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# THE SAGEBRUSH-GRASS REGION: A REVIEW OF THE ECOLOGICAL LITERATURE



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**E.W. Tisdale and M. Hironaka**

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## FOREWORD

This publication is the result of a long-standing interest in the sagebrush-grass vegetation of North America. From 1948 to 1980 we have witnessed and participated in greatly increased research on the major vegetation region.

The lack of any comprehensive review of the accumulated ecological information led us to undertake this task, which proved to be larger than was first contemplated. We have tried to include all the more relevant publications, and can only apologize for those which are omitted. A major fact which emerged during our search was that a large amount of unpublished material in theses, project reports, etc., largely remains unavailable. It also became apparent that relatively more research has been done on the northern portion of the sagebrush region than on the southern part.

We would like to acknowledge our indebtedness to co-workers who have shared in the study of sagebrush vegetation over the past 3 decades and with whom we have shared observations and ideas. These include university researchers and scientists from federal, state, and private agencies. We hope they will approve of our present effort.

# The Sagebrush - Grass Region: A Review of the Ecological Literature

E.W. Tisdale and M. Hironaka

## INTRODUCTION

The objective of this paper is to provide a comprehensive review of literature on the vegetation of the sagebrush region of North America. Despite its prime importance as a grazing resource, and the problems produced by its use and misuse, research on this large and varied ecosystem was quite limited during the first half of this century. Increased activity began in the 1950s and has expanded greatly during the last two decades, stimulated by federally supported regional projects, the International Biological Program, and establishment of the U.S. Department of Agriculture Forest Service Shrub Sciences Laboratory at Provo, Utah. The result has been an impressive increase in the technical literature, appearing in a wide variety of media. Much additional material of value exists in unpublished theses and reports. Although bibliographies for particular topics have been compiled, no comprehensive attempt has been made so far to cover the whole range of research and publication dealing with the sagebrush-grass vegetation.

The present review developed from a continuing involvement with the ecology of sagebrush vegetation in Idaho, including participation in two U.S. Department of Agriculture (USDA) regional projects (W-25 and W-89), and subsequent research on classification of sagebrush vegetation for the USDA Forest Service.

Since the objective is to document the current status of knowledge of sagebrush vegetation, emphasis has been

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placed on thorough coverage of recent contributions. Inclusion of older work has been made more selective, particularly where the results are included in subsequent publications.

The overall emphasis is on the characteristics of sagebrush-grass vegetation and its major component species. Manipulation and replacement receive less attention. This subject area was intensively reviewed in the Sagebrush Ecosystem Symposium, held at Utah State University, Logan, in 1979.

Although the total vascular flora of sagebrush-grass vegetation is extensive, a relatively small number of species comprise the bulk of the biomass (Tisdale et al. 1969). Of the shrubs which give this vegetation its distinctive physiognomy the most abundant are woody species of sagebrush (*Artemisia*). Other common shrubs include rabbitbrush (*Chrysothamnus*) and bitterbrush (*Purshia*). Shrubs which occur less commonly in the sagebrush-grass region, but which dominate closely related communities include serviceberry (*Amelanchier*), mountain-mahogany (*Cercocarpus*), wild cherry (*Prunus*) and snowberry (*Symphoricarpos*).

The principal herbaceous species are grasses, especially wheatgrass (*Agropyron*), fescue (*Festuca*), bluegrass (*Poa*), needlegrass (*Stipa*), bromegrass (*Bromus*), and squirreltail (*Sitanion*). Forbs are less abundant, but species of phlox (*Phlox*), milk-vetch (*Astragalus*), and fleabane (*Erigeron*) are widespread and often abundant, especially in the moister parts of the region.

The woody section of *Artemisia*, the Tridentatae, has been studied and revised by several workers, including Hall and Clements (1923), Ward (1953), Beetle (1959, 1960), Beetle and Young (1965), and Winward (1970). The

treatment followed in this paper is essentially that of Beetle (1960), but with modifications in the *A. tridentata* group. Nine species and several subspecies and other subdivisions of woody *Artemisia* are recognized in the region described. The species, in approximate order of area occupied are: big sagebrush (*A. tridentata*), silver sagebrush (*A. cana*), low sagebrush (*A. arbuscula*), black sagebrush (*A. nova*), Bigelow sagebrush (*A. bigelovii*), threetip sagebrush (*A. tripartita*), stiff sagebrush (*A. rigida*), early low sagebrush (*A. longiloba*), and Rothrock sagebrush (*A. rothrockii*). Although the genus *Artemisia* has its origin in Asia, the section Tridentatae, distinguished by woody stems and a lack of ray florets, appears to have evolved in North America, and to differ from the woody *Artemisias* of the Old World (Stebbins 1971, McArthur and Plummer 1978, Kelsey and Shafizadeh 1979). This North American section has evolved species and lesser taxa to fit a wide variety of habitats in the area now occupied by its members. Other woody sages, including California sage (*A. californicum*) in coastal California and sand sage (*A. filifolia*) on sandy soil of the Southern Great Plains, do not belong in the section Tridentatae, and are not covered in this review.

### AUTECOLOGY OF MAJOR SPECIES

Current knowledge of the ecology of individual species of the sagebrush region is still inadequate, although much has been accomplished during the past three decades. The available information is usually scattered over a number of studies, each limited to certain phases of the plant's ecology, often done with different methods and with populations of different character. A common weakness has been failure to identify the source and nature of the populations studied (Tisdale 1962). The importance of the "provenance" approach has been well demonstrated in research on forest tree species (Callahan 1963).

