to make little use of the steep slopes which compose the bulk of the canyon grasslands. The third injurious factor was the grazing season, which usually included heavy utilization in late spring and early summer during growth stages in which the major grasses, Agropyron spicatum and Festuca idahoensis, are highly vulnerable (Mueggler 1975, McLean and Wikeem 1985).

Pressure by domestic livestock was at its greatest from 1880 through the 1930s. Since that time, decreased stocking rates and improved management have eased the pressure in many areas, but poor grazing distribution and improper season of use continue to be problems, even where actual stocking rates seem reasonable in relation to the total grazing resource.

This grazing pressure, extending over approximately a century, produced the following changes:

- 1. a major decline in abundance of the climax bunchgrasses;
- 2. a variable response, usually involving eventual reduction of most other native perennials;
- 3. a great increase in exotic species.

1. Native Grasses

The decrease in native grasses has been particularly drastic in the case of the two dominants, *A. spicatum* and *F. idahoensis*. Both are highly palatable, and have decreased in proportion to intensity and duration of grazing pressure. The extent of the reduction in the case of *A. spicatum* is illustrated by standing crop data from nine depleted sites in the *Agropyron/Poa/Balsamorhiza* and *Agropyron/Opuntia* hts (Tisdale 1976).

These sites show an average of 6 percent perennial grass, 57 percent annual grasses and 37 percent forbs (mostly exotic annuals). The principal perennial grass component is an exotic, *Poa pratensis*. *A. spicatum* produced less than 1 percent of the total. By contrast, our relatively undisturbed stands of the same habitat types sampled in the current study show a perennial native grass component of 70 percent, perennial forbs 19 percent, annual grasses 5 percent, and annual forbs (mostly native) 5 percent.

Other native grass species show more varied response to heavy grazing use. *Poa sandbergii*, while highly palatable in early spring, tends to be less harmed due to its low stature and early seasonal drying of its foliage (Rickard et al. 1975). This species decreases much less quickly under cattle grazing than A. spicatum or F. idahoensis, but is finally reduced to small populations on highly depleted sites.

Sporobolus cryptandrus plays a variable role in reaction to heavy grazing, increasing at the expense of A. spicatum on some sites, but decreasing on others in competition with Aristida longiseta. The latter species is the only native perennial grass which has increased consistently under heavy grazing (Evans and Tisdale 1972).

2. Native Forbs

The reaction of native forbs has been more varied than that of the major perennial grasses. Most of the perennial forbs are less palatable to cattle than are the climax bunchgrasses, but, because of the historical pattern of livestock use in the canyon grasslands, virtually all depleted areas have been grazed at one time or other by both cattle and sheep. Thus, the present status of perennial forbs on cattle ranges may reflect changes caused much earlier by sheep, to which many of these forbs are palatable.

Despite the differences in palatability, most highly depleted stands in the canyon grassland are low in native perennial forbs. Many of these species have persisted or even increased initially with reduction in the perennial bunchgrass cover, but in most cases they eventually succumbed to the effects of continued use and competition with aggressive exotics.

Seral sequences reported by Johnson and Simon (1985) show many instances of this pattern of initial increase of abundance for some perennial forbs, followed by a decrease under more depleted range condition. Their data also indicate the variability of response for the same herbaceous species in different communities.

Currently, the most common native perennial forbs on depleted communities are Achillea millefolium var. lanulosa, Lupinus spp., several species of Lomatium (L. macrocarpum, L. triternatum, L. cous), and, in certain types, Balsamorhiza sagittata.

Native annuals have fared better than perennials under heavy grazing, although many have also decreased under competition with exotics. Native species most abundant on depleted stands include one grass, *Festuca megalura*, and two forbs, *Epilobium paniculatum* and *Stellaria nitens*. Other common forbs include *Amsinckia retrorsa*, *Clarkia pulchella*, *Collinsia parviflora*, *Madia gracilis* and *Polygonum majus*.

Exotic Species

Exotic species have largely filled the gaps in the canyon grasslands caused by the destruction of native perennials. This process started about 1890 with the first records

of an annual, Bromus tectorum, an alien from the Mediterranean area. This species, with its enormous seed-producing capacity, rapid and flexible germination behavior, and ability to out-compete seedlings of A. spicatum (Harris 1967, Mack and Pyke 1983) is the archetype of these exotics, and has become the most abundant. Bromus species that require more mesic habitats, including Bromus brizaeformis. B. japonicus and B. mollis (Hulbert 1955) became abundant also, along with annual forbs such as Draba verna, Erodium cicutarium and Lactuca serriola, and the biennial Tragopogon dubius. One exotic perennial grass, Poa pratensis, also has invaded the canyon grasslands in large amounts, mostly in the more mesic parts. It has a remarkable range ecologically, however, and occurs with Aristida longiseta in relatively dry sites in parts of the Snake and Salmon River systems. It is highly palatable, but persists due to high tolerance to grazing and a strong system of vegetative reproduction.