The attempt here is to assemble and evaluate pertinent data concerning major species of the sagebrush region. The material is presented under the headings of taxonomy, intraspecific variation, growth development, habitat relationships (physical and biotic) and physiological factors.

#### *Artemisia tridentata* (Big sagebrush)

Within the sagebrush group, most attention has been given to this species, doubtless because of its great abundance and wide distribution. Adjustment to environment has produced sufficient differences to warrant the recognition of subspecific units. These include three subspecies: *tridentata*, *vaseyana*, and *wyomingensis*, and one form *vaseyana spiciformis*. Another entity, known only as "big sagebrush X" has also been recently described (Winward and Tisdale 1977).

These subdivisions of *A. tridentata* are separable by morphological, phenological, cytological, and chemical characteristics, and their recognition is indispensable for

classifying big sagebrush vegetation (Kelsey et al. 1976, Winward and Tisdale 1977, and Winward 1980), and as indicator plants in other communities (West et al. 1978). Basin big sagebrush (*A. tridentata tridentata*) occurs in areas of dry climate but on relatively deep, well drained soils. Wyoming big sagebrush (*A. tridentata wyomingensis*) occurs in warmer and often drier sites on shallower, sometimes slightly saline soils. Mountain big sagebrush (*A. tridentata vaseyana*) grows in areas of more moisture and lower temperatures. Subalpine big sagebrush, form *spiciformis* of *A. vaseyana*, is limited to mesic sites at high altitudes. The "X big sagebrush" shares characteristics with subspecies *tridentata* and *vaseyana*. It appears to be restricted to areas of intermediate elevation where the climate is moister than in sites occupied by subspecies *wyomingensis* but warmer than the higher elevations where *A. vaseyana* occurs (Winward and Tisdale 1977). Since external differences among these taxa are not great, and some intergrading occurs, use of all possible criteria for identification is advisable. Chemical tests, using thin layer chromatography have been used to detect the presence of diagnostic fluorescent compounds (Holbo and Mozingo 1965, Winward 1970, Hanks and Jorgensen 1973, Hanks et al. 1973, Kelsey et al. 1976). Simple fluorescence tests have also been devised for use under field conditions (Winward and Tisdale 1969, Stevens and McArthur 1974).

Genecological variation also occurs. This type of variation involves the development of local populations or races within a species which differ genetically and physiologically but do not show sufficient morphological differences to be recognized taxonomically. Since its first recognition by Turesson (1922) this kind of variation has been found to be common in species of wide distribution. Detection of these differences requires special techniques including growing populations from different sources in a common environment, and this has been done for few species of the sagebrush region. Knowledge of this type of variation is significant for the understanding and management of range vegetation (Tisdale 1962).

In the case of *A. tridentata*, Marchand et al. (1966) found differences in survival rate and phenology among populations of both *A. tridentata tridentata* and *A. tridentata vaseyana* grown in experimental gardens. Hanks and coworkers (1971, 1973) used paper chromatography to separate populations within each of the three subspecies of *A. tridentata*. These populations varied in habitat and in palatability to grazing animals. Further studies are likely to reveal more genecological variation in big sagebrush (Plummer 1971, McArthur and Plummer 1978).

The most complete account of the developmental history of *A. tridentata* is that presented by Daubenmire (1975a), which includes studies by Goodwin (1956) and Price (1965), all in eastern Washington. Other sources of data include Robertson (1943), Mueggler (1956), Payne (1957), Beetle (1960), Marchand et al. (1966), Schlatterer

and Tisdale (1969), Winward (1970), McDonough and Harniss (1974a, 1974b), Harniss and McDonough (1975, 1976), McArthur and Welch (1978), Caldwell (1979), McArthur et al. (1979).

The following treatment applies to *A. tridentata* as a species, with exceptions due to subspecific differences where these have been documented. The species is a prolific seed producer and 300,000 or more achenes may be produced annually on one mature plant. Flowering usually occurs during September and seed ripens by late October or early November. These stages occur 2 to 5 weeks earlier in the higher elevation forms, subspecies *vaseyana* and *A. tridentata* "X." Seed is shed during late fall and winter. Dissemination is by wind, water and animals, with most seed remaining fairly close to the parent plant. Germination occurs in late winter and early spring.

Under laboratory conditions seed germinates under a wide range of temperatures, and germination is favored by light. Seed of subspecies *tridentata* and *wyomingensis* germinates at rates of 60 percent or more without stratification. Germination of subspecies *vaseyana* is low (15 percent approximately) under these conditions, but increases to 80 or 90 percent following 30 to 60 days of stratification (McDonough and Harniss 1974a). Most seed germinates in the spring following its formation, but some can lie dormant in the soil for periods up to 4 years. It appears that the revegetation of large areas from which *A. tridentata* has been removed by fire or other means is accomplished largely by seed remaining in the soil (Mueggler 1956, Bartolome and Heady 1978). Seedlings may appear in vast numbers (600 per sq ft) in years of favorable moisture conditions, but mortality is usually heavy by the end of the first season. Young sagebrush plants grow slowly where competition from other vegetation is severe, but respond well to lessened competition, as on areas recently disturbed by insects or fire. Plants usually begin reproduction at an age of 3 to 4 years but may start at 2 years under highly favorable conditions.

Growth begins in early spring, and is largely completed by late July. Winward (1970) found significant differences in the soil moisture regime of the three subspecies of *A. tridentata* in southern Idaho. Moisture became deficient by mid-July on sites dominated by subspecies *wyomingensis*, by late July or early August for subspecies *tridentata*, and by September on *A. vaseyana* sites. Despite the seasonal pattern of moisture stress, many plants of the *A. tridentata* complex flower and produce seed in normal years.