Although these species, especially the annual bromes, remain abundant on depleted areas, a major feature of the annual-dominated communities is their instability, as marked by the continued invasion of additional exotics. This list includes a perennial, *Hypericum perforatum*, which appeared in the canyon grasslands in the 1930s and increased to become a major species on depleted ranges until controlled by biological means in the 1950s (Tisdale 1976). It remains a widely distributed, but rarely abundant, species. The next major arrival was an annual grass, *Taeniatherum asperum (Elymus caput-medusae)* which out-competes the annual bromes in many areas, especially on heavier-textured soils (Dahl and Tisdale 1975).

More recent invaders include a number of perennial forbs, several of which are currently increasing on depleted stands of canyon grasslands. The genus which may have the greatest potential for increase is *Centaurea*, represented by *C. diffusa*, *C. maculosa*, *C. repens* and *C. solstitialis*. These species are well adapted to much of the canyon grassland environment, and unattractive to most herbivores. *C. solstitialis*, in particular, has invaded sizeable areas in the Clearwater and lower Snake River valleys during the past decade, replacing annual *Bromus* spp. which had been dominant there for many years.

Other recent additions to the exotic forb list include two perennials, *Chondrilla juncea* and *Linaria dalmatica*; an annual, *Crupina vulgaris*; and an annual grass, *Ventenata dubia*. All are abundant in a few localities in the canyon grasslands.

From a grazing viewpoint, replacement of the annual bromes by any species listed above would represent a further downward stage. Bromes, while highly variable in yield from year to year and short in their season of providing green feed, still constitute a major grazing resource. Most of the exotic perennials are much less palatable, and many are also physically repellent or poisonous.

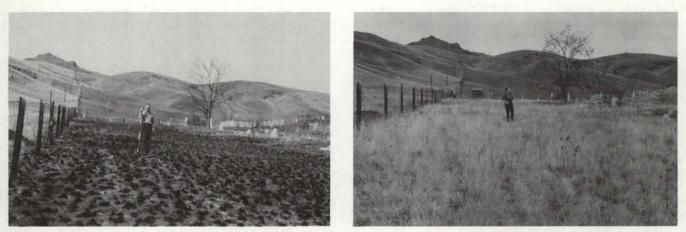


Fig. 12. Stand of Aristida longiseta and annual bromes species were burned one spring (1) and the same area was photographed one year later (r). Little damage was done to the vegetation in spite of an intense burn that consumed most litter and standing vegetation.

EFFECTS OF INSECTS

Insects constitute a little-studied influence on the canyon grasslands. A study of grasshoppers, one of the more conspicuous of the defoliating groups, by Banfield and Brusven (1973) suggests that these insects may exert severe stress on major plant species including *Festuca idahoensis*, *Sporobolus cryptandrus*, *Lupinus* spp., and *Pentstemon* spp. as well as the exotic *Poa pratensis* and *Bromus tectorum* (early growth stages only). All are eaten readily by *Camnula pellucida*, the clear-winged grasshopper, and other common species of grasshopper. The pressures exerted by these insects during periods of high population level, added to those of livestock use, can be critical for climax native species, and no doubt have contributed to depletion of some grassland areas.

Other types of insect predation on native species have been reported. Spears and Barr (1985) found that larvae of the genus *Tetramesa* (jointworms) are common in canyon grassland species including *Aristida longiseta*, *Sporobolus cryptandrus* and *Stipa comata*. These insects infest grass culms, and were found to reduce the number of spikelets per inflorescence, seed weight, percent germination, and rate of germination. How much this affects the ability of these species to maintain their populations has not been determined. In the case of *A. longiseta*, a detrimental effect could be useful as a control measure, although the fact that the insect predators are native diminishes the prospects for biological control because their populations are also controlled by disease and predators.

EFFECTS OF FIRE

In view of the known importance of fire in grasslands, observations were made throughout this study on effects of this factor. In some respects, the study area is prone to natural fire since the pattern of dry, hot summers produces a ready fuel supply, and lightning-caused fires are common in adjacent forests. Furthermore, fire may have been used by Indians prior to white settlement (Shinn 1980), but the comparative lack of big game in the area and scarcity of shrubby vegetation may have largely removed motivation for such action.

Horton (1972) concluded that fire has not been a major influence on the canyon grasslands, despite its importance in some of the neighboring forest types.

Whatever the primeval situation may have been, fire has been a minor factor in these grasslands in the century since white settlement began. Both direct control and scarcity of fuel on overgrazed ranges have contributed to this situation. Above-normal precipitation also may have been a factor during the past four decades (Leaphart and Stage 1971).

No signs of major changes in composition or boundaries of the major grassland communities appear to have resulted from this presumed decrease in fire frequency. Although minor increases may have occurred in some shrub types (*Cercocarpus ledifolius* and *Symphoricarpos albus*), there has been no widespread invasion of woody species such as those reported for *Juniperus occidentalis* in southwestern Idaho and adjacent Oregon (Burkhardt and Tisdale 1976), or of *Pseudotsuga menziesii* in western Montana (Sindelar 1971).

The available data indicate that many and perhaps most of the major species of the canyon grassland are fairly tolerant to fire. Among the dominant grasses, Agropyron spicatum is known to recover quickly from all but the hottest fires and normally shows little mortality or loss of subsequent growth. Festuca idahoensis is more susceptible, especially during late summer, and may require several years for recovery, but is unlikely to be eliminated by fire (Mueggler and Blaisdell 1958, Wright et al. 1979). Koeleria cristata is highly fire resistant (Blaisdell 1953). Information on other species is scanty, but observations made during the current study provide some data. During the 1960s, ranchers in the Slate Creek area of the Salmon River attempted to control the undesirable bunchgrass, Aristida longiseta, by burning. Not only did this species prove to

be relatively unharmed by the treatment, but so did many associated species, including Sporobolus cryptandrus, Achillea millefolium, Astragalus inflexus, Cirsium undulatum, and Lomatium spp. Johnson and Simon (1985) report that many perennial forbs including Achillea millefolium, Balsamorhiza sagittata, Castilleja hispida and Lupinus spp. are little affected by fire.

It does not appear that the current composition or pattern of the climax grassland vegetation in the study area has been significantly affected by fire. Vegetational boundaries seem stable, and the pattern of communities can be logically explained by climatic, soil and physiographic factors. In this respect, the situation resembles that described by Daubenmire (1970) for the grasslands and sagebrush vegetation of Washington.

COMMUNITY CLASSIFICATION

The grassland habitat types described are separated clearly by differences in species composition, and these separations are corroborated by differences in site characteristics (Tisdale and Brodahl 1983). It is apparent from the data, however, that considerable variability exists within each type. The extent of this variability was investigated by several methods, including determination of homogeneity index (Curtis and Greene 1949); similarity indices and ordination (Mueller-Dombois and Ellenberg 1974). The results of these analyses are reported by habitat types.

Carex hoodii/Festuca idahoensis ht

This is the most uniform of the communities described. The homogeneity index (32) is the highest, and the similarity and ordination results also indicate a high degree of uniformity. This same is true for site characteristics; for example, it is the only community whose soils are classified in one soil family (loamy skeletal Mixed Cryumbrepts). Factors contributing to this degree of uniformity include a limited range of surface geological and physiographic characteristics.

A subdivison of this type obtained by separating sites in which *Danthonia intermedia* is abundant has been proposed by Johnson and Simon (1985). Examination of my data, in which 5 of the 12 sites contain *D. intermedia*, shows no significant difference in either species composition or site characteristics between samples containing this species and those from which it is absent.

Festuca idahoensis/Koeleria cristata ht

This type occupies a wide range ecologically, and was sampled more intensively than any other. The homogeneity index (18) is relatively low, but no lower than for the two habitat types of the *Agropyron* series. Similarity and ordination tests show considerable variability, but no clear-cut separation into sub-groups. This ht occupies an exceptionally wide elevational belt (1560 m or 5120 ft), and Johnson and Simon (1985) have proposed a division based on this factor, with a separation point of 1158 m (3800 ft). These authors distinguish the two groups by differences in absolute and relative cover of *F. idahoensis* and *A. spicatum*, by differences in perennial forb composition, and in cover of cryptogams ("moss"), gravel, and bare ground. Differences also occur in aspect, steepness of slope, and solum depth.

My samples of this ht include 11 in the lower elevational range, and 10 in the higher areas. Comparison of these two groups shows differences in species composition, in proportion of perennial grass species, and in ground cover. Site factors show no significant difference except in the case of aspect (Fig. 10). Differences in constancy occur among the perennial forbs with three species, *Eriogonum heracleoides, Arnica sororia*, and *Senecio integerrimus* being more common in the high elevation group and *Lithospermum ruderale, Cerastium arvense*, and *Hypericum perforatum* occurring more frequently at the lower elevations.

These differences in species composition groups do not match with those listed by Johnson and Simon. Three perennial forbs, *Castilleja hispida*, *Geum triflorum*, and *Hieracium albertinum* listed as infrequent or absent in their low elevation group are common in my samples from low elevations. Similarly, *Cerastium arvense* and *Hypericum perforatum*, confined in my data to the low elevation series, occur commonly in their high elevation group. The common occurrence of *Eriogonum heracleoides* at higher elevations and infrequence of this species at the lower elevations seems to be the only feature in common so far as species occurrence is concerned.