*Artemisia tridentata* is evergreen as a result of the production of two series of leaves each year. The first series is produced from buds which have over-wintered. These "ephemeral" leaves are usually larger than those of the second, "persistent" series which develop later in the season and remain on the plant over winter.

Big sagebrush exhibits a characteristic growth form with a single, multi-branched main stem. The subspecies differ in stem diameter, crown form and height of mature plants. Subspecies *tridentata* and *wyomingensis* have irregular crowns and relatively thick trunks, while subspecies *vaseyana* and its form *spiciformis* have more slender trunks and flat-topped crowns. Height of mature plants varies with site conditions, but subspecies *tridentata* commonly grows to 120 to 180 cm (4-6 ft) and occasional plants may reach 240 cm (8 ft) or more. Subspecies *wyomingensis* is shorter, usually reaching 45 to 100 cm (18-40 inch). *Artemisia tridentata* is long-lived and forms well defined rings which enable both age and fluctuations in growth to be determined (Ferguson 1964). Ages of 40 to 50 years are common, with some plants exceeding 100 years. Slow-growing individuals on unfavorable sites attain the greatest age.

Root systems of all three subspecies of *A. tridentata* have been studied, although the number of such investigations has been limited (Goodwin 1956, Tabler 1964, Winward 1970, Hull and Klomp 1974, Fernandez and Caldwell 1975, Daubenmire 1975a, Sturges 1977, Sturges and Trlica 1978). Caldwell (1979) has summarized much of the available data. Essentially there is a basic root pattern for the species, with significant variation due to differences among subspecies and sites. The basic plan is a tap root extending from 1 to 2 m, with a lateral spread up to 1.5 m. There is a marked concentration of fine roots in the upper 20 to 30 cm of soil, but a considerable development at greater depths also.

A comparison of subsp. *vaseyana* growing on the bottom and midslope of a ridge and subsp. *wyomingensis* on the ridge top showed a greater depth of root penetration for the former, but lateral spread was the same for both subspecies. Root depth was definitely related to depth of water recharge. In total, the root system of the *A. tridentata* complex is well adapted to extract moisture and nutrients from both shallow and deeper portions of the soil profile, and must be considered as highly competitive with the principal grasses and forbs of the sagebrush region.

Big sagebrush is highly susceptible to fire and no resprouting occurs (Blaisdell 1953). As a result, large amounts of *A. tridentata* are killed periodically by wild-fires, and planned burning has been used as a tool for sagebrush control (Pechanec et al. 1965).

The species is also affected by several dipterous insects, many of which cause formation of galls on the plant (Fronk et al. 1964, Jones 1971). These reduce plant vigor when abundant, but do not usually cause death. Other leaf chewing insects are more harmful. Most common is *Aroga websteri*, a moth, whose larvae feed exclusively on foliage of *A. tridentata* and related species: *A. arbuscula*, *A. nova* and *A. cana* (Henry 1961). Periodically, populations of *A. websteri* increase to a point where

significant damage is done, with mortality ranging up to 80 or 90 percent of sagebrush stands in severe cases. Large outbreaks occurred in southeastern Oregon and southwestern Idaho in 1962-1963 (Gates 1964). The insect populations become heavily parasitized during peak periods, however, and usually decline abruptly after 1 or 2 years at peak level (Fillmore 1965). The sagebrush then gradually repopulates the affected area.

Another insect, *Trirhabda pilosa* (Blake 1931), appears to have a high potential for destroying big sagebrush, but recorded outbreaks are rare. Pringle (1960) found severe damage to *A. tridentata* in southern British Columbia in 1956-1958, but the insect population declined soon after and has not reappeared in significant numbers. Fisser and Lavigne (1961) reported a severe infestation of *Trirhabda attenuata* on *A. tripartita* subsp. *rupicola* in Wyoming.

Mueggler (1967) reported extensive damage by voles (*Microtus* spp.) to *A. tridentata* in western Montana during the winter of 1963-1964. The mode of damage was by stripping bark, and mortality of plants ranged from 10 to 84 percent. Similar increases of voles have occurred in other parts of the sagebrush region. Frischknecht and Baker (1972) have suggested that voles could be utilized for improvement of certain sagebrush ranges.

Grasshoppers, common insects of the sagebrush region, usually prefer the associated herbaceous species, but under certain conditions may damage stands of sagebrush. Allred (1941) reported severe damage (over 50% mortality) to *A. tridentata* in the Powder River drainage of Wyoming and Montana in 1936 due to concurrence of a peak population of grasshoppers and drought conditions. Comparable damage to *A. tridentata wyomingensis* was observed by the present authors on a 1000-acre area near King Hill, southern Idaho in 1965.

The biotic agents discussed are native to the sagebrush region, and presumably have co-existed with *A. tridentata* and allied species for a long time. Although considerable mortality of big sagebrush occurs periodically due to one or more of these agents, this does not prevent the species from maintaining itself within the area of suitable climate and soils. This also applies to the effects of natural fires. Only persistent use of fire, herbicides or mechanical methods will permanently reduce the population of sagebrush.

Big sagebrush is also sensitive to herbicides, including 2,4-D; 2,4,5-T; and picloram, when applied during the period of active growth (Pechanec et al. 1965, Tueller and Evans 1969, Evans et al. 1970b, Evans and Young 1977b). This method has been widely used in management of sagebrush-grass ranges, but can have detrimental effects on sagegrouse (Klebenow 1970) and other wildlife species.