The above data are significant in depicting the problems of separating valid subgroups within well-defined communities such as the *Festuca/Koeleria* ht. The two proposed subdivisions have most of their floristic characters in common, for the principal grass species are the same, and 11 of the 13 perennial forbs rated as common for the ht retain this status within each subgroup. Enough differences remain in relative abundance of the two dominant grasses and of *Koeleria cristata*, and in nature of the ground cover to warrant a separation, at least for management purposes. Such subdivision must reckon with the paucity and variability of floristic indicators however, plus the fact that intermediates between the two sub-types are likely to be common.

A variant of the *Festuca/Koeleria* ht occurs on coarsetextured soils, but this kind of habitat was encountered rarely in the study area. The two sites sampled are on southerly exposures at an elevation of 1585 m (5200 ft). The soils are moderate in depth (70 cm), very stony, with loam texture in the "A" horizon and sandy loam for the remainder of the profile. These soils are classed as a frigid Pachic Ultic Haploxeroll, and are immature in development and low in organic matter for the ht. The vegetation shows a 2:1 cover ratio of *F. idahoensis* to *A. spicatum*, relatively high cover of K. cristata and abundance of Eriogonum heracleoides. The ground cover is notable for a low percentage of cryptogams and large amounts of surface gravel and rock. These characteristics apply also to the high elevation phase of the Festuca/Koeleria ht. Species composition is different, however. Half of the perennial forb species common to the Festuca/Koeleria ht are absent from the two sites in question. Their place is taken by species including Phacelia heterophylla, Allium acuminatum, Arenaria congesta, Eriophyllum lanatum, Erysimum asperum, and Gilia aggregata, which are characteristic of coarse-textured, or rocky soils. Two samples in areas of limited extent are scarcely sufficient for recognition of a vegetation type, but show the extent to which differences in vegetation can result from local variation in habitat.

Festuca idahoensis/Agropyron spicatum ht

This type has a fairly high homogeneity index (23). The similarity matrix and ordination tests showed no indications of sub-grouping. A feature of the type is the wide difference in ratio of foliage cover of F. *idahoensis* to that of *A. spicatum*. This ratio varies from 7.3 to 0.5, but contrary to results from the *Festuca/Koeleria* ht, the difference in ratio of the two dominants appears to be unrelated to other vegetational or environmental characteristics.

Johnson and Simon (1985) have proposed a separation of the *Festuca/Agropyron* ht into two subdivisions on the basis of soil depth. It was not possible to test this hypothesis, since occurrence of this ht on shallow soils is infrequent in my study area, and only one of 14 sites sampled falls into this category.

Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata ht

This type has a low homogeneity index (18), and shows the poorest agreement in classification by floristic versus site characteristics of any of the five hts tested (Tisdale and Brodahl 1983). Similarity and ordination tests confirmed this variability and pinpointed two samples that show sufficient deviation from the norm to warrant consideration as possible sub-types or phases.

One of these sites occurs in sandy soil on lower slopes of the Salmon River Valley. The vegetation shows the usual dominance by *A. spicatum* and abundance of *P. sandbergii*, but differs in other respects from the pattern of the ht. Six of the eight common perennial forb species, including *B. sagittata* are absent, as are two of the common annual bromes, *Bromus brizaeformis* and *B. japonicus*. Species that occur abundantly on the site, but infrequently in the ht, include *Sporobolus cryptandrus*, *Chrysopsis villosa*, *Erysimum asperum*, and *Chrysothamnus nauseosus*. All are associated with coarse-textured soils in the canyon area. The soil texture is loamy sand to sandy loam. Solum depth and pH are high for the ht, and organic matter is low. The other aberrant site is situated at low elevation in the Snake River Valley west of Lewiston. This location is in the northwest corner of the study area where total precipitation and the percent falling in May and June are less than in most of the canyon grassland region. Agropyron spicatum is strongly dominant on this site, perennial forb cover is sparse, and five of the eight common species of the ht are absent, including Balsamorhiza sagittata. Except for the presence of Bromus brizaeformis and B. japonicus, the species composition resembles the A. spicatum/P. secunda (sandbergii) ht reported by Daubenmire (1970) in Washington rather than the A. spicatum/P. sandbergii/B. sagittata ht described in this report.

The vegetational differences shown by the two sites just described illustrate the kinds of local variation that can occur within a habitat type of wide ecological amplitude. In such situations, more intensive sampling would probably establish valid sub-types.

Agropyron spicatum/Opuntia polyacantha ht

This type has a fairly low homogeneity index (19). The similarity and ordination tests revealed considerable variation, but no clear evidence of subgrouping. The three most deviant sites are characterized by absence of Poa sandbergii, and of two of the common perennial forbs of the type, Erigeron pumilis and Phlox colubrina. One of the common annual bromes, Bromus japonicus, is also lacking in these samples. The ground cover of these sites is higher in surface gravel and lower in cryptogams than the average for the type. No other significant differences in habitat characteristics between these three sites and the remainder of the samples could be detected. The occurrence of P. sandbergii is highly variable in this ht, with frequencies ranging from 90 percent to zero. Little is known of the site requirements of this species, but its shallow rooting system makes it susceptible to frostheaving or other surface disturbance from which the sparse cover of this ht gives little protection.

COMMUNITY STABILITY

The grassland types described appear to be highly stable, with boundaries that are not likely to change without a sizeable shift in climate. Interfaces between grassland and conifer forest, which are common in the canyon ecosystem, also appear stable and usually quite sharp. Changes in the composition of the grassland communities caused by heavy grazing do not appear to have altered their pattern of distribution.

The shrub communities present a somewhat different situation. The Artemisia rigida/Poa sandbergii ht is restricted to a special edaphic condition, and is unlikely to spread beyond this habitat. Cercocarpus ledifolius is also restricted in habitat, but less strongly so than A. rigida, and may have increased its area of dominance in recent years due to reduced fire influence (Gruell et al. 1985). Other species, including Symphoricarpos albus and Rhus glabra, have a wider ecological amplitude and greater potential range. Both these shrubs spread vegetatively as well as by seed, and *S. albus* in particular tends to form dense stands which exclude most other species.

Johnson and Simon (1985) report evidence for recent increases of *S. albus* stands in the middle Snake River Valley and suggest grazing, fire, and/or climatic change as causal factors. *S. albus* appears little affected by current levels of grazing use over most of my study area, but may have been inhibited by heavier use in the past. It may also have benefited from the comparative scarcity of fires during the past century. Climatic influences may be involved, for Leaphart and Stage (1971) have shown by tree ring studies that precipitation in this part of Idaho has been above average since 1940, following a drier spell which lasted for a quarter of a century.

The evidence for stability of *Rhus glabra* stands is mixed. Daubenmire (1970) cites evidence for stability, while Johnson and Simon (1985) report that "this species is invading some more mesic grasslands" in the Snake River Valley. *Rhus glabra* rates low in preference by livestock and thus stands to benefit from the heavy grazing use which is common at lower elevations where this species occurs. Observations in my study area indicate that *Rhus* may be increasing slightly in the lower grassland areas, especially on sites dominated by *Aristida longiseta* or *Sporobolus cryptandrus*.

CONCLUSIONS

This study is a first attempt to classify the grasslands and shrublands of the study area and to determine their relationship to environmental factors. Emphasis has been placed on recognizing ecosystem units, series and habitat types that are clearly separable by floristic data alone, but also well defined by habitat characteristics. The priority given to clearly defined vegetational units plus limitations of sampling have resulted in the recognition of a relatively small number of climax communities. The study has left unresolved the seral status of certain communities dominated by *Sporobolus cryptandrus* and *Aristida longiseta*.

The canyon grasslands are recognized as a distinctive unit within the Pacific Northwest Bunchgrass region. Two of the series, the Agropyron spicatum and Festuca idahoensis, are widespread in the region, but the third, characterized by Carex hoodii, appears to be restricted to the study area, but may have relationships to the mountain grasslands of central Idaho. The five habitat types recognized appear to be distinctive to the canyon grasslands.

Sampling of the shrub communities associated with the grasslands was less intensive, but sufficient to establish the climax status of five types. These communities need further study, especially to investigate the relationships of vegetation to soil and topography, and to document the size and age structure of the dominant woody species.

Given the internal variability of the communities described, additional study probably will lead to recognition of finer subdivisions. This would be similar to developments in soil classification where the concept of soil series has been refined and the number of series greatly increased as a result of continuing study (USDA 1975). Progress in soils classification, however, has come through a continuing, highly organized effort while vegetational classification has been pursued independently by various researchers with little coordination or agreement on basic principles and procedures. There is a pressing need for joint consideration of such problems, especially for agreement on criteria for classification, including the relative weight accorded to species occurrence compared to abundance or productivity and the extent to which environmental characteristics should be used.

Specific measures needed for a better understanding of the grassland vegetation of the study area include additional sampling to test the significance of differences within groups. A population of 15 to 20 samples, obtained for most types in this study, may give adequate representation to a relatively uniform community, but is minimal for the exploration of internal variability.