Most investigations of the physiology of big sagebrush have been made during the past decade, although the effects of defoliation were studied earlier. An excellent summary of existing knowledge was provided by Caldwell (1979). This species shows a marked capacity for photosynthesis at low temperatures, but assimilation is greatly reduced by leaf temperatures above 30° C and also by moisture stress (Dina and Klikoff 1973, Deputit and Caldwell 1973, 1975, Pearson 1975). The species shows a considerable photosynthetic acclimatization potential, greater than that of the less widely distributed species, *A. arbuscula* and *A. nova* (West and Mooney 1972). The ability of *A. tridentata* to carry on photosynthesis at a high rate at low temperatures makes it well suited to its environment, where the low temperatures of spring coincide with abundant soil moisture. In addition, the plants are capable of rapidly resuming a high rate of photosynthesis later in the season, whenever moisture and temperature conditions become favorable (Pearson 1975).

Big sagebrush also has the capacity to extract water from dry soils when soil water potentials are as low as -70 bars (Campbell and Harris 1977). The root system becomes active early in spring and may begin growth as much as a month before aerial growth (Fernandez and Caldwell 1975).

Caldwell (1979) summed up the physiological factors for success of *A. tridentata* as including capacity for photosynthesis at low temperatures, capacity for temperature acclimatization, maintenance of large leaf area throughout the year, sensitive stomatal control of water loss, capacity of the root system to remove water from dry soils and possible presence of secondary compounds which may deter predators and plant competitors.

The effects of clipping have been investigated by several workers. Cook and Stoddart (1960) found that *A. tridentata* can tolerate about 60 percent use during winter, but allowable use during late spring was only 35 percent. Pearson (1965) found severe damage from one season of 100-percent use. Wright (1970) found that an 80-percent use rate was most harmful in midsummer (July) when carbohydrate reserves were lowest, and least harmful during the late summer, fall and winter months. Cook and Child (1971) and Trlica and Cook (1971) found that *A. tridentata* and *A. nova* both recovered slowly from severe defoliation, and that carbohydrate reserves were directly related to previous defoliation.

### *Artemisia arbuscula* (Low sagebrush)

This species is second in abundance only to *A. tridentata* in the northern intermountain area. It is characterized by a compact crown and low stature (30-50 cm). It is distinguished from *A. tridentata* by its smaller size, shorter leaves, and narrow paniculate inflorescence. Two subspecies are recognized: subsp. *arbuscula* with coarse,

cuneate leaves; and subsp. *thermopola* with fine, deeply trifid leaves (Beetle 1960). Subspecies *thermopola* is confined to areas of gravelly, immature soils close to the forest boundary in western Wyoming and eastern Idaho. Subspecies *arbuscula* is the dominant shrub over large areas at medium to high elevation which are similar climatically to those occupied by *A. tridentata*, especially subsp. *tridentata* and *vaseyana*. The difference in habitat is edaphic, for both subspecies of *arbuscula* occupy soils which are either less than 33 cm to an impermeable "B" horizon bedrock, or if deeper, have 30 percent or more gravel and cobbles in the horizon (Fosberg 1964, Fosberg and Hironaka 1964). This edaphic restriction of *A. arbuscula* has been confirmed by a number of investigators in various parts of the sagebrush region (Tueller 1962, Hall 1967, Summerfield 1969, Zamora and Tueller 1973, Sabrinski and Knight 1978). The shallow soils result from periglacial erosion and tend to be waterlogged in the spring. Both this type and the deeper, gravelly soils are low in moisture retaining capacity and become very dry by mid-summer. This appears to be the main factor which prevents *A. tridentata* from growing on these soils, although the effects of poor aeration in the spring period may also be a factor, since *A. tridentata* roots are known to have high oxygen requirements (Lunt et al. 1973). Sites with alternating areas of shallow or gravelly and deeper, finer soils commonly support a mosaic of *A. arbuscula* and *A. tridentata*, each confined to its preferred soil. In total, the area in which *A. arbuscula* occurs on shallow soils with an impermeable layer far exceeds its occurrence on deeper, gravelly soils. The latter condition is reported on soils derived from glacial outwash in western Wyoming (Sabrinski and Knight 1978), but is not widespread in the sagebrush region. This distribution, in relation to soils, plus the similarity to sites occupied by *A. longiloba* does not support Beetle's (1979) idea that *A. arbuscula* developed as a type adapted to glacial till soils.

Apart from its edaphic relationships, little has been published on *A. arbuscula*. The phenology appears similar to that of *A. tridentata*, with new growth noticeable in May, flowering in September and seed ripening in late October and November (Beetle 1960 and authors' personal observations). The species is a nonsprouter and is susceptible to fire and defoliating insects, especially *Aroga websteri* (Furniss and Barr 1975) and to herbicides (Eckert and Evans 1968). Fire is not common in *A. arbuscula* vegetation due to the scarcity of fuel (Gipe 1976).

#### *Artemisia nova* (Black sagebrush)

This is a low-growing evergreen species, similar in many ways to *A. arbuscula*, but generally lower in stature (20-40 cm), (8-16 inch), with smaller leaves and an inflorescence which is dark brown and persistent in the year following its production (Beetle 1960). The crushed leaves are highly pungent and usually sticky. This species is widely distributed over the sagebrush region. *Artemisia nova* occurs primarily on soils which are shallow and gravelly, well drained, and often calcareous (Thatcher 1959, Hironaka

1963, Zamora and Tueller 1973). Where *A. arbuscula* and *A. nova* meet, as in parts of eastern Idaho, the former generally occupies higher elevations or slightly moister habitats (Ward 1953). *Artemisia nova* tends to occur in drier areas than those occupied by *A. arbuscula* or *A. tridentata wyomingensis*. It has a shallower root system than *A. tridentata*, and its annual growth is more dependent on amounts of water near the soil surface (Stevens et al. 1974).

*Artemisia nova* is most abundant in the southern part of the Intermountain region where it occurs in stands of varying size surrounded by larger areas of salt-desert vegetation (Hutchings and Stewart 1953). A form of *A. nova* with canescent leaves occurs in parts of Utah, Nevada, and in southeastern Idaho. It appears to differ from the typical form of the species in animal preference and possibly other characters of significance for management, but no definitive studies of it have been made (Winward 1980).

The phenology of the species is similar to that of *A. arbuscula*, but slightly earlier (Beetle 1960). *Artemisia nova* is also a nonsprouter and can be killed by fire or insects. The sparse vegetation of most stands makes them virtually fireproof.

#### *Artemisia bigelovii* (Bigelow sagebrush)

This species differs from all others in the section Tridentatae by having ray as well as disk flowers. Some authorities consider it to belong to the section Abrotanum, but the weight of evidence seems to place it in the Tridentatae (McArthur 1979).

This sagebrush is a low growing species (20-40 cm tall), with numerous spreading vegetative branches and slender erect flowering stems with long narrow panicles. The vegetative leaves are tridentate like those of *A. tridentata*, but more shallowly and sharply dentate (Beetle 1960). Bigelow sagebrush is more southern in distribution than the other species of the section Tridentatae, and occurs mainly in the drainage of the Colorado River and its territories, in the states of Utah, Colorado, Arizona, and New Mexico.

Few published data are available for this species, although Beetle (1960) rates it fifth among the sagebrush species in area occupied. It is considered to be highly drought resistant and a nonsprouter after fire or cutting. It seems to be relatively free from the insect galls which are common to the other sagebrush species. Data on soil relationships appear to be lacking.

#### *Artemisia tripartita* (Three-tip sagebrush)

*Artemisia tripartita* is a species of moderate size, averaging 40 to 80 cm (16-32 inch) and distinguished by its slender, deeply three-cleft leaves and relatively open inflo-

rescence. Two subspecies are recognized, but one of these, subsp. *rupicola*, is found only east of the Continental Divide, while subsp. *tripartita* occurs throughout the northern and central parts of the sagebrush region (Beetle 1960). Subspecies *tripartita* frequently occurs adjacent to stands of *A. tridentata* and the habitat factors responsible for the distribution of the two species are not well understood. *Artemisia tripartita* occurs on soils of moderate depth with good fertility and drainage (Thatcher 1959, Passey and Hugie 1962b, Tisdale et al. 1965). Although the soil relationships of *A. tripartita* appear generally similar to those of *A. tridentata*, its moisture requirements seem greater than those of subsp. *tridentata* and *wyomingensis*. Where it occurs adjacent to either of these, *A. tripartita* is confined to north and east slopes or to shallow depressions (Tisdale et al. 1965, Daubenmire 1970). In eastern Oregon and western Idaho, *A. tripartita* often occurs in isolated stands in depressions surrounded by *A. tridentata wyomingensis*, but is more abundant and widespread in eastern Idaho where soil moisture in summer is less limiting due to a higher proportion of summer rainfall and lower temperatures (Hironaka 1963).

*Artemisia tripartita* sprouts after fire, cutting, or even herbicide treatments (Beetle 1960, Pechanec et al. 1965), regenerating by sprouts from shallow lateral roots and from adventitious buds on the base of stems (Daubenmire 1970).

The phenology of *A. tripartita* as recorded by Blaisdell (1958) in eastern Idaho shows leaf growth starting in late April, shoot growth in mid-June, full flower in mid-September and seed ripe by mid-October. The pattern is similar to that of *A. tridentata* subsp. *tridentata*.

Wright (1970) found that *A. tripartita* reacted the same as *A. tridentata* to clipping in mid-summer, but was less tolerant than the latter to clipping during fall and winter.

### *Artemisia cana* (Silver sagebrush)

*Artemisia cana* is moderate in size, 50 to 90 cm (20-36 inch), with leaves which are entire, or partially lobed, relatively long and often whitish pubescent. This species occurs primarily east of the Continental Divide and is the principal sagebrush in much of the Great Plains, where it occurs widely though usually in rather sparse stands (K.L. Johnson 1979). The form occurring on the Great Plains, subsp. *cana*, occurs on a wide variety of sites, but is particularly adapted to deep light textured soils (Hazlett and Hoffman 1975). Only the subspecies *viscidula* and *bolanderi*, distinguished by their narrower, often divided leaves, occur west of the Rockies (Beetle 1960). Subspecies *viscidula*, with greenish leaves, occurs mainly on stream banks, meadows, and depressions in the central part of the sagebrush region. Subspecies *bolanderi*, distinguished by its canescent leaves, grows on poorly drained soils in the far western part of the sagebrush region in central Oregon and eastern California.

*Artemisia cana* is a shrub of moderate size, with a rounded crown and an inflorescence of dense, narrow leafy panicles. It reproduces vegetatively by root sprouting and sprouts readily after fire or grazing (McArthur et al. 1979).