There is also a need for more intensive methods of study in problem areas, such as communities of doubtful seral status. Direct experimentation, including removal and/or addition of transplants or propagules, and disturbance by fire, grazing (clipping), etc., are needed to solve problems not susceptible to the methods of observation and correlation employed in the present investigation.

This study and others of a similar nature are handicapped by deficiencies of basic information regarding the ecosystems involved. A principal deficiency is the lack of autecological information regarding the species in these communities. No comprehensive study has been made of the dominant species of the canyon grasslands, or of any of the 45 species rated as common in these types. Furthermore, existing studies have usually involved only limited populations. These results must be interpreted with caution due to the existence of ecotypic variation in many of the species concerned, including Agropyron spicatum and Festuca idahoensis (Dobrowolski 1979, Tisdale 1961) and its probable occurrence in other species of the region. Lack of autecological data limits the ability of the investigator to assess the significance of species distribution, or of species reaction to differences in environmental characteristics or disturbance factors. Information is needed not only for native species, but also for exotics which have invaded the canyon grasslands.

There are also many unanswered questions concerning special characteristics of soils of the canyon region. Such questions include the effects of steep slopes (50-100%) on soil development and soil-plant relationships, and the effects of differences in aspect coupled with steep topography. Other items include the effect of large amounts of stones and gravel in the profile, and the significance of surface soil cover involving varying amounts of cryptogam, litter, and surface gravel and rock.

LITERATURE CITED

Aller, A., M.A. Fosberg, M. Lazelle, and A. Falen. 1981. Plant communities and soils of north slopes in the Palouse region of eastern Washington and northern Idaho. Northwest Sci. 55:248-262.

Arnow, L.A. 1981. Poa secunda Pres L. versus P. sandbergii Vasey (Poaceae). Syst. Bot. 6:412-421.

- Banfill, J.C., and M.A. Brusven. 1973. Food habits and ecology of grasshoppers in the Seven Devils Mountains and Salmon River breaks of Idaho. Melanderia 12:1-21. Washington State Entomological Society. Pullman.
- Blaisdell, J.P. 1953. Ecological effects of planned burning of sagebrush-grass range on the Upper Snake River Plains. USDA Tech. Bull. No. 1075. 39 pp.

Bryan, R., and J. Madden. Personal correspondence. 1979.

- Buechner, H.K. 1953. Some biotic changes in the State of Washington, particularly during the century of 1853-1953. Wash. State Univ. Res. Studies 21:154-192.
- Campbell, John D. 1962. Grasslands of the Snake River drainage in northern Idaho and adjacent Washington. M.S. Thesis, University of Idaho, Moscow. 86 pp.

Crawford, R.C. and F.D. Johnson. 1985. Pacific yew dominance in tall forests, a classification dilemma. Can. J. Bot. 63:592-602.

- Curtis, J.T., and H.C. Greene. 1949. A study of relic Wisconsin prairies by the species-presence method. Ecology 30:83-92.
- Dahl, B.E., and E.W. Tisdale. 1975. Environmental factors related to medusahead distribution. J. Range Manage. 28:463-468.
- Daubenmire, R. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecol. Monogr. 12:53-79.

_____. 1952. Forest vegetation of northern Idaho and adjacent Washington and its bearing on concepts of classification. Ecol. Monogr. 22:301-330.

_____. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43-64.

_____. 1960. An experimental study of variation in the Agropyron spicatum-A. inerme complex. Bot. Gazette 122: 104-108.

_____. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. No. 62. Pullman. 131 pp.

_____. 1972. Annual cycles of soil moisture and temperatures as related to grass development in the steppe of eastern Washington. Ecology 53:419-424.

_____. 1982. The distribution of Artemisia rigida in Washington: A challenge to ecology and geology. Northwest Sci. 56:162-164.

- Daubenmire, R., and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. No. 60. Pullman. 104 pp.
- Dewey, D.R. 1983. Historical and current taxonomic perspectives of Agropyron, Elymus, and related genera. Crop Science 23:637-642.
- Dobrowolski, J.P. 1979. A numerical taxonomic analysis of *Agropyron spicatum* with special reference to ecotypic variation. M.S. Thesis, Washington State Univ., Pullman.

- Evans, G.R. 1967. Ecology of Aristida longiseta in north central Idaho. M.S. Thesis, Univ. of Idaho, Moscow. 69 pp.
- Evans, G.R., and E.W. Tisdale. 1972. Ecological characteristics of Aristida longiseta and Agropyron spicatum in west central Idaho. Ecology 53:137-142.
- Frank, E.C., and R. Lee. 1966. Potential solar beam irradiation on slopes. USDA Forest Serv. Res. Paper RM-18. 116 pp.
- Gruell, G., S. Bunting, and L. Neuenschwander. 1985. Influence of fire on curlleaf mountain-mahogany. Pages 58-72 in Proc. Symp. Effects of Fire on Wildlife Habitat. March 1984. Missoula, Mont. USDA Forest Serv., Intermtn. Sta. Gen. Tech. Rep. 1986.
- Harris, Grant. A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. Ecol. Monogr. 37:89-111.
- Heidel, B., E.J. Christy, and A.J. Gilmartin. 1982. Numerical phenetic analysis of variation in populations of Poa secunda Presl. and Bromus japonicus Thunb. (Poaceae). Northwest Sci. 56:108-120.
- Hironaka, M., M.A. Fosberg, and A.H. Winward. 1983. Sagebrush-grass habitat types of southern Idaho. FWR Exp. Sta. Bull. No. 35. Univ. of Idaho, Moscow. 44 pp.
- Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle. 730 pp.
- Holdridge, L.R. 1967. Life zone ecology. Revised ed. Tropical Sci. Center, San Jose, Costa Rica. 206 pp.
- Horton, L.E. 1972. Ecological Analysis: A preliminary investigation of vegetation structure and ecosystem function of the lower Salmon River. USDA Forest Serv., Intermtn. Reg. Rep. 85 pp.
- Hulbert, L.C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Monogr. 25:181-213.
- Huschle, G. 1975. Analysis of the vegetation along the middle and lower Snake River. M.S. Thesis, Univ. of Idaho, Moscow. 271 pp.
- Huschle, G., and M. Hironaka. 1980. Classification and ordination of seral plant communities. J. Range Manage. 33:179-182.
- Johnson, C.G. 1981. Synecological relationships in the Billy Meadows area, Wallowa-Whitman National Forest. USDA Forest Serv. Spec. Rep. Baker, Ore. 295 pp.
- Johnson, C.G., and S.A. Simon. 1985. Plant associations of Hells Canyon National Recreation Area. USDA Forest Serv. Interm. Rep. Wallowa-Whitman National Forest. 258 pp.
 - Lambert, J.M., S.E. Meacock, J. Barrs, and P.F.M. Smartt. 1973. AXOR and MONIT: Two new polythetic-devisive strategies for hierarchical classification. Taxon 22:173-176.
 - Leaphart, C.D., and A.R. Stage. 1971. Climate-A factor in the origin of the pole blight disease of *Pinus* monticola. Ecology 52:229-239.
 - Mack, R.N. 1984. Invaders at home on the range. Natural History 2:40-46.
 - Mack, R.N., and D.A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. J. Ecol. 71:69-93.
 - McLean, A. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationship to soils. Ecol. Monogr. 40:403-424.
- McLean, A., and S. Wikeem. 1985. Influence of season and intensity of defoliation on bluebunch wheatgrass survival and vigor in southern British Columbia. J. Range Manage. 38:21-26.

- Mueggler, W.F., and J.P. Blaisdell. 1958. Effects on associated species of burning, rotobeating, spraying, and railing sagebrush. J. Range Manage. 11:61-66.
- Mueggler, W.F., and C.A. Harris. 1969. Some vegetational and soil characteristics of mountain grasslands in central Idaho. Ecology 50:671-678.
- Mueggler, W.F., and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Forest Serv. Gen. Tech. Rep. INT-66. 154 pp.
- Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, Inc. New York. 547 pp.
- Olson, O.C., and D.H. Crockett. 1965. Relation of two soil substrata conditions to forest cover and nonforested openings in the Seven Devils Mountains. Pages 189-197 *in* C.T. Youngberg (ed.) Forest-soil relationships in North America. Oregon State Univ. Press, Corvallis.
- Parsons, D.C., L.M. Lavkulich, and A.L. Van Ryswyk. 1971. Soil properties affecting the vegetative composition of Agropyron communities at Kamloops, British Columbia. Can. J. Soil Sci. 51:269-276.
- Pelton, J. 1953. Studies on the life history of Symphoricarpos occidentalis Hook in Minnesota. Ecol. Monogr. 23:17-39.
- Pickford, G.D., and E.H. Reid. 1942. Basis for judging subalpine grassland ranges of Oregon and Washinton. USDA Circular No. 655. 38 pp.
- Poulton, C.E. 1955. The ecology of non-forested vegetation of Umatilla and Morrow Counties, Oregon. Ph.D. Thesis, Washington State Univ., Pullman. 166 pp.
- Reid, E., G. Strickler, and W. Hall. 1980. Green fescue grassland: 40 years of secondary succession. USDA Forest Serv. PNW Res. Paper No. 274. 39 pp.
- Richmond, C.M., R. Fryxell, G.G. Neff, and P.L. Weis. 1965. The Cordilleran ice sheet of the northern Rocky Mountains and related Quaternary history of the Columbia Plateau. Pages 231-242 in H.E. Wright, Jr., and G.D. Frey, eds., Quaternary of the United States. Princeton Univ. Press, Princeton, N.J.
- Rickard, W.H., D.W. Uresk, and J.F. Cline. 1975. Impact of cattle grazing on three perennial grasses in south-central Washington. J. Range Manage. 28:108-111.
- R.I.S.C. 1983. Guidelines and terminology for range inventories and monitoring. Rep. of the Range Inventory Standardization Committee. Society for Range Manage., Denver, Colo. 13 pp.
- Ross, C.P., and J.D. Forrester. 1958. Outline of the geology of Idaho. Idaho Bureau Mines and Geology and U.S.Geological Survey Bull. No. 15. 74 pp.
- Scheldt, R.S., and E.W. Tisdale. 1970. Ecology and utilization of curlleaf mountain-mahogany in Idaho. Forest, Wildlife and Range Exp. Sta. Note 15, Univ. of Idaho, Moscow. 2 pp.
- Schlatterer, E.F. 1972. A preliminary description of plant communities found in the Sawtooth, White Cloud, Boulder and Pioneer Mountains. USDA Forest Serv. Intermtn. Reg. 111 pp.
- Shinn, D.A. 1980. Historical perspectives on range burning in the Inland Pacific Northwest. J. Range Manage. 33:415-422.
- Sindelar, B. 1971. Douglas-fir invasion of western Montana grasslands. Ph.D. Dissertation. Univ. of Montana, Missoula. 130 pp.
- Smith, Mia. 1979. Big game-livestock relations on Idaho winter range. M.S. Thesis. Univ. of Idaho, Moscow. 102 pp.