### *Artemisia longiloba* (Early low sagebrush)

*Artemisia longiloba* is a low growing species, 20 to 40 cm (8-16 inch), similar in many respects to *A. arbuscula*, but distinguished by larger leaves with obtuse lobes, larger flowering heads and early maturity (Beetle 1960). This species is confined to shallow, poorly drained soils, generally with dense clay "B" horizons (Passey and Hugie 1962b, Robertson et al. 1966, Tisdale et al. 1969, Zamora and Tueller 1973). The common name "alkali sagebrush" suggested for this species and the statement that it occurs on "alkaline soils" are misleading, as these soils are neutral rather than alkaline, as shown by the studies listed above. This species generally occurs in small, sharply defined stands. When associated with *A. arbuscula* it usually occurs on lower lying areas where soil moisture is slightly higher.

### *Artemisia rigida* (Stiff sagebrush)

*Artemisia rigida* is a low growing species, 30 to 40 cm (12-16 inch), with silvery canescent leaves which are deeply divided into three to five narrow segments. Unlike the sagebrush species described previously, *A. rigida* is fully deciduous; the plants remain bare of leaves all winter. It occurs on soils that are extremely shallow to bedrock, usually basalt (Hall 1967, Daubenmire 1970). This species is confined to the northwestern portion of the sagebrush region, mainly in Washington and eastern Oregon (Beetle 1960). Its occurrence in Idaho is limited to small areas close to the western border of the state.

*Artemisia rigida* grows in a fairly wide range of climatic conditions, and may occur adjacent to stands of *A. tridentata* subsp. *tridentata* or subsp. *vaseyana*, or *A. tripartita*, but is clearly limited by edaphic factors. Little is recorded concerning the effects of fire or biotic factors on *A. rigida*. The sparse, herbaceous understory and open nature of the stands make them virtually immune to fire. Preliminary tests suggest that the species does not sprout after clipping to a height of 3 to 4 cm.<sup>1</sup>

### *Artemisia rothrockii* (Rothrock sagebrush)

This is a relatively low-growing, flat-topped species which resembles *A. tridentata* subsp. *vaseyana*, with which it often has been confused. *Artemisia rothrockii* is distinguished by the densely canescent, three-lobed leaves of the vegetative shoots and by the short, interrupted spike-like inflorescence. Layering is common in this species. The distribution is strictly at high elevations, in California, Colorado, and western Wyoming (Beetle 1960, McArthur et al. 1979). Material from the mountains of

<sup>1</sup> E. W. Tisdale. 1980. Unpublished data on file. College of Forestry, Wildlife and Range Sciences. Univ. of Idaho, Moscow.

southeastern Idaho, Utah, and Nevada which has been assigned to this species probably belongs to *A. tridentata vaseyana* or to an undescribed taxon (Winward 1976, McArthur et al. 1979).

Beetle (1960) reports that *A. rothrockii* occurs on "deep soils," and that new growth starts in May with seed maturing in September to October. Apart from these observations, no data on the ecology of this species have been found.

### *Chrysothamnus* (Rabbitbrush)

Two widely distributed species of this genus are important in the sagebrush-grass region. *Chrysothamnus nauseosus* (rubber rabbitbrush) is a deciduous shrub of variable size, 60 to 120 cm (24-48 inch), with narrow leaves, numerous yellow flowering heads, and twigs covered by feltlike hairs. The species is variable, morphologically and ecologically. Hitchcock and Cronquist (1974) list six varieties, four of which, i.e., *nauseosus*, *albicaulis*, *glabratus* and *artus*, occur in the sagebrush region. Anderson (1966) recognized subspecies *albicaulis*, *consimilis*, *graveolens* and *salicifolius*. Of these, var. or subsp. *albicaulis* seems to be the same taxon, while var. *glabratus* of Hitchcock apparently equals subsp. *graveolens* of Anderson, and var. *artus* equals subsp. *consimilis*. Subspecies *salicifolius*, a high elevation form common in northern Utah, is not listed by Hitchcock. Hanks and co-workers (1975) were able to separate subspecies *albicaulis*, *graveolens*, *consimilis* and *salicifolius* by paper chromatography and among these taxa to demonstrate differences in habitat and in palatability to grazing animals. Generally, recognition of *C. nauseosus* has not been made to subspecific level, although Daubenmire (1970) has designated the material in eastern Washington as var. *albicaulis*.

Galls produced by tephritid flies are common on several species of *Chrysothamnus* (Furniss and Barr 1975). McArthur et al. (1979) report that the type of gall may be related to subspecific differences in *C. nauseosus*. Subspecies *albicaulis* was commonly infested with a round, firm stem gall, while subsp. *consimilis* and *graveolens* had fluffy, less persistent galls. These differences were fairly constant over much of the Great Basin. Wangberg (1976), in a study of tephritid gall-formers on *Chrysothamnus* in Idaho, found that the same insect species, *Aciurina bigeloviae*, form three different types of galls on *C. nauseosus* subsp. *albicaulis*, depending on the geographical location of the host. The same insect forms different types of galls on subsp. *consimilis*, also on another host species, *C. parryi*. Gall host specificity shows promise as an additional means of identifying *Chrysothamnus* taxa, but the relationship of predator and host is not simple.