Sosebee, R.E. (Ed.). 1977. Rangeland plant physiology. Range Sci. Ser. No. 4. Society for Range Manage. Denver, Colo. 290 pp.

- Spears, B.M., and W.F. Barr. 1985. Effect of jointworms on the growth and reproduction of four native range grasses of Idaho. J. Range Manage. 38:44-46.
- Steele, R., S.F. Arno, and R.D. Pfister. 1976. Preliminary forest habitat types of the Nezperce National Forest. USDA Forest Serv. Intermtn. Forest and Range Exp. Sta. review draft. 71 pp.

Steele, R., R.D. Pfister, R.A. Ryker, and J.A. Kittams. 1981. Forest habitat types of central Idaho. USDA Forest Serv. Intermtn. Forest and Range Exp. Sta. Gen. Tech. Rep. INT-114. 138 pp.

Tisdale, E.W. 1947. The grasslands of the southern interior of British Columbia. Ecology 28:346-382.

. 1961. Ecological changes in the Palouse. Northwest Sci. 35:134-138.

. 1961a. Intraspecific variation in *Festuca*. II. Carnegie Inst. of Washington Yearbook. 60:388-391.

. 1976. Vegetational responses following biological control of *Hypericum perforatum* in Idaho. Northwest Sci. 50:61-75.

_____. 1979. A preliminary classification of Snake River canyon grasslands in Idaho. Forest, Wildlife, Range Exp. Sta. Note 32., Univ. of Idaho, Moscow. 8 pp.

. 1982. Grasslands of western North America: The Pacific Northwest Bunchgrass type. Pages 223-245 in Proc. Symp: Grassland Ecology and Classification. British Columbia Ministry of Forests. Victoria, B.C.

Tisdale, E.W., and Mary Bramble-Brodahl. 1983. Relationships of site characteristics to vegetation in canyon grasslands of west central Idaho and adjacent areas. J. Range Manage. 36:775-778.

USDA. 1975. Soil taxonomy. USDA Soil Cons. Serv. Handbook No. 436., Washington, D.C.

_____. 1976. Reconnaissance soil survey, Nez Perce County, Idaho. USDA Soil Cons. Serv. 97 pp.

. 1976. Soil Cons. Serv. National Range Handbook, Washington, D.C.

_____. 1980. Soil Survey of Whitman County, Wash. USDA Soil Cons. Serv. 185 pp.

_____. 1982. Soil survey of Idaho County, Idaho. Western part. USDA Soil Cons. Serv. 266 pp.

Waller, S.S., and J.K. Lewis. 1979. Occurrence of C₃ and C₄ photosynthetic pathways in North American grasses. J. Range Manage. 32:12-28.

White, D.L. 1974. Geology of the Pittsburg Landing-Big Canyon Creek area, Snake River Canyon, Idaho and Oregon. Northwest Sci. 48:72-79.

Wright, H.A., L.F. Neuenschwander, and C.M. Britton. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities. USDA Forest Serv. Intermtn. Forest and Range Exp. Sta. Tech. Rep. INT-58, Ogden, Utah. 48 pp.