*Chrysothamnus viscidiflorus*, the other common species of rabbitbrush in the sagebrush region, is also a variable species. It is a moderately low shrub, 60 to 100 cm

(24-40 inch), distinguished from *C. nauseosus* by glabrous or puberulent twigs and leaves, the latter often twisted. Hitchcock et al. (1955) described seven varieties, namely, *lanceolatus*, *humilis*, *puberulus*, *pumilis*, *stenophyllus*, *viscidiflorus* and *latifolius*. The varieties are characterized by Hitchcock and Cronquist (1974) as "only obscurely or scarcely correlated with ecology and geographic distribution." Since few workers have identified their material to subspecies, it is difficult to judge the accuracy of this statement. Winward (1970) found that in southeastern Idaho var. *pumilus* was associated with habitat types dominated by *A. tridentata* subsp. *tridentata* and *wyomingensis*, while var. *viscidiflorus* was associated with moister sites dominated by *A. tridentata* subsp. *vaseyana*. Lauer and Peek (1976) report a similar situation in east central Idaho with var. *pumilus* on the drier sites and vars. *lanceolatus* and *viscidiflorus* on more mesic situations. McArthur et al. (1978a) used paper chromatographic analysis of phenolic compounds in *C. viscidiflorus* to separate the subspecies. They found this method particularly useful in view of the difficulty of identifications by morphological characters, many of which are highly variable. These workers found subsp. *viscidiflorus*, *stenophyllus*, *lanceolatus*, and *puberulus* to be the most abundant in the Great Basin. It is likely that additional ecological differences within both species of rabbitbrush will be found when identification to the varietal level is made more commonly.

Since ecological information on both species of *Chrysothamnus* is scarce and since they are similar in many respects, they will be discussed together with differences noted where these have been observed. Both species occur throughout the sagebrush region, but usually as minor components of relatively undisturbed sagebrush-grass stands (Eckert and Evans 1968, Tisdale et al. 1969, Hironaka and Fosberg 1979). Disturbance by fire or mechanical damage favors *Chrysothamnus* and results in a marked increase in both species (McKell and Chilcote 1957, Blackburn et al. 1969, Daubenmire 1975b, McArthur et al. 1979). This reaction is due primarily to the ability of both species to sprout and to their high rate of reproduction from seed when competition from other species has been reduced (McKell and Chilcote 1957). The plumed seeds of *Chrysothamnus* are well adapted for dispersion by wind and greatly excel *Artemisia* in this respect. Growth of *Chrysothamnus* begins in early spring, usually at the same time as associated species of *Artemisia*, but development proceeds more rapidly, to flower production in late July and August, and seed ripening and shedding in September (McKell and Chilcote 1957, Blaisdell 1958). McKell and Chilcote (1957) reported seed germination of only 16 to 31 percent under laboratory conditions, but seed production was heavy in vigorous plants. Seedlings usually appear in abundance in the spring months if moisture conditions are favorable.

A phenological study of *C. viscidiflorus* near Reno, Nevada by Young and Evans (1974) showed growth starting

the end of February, but proceeding very slowly until early May due to low temperatures. A rapid growth period followed until the end of June, after which growth slowed again. Flowering occurred from mid-August until mid-September, with abundant production of achenes. Only 2 percent of the plants on this site, burned 12 years earlier, were from root sprouts, indicating the importance of reproduction from seed in this species. Growth was affected strongly by amount of competition and age of plant, with young plants growing much more rapidly than older ones.

*Chrysothamnus* grows on a wide range of soils. *Chrysothamnus nauseosus* appears to be favored by deep, sandy soils (Daubenmire 1942), but is not restricted to them. Some varieties of *C. viscidiflorus* can tolerate relatively saline soils (Plummer et al. 1968). Branson et al. (1976) found total root mass per unit area greater for *C. nauseosus* than for *Artemisia tridentata*, although effective rooting depth was less. Frischknecht (1963), however, found *C. nauseosus* less competitive with crested wheatgrass than was *Artemisia tridentata*.

The general response of *Chrysothamnus* to fire or mechanical injury is sprouting from adventitious buds formed at the summit of the roots (Daubenmire 1975b). Sprouting can occur within a few months of injury and those shoots can flower during the same season (McKell and Chilcote 1957). *Chrysothamnus* is also relatively resistant to many herbicides and often survived applications of 2,4-D which are sufficient to kill most species of *Artemisia* (Blaisdell and Mueggler 1956b, Robertson and Cords 1957, Hyder et al. 1962, Laycock and Phillips 1968, Mohan 1973). Heavier applications of 2,4-D and picloram, plus better timing of application, have been effective in killing rabbitbrush (Eckert and Evans 1968, Laycock and Phillips 1968, Mohan 1973, Evans and Young 1975).

A number of insects including species of *Trirhabda*, *Crossidius*, *Agrius*, *Aciurina*, *Procecidochares*, *Apterona* and *Synnoma* are known to feed on *Chrysothamnus* (Furniss and Barr 1975). While several of these insects cause significant damage locally and periodically, the most important seem to be *Trirhabda*, especially *T. mitidicollis* and *T. lewisii*. Massey and Pierce (1960) report that larvae of this beetle killed "large areas" of *C. nauseosus* in western New Mexico in 1957. Comparable outbreaks are not known to have occurred elsewhere. Overall, it does not appear that *Chrysothamnus* is affected as seriously by any insect as *Artemisia* is by *Aroga websteri*.

Clipping studies indicate that *Chrysothamnus* responds to continued harvesting in much the same way as other shrubs of the sagebrush region. Garrison (1953) found that *C. nauseosus* produced well when 73 percent of the annual growth was clipped during autumn for 4 years, but crown cover of the plants declined. It appeared that 50 percent would be a safe rate of use in the fall and winter seasons.

It is apparent that both species of *Chrysothamnus* have sufficient ecological amplitude to enable them to occupy a wide variety of sites within the sagebrush-grass region. They are well adapted to tolerate many forms of disturbance and to quickly occupy disturbed sites. This is their principal role in the region (Young and Evans 1974).

### *Purshia* (Bitterbrush)

Two species, *Purshia tridentata* (antelope bitterbrush) and *P. glandulosa* (desert bitterbrush), occur in the sagebrush-grass region. Of these, *P. tridentata* is abundant and widely distributed in the region, while *P. glandulosa* is primarily a desert species, reaching the sagebrush type only in southwestern Utah, southern Nevada, and northwestern Arizona.

*Purshia glandulosa* is a compact, usually erect shrub with evergreen, glandular leaves, and relatively large flowers (20 mm bract). By contrast, *P. tridentata* is intricately branched, highly variable in growth form with deciduous, nonglandular leaves and small flowers (8 mm bract). *Purshia glandulosa* is thought to have developed as a hybrid between *P. tridentata* and *Cowania mexicana* var. *stansburiana* (cliffrose).

*Purshia tridentata* occurs in several communities of the sagebrush-grass region and in the mountain shrub, pinyon/juniper and ponderosa pine regions. The high preference rating shown for it by native herbivores and domestic livestock make it especially important as a browse species (Hormay 1943, Nord 1965). The forage value, abundance and wide distribution of antelope bitterbrush have resulted in more information concerning it than is available for most native shrubs. Two annotated bibliographies for this species have been published (Basile 1967, Clark and Britton 1979); Clark (1979) has provided a literature review with emphasis on response to burning and cutting.

Antelope bitterbrush occurs over a large area in North America, including the Rocky Mountain and Pacific coastal states. No taxonomic subdivisions of the species are recognized (Hitchcock and Cronquist 1974). Ecotypic variation occurs, however, for Nord (1965), Alderfer (1977), Monsen and Christiansen (1975), and Wright et al. (1979) report heritable, habitat-related differences in stature and growth form.

Seasonal development of antelope bitterbrush as reported by Blaisdell (1958) in eastern Idaho, showed leaf growth beginning in early spring, at about the same time as associated species of *Artemisia*. Flower bud formation and flowering occurred in early and late May respectively, about 3 months earlier than in most species of *Artemisia*. Seed of *Purshia* was ripe by mid-July and shed by early August. The leaves were drying by this time and were shed in early

winter. Actual dates of these growth stages vary over the range of the species, and Nord (1965) reports flowering in March in some parts of California.

Nord (1965) reports that seed production under natural conditions begins when plants are about 10 years old. Seed production depends on climatic conditions and plant vigor, and abundant seed crops are produced only three or four times each decade. The relatively large, heavy seeds drop close to the parent plant and are disseminated mainly by rodents. The latter eat a high proportion, but also aid seedling establishment by burying seed (Sanderson 1962). The seeds are dormant when shed, and require stratification before germination (Evans and Young 1977a). This process normally occurs over winter, and germination comes in early spring. Seedling survival depends primarily on soil moisture during the first growing season, and seedling mortality is usually high (Holmgren 1956, Ferguson 1972). Seed which fails to germinate in the first season following production rarely survives to a second year.

Vegetative propagation can occur by layering or by sprouting from the base after fire or cutting. The amount of sprouting after fire varies greatly according to geographic location. It is uncommon over much of the area occupied by bitterbrush, sporadic in California (Nord 1965) and common in eastern Idaho (Blaisdell 1953, Blaisdell and Mueggler 1956a). The latter found that intensity of the fire and soil moisture conditions during and shortly after burning were key factors affecting amount of sprouting. Clark (1979), in eastern Oregon, found that cutting bitterbrush plants to ground level was less injurious than burning them. Burning in the fall caused complete mortality, but survival of 30 to 50 percent occurred after spring burning. The addition of water to the sites just before or after burning improved survival rates slightly. An erect form of *P. tridentata* was damaged more severely than a decumbent form by either fire or cutting. Bitterbrush plants are long-lived, commonly attaining ages of 80 years or more except when grazed excessively (Nord 1965, McConnell and Smith 1977).

Antelope bitterbrush is generally found on deep, well-drained, often coarse-textured, nonsaline soils, including sands and volcanic ash (Nord 1965, Daubenmire 1970, Chadwick and Dalke 1965). Some populations can also grow on shallow, rocky soils (Mueggler and Stewart 1980), or even on clay soils (Alderfer 1977). It tends to occur in the moister parts of the sagebrush zone, usually associated with *A. tridentata* subsp. *tridentata* and subsp. *vaseyana*, or with *A. tripartita*.

The tolerance of antelope bitterbrush to clipping or grazing is similar to that of associated shrubs in the sagebrush-grass region. Garrison (1953) found that plants on favored sites produced maximum foliage when clipped in the fall at a rate of 75 percent of the annual growth, but failed to make normal growth in height. A safe rate of utilization was estimated to be about 60 percent on these

sites and only 50 percent on poorer sites. Trlica et al. (1977) reported slow recovery after three defoliations of 90 percent. Buwai and Trlica (1977) found that defoliation during the latter part of the growing season was more detrimental than the same treatment applied earlier, at a time when regrowth was still possible. McConnell and Smith (1977) report that browse production per acre increased for the short term with heavy grazing in spring and summer, but then declined due to the premature death of many plants.

Bitterbrush is host to a variety of insects (Furniss and Barr 1975), the most harmful of which is the western tent caterpillar (*Malacosoma californicum*) whose larvae eat the leaves. The seasonal feeding period of the insect coincides with the period of maximum vulnerability of the plants, and two consecutive defoliations can kill plants whose vigor has already been lowered by heavy grazing or other factors (Clark 1956). A number of insects, including thrips and gall midges, reduce seed production of bitterbrush by feeding on the buds and flowers (Ferguson et al. 1963, Furniss and Barr 1975).

*Purshia* is more resistant to herbicides such as 2,4-D and 2,4,5-T than are most species of *Artemisia*. This differential response has been utilized in attempts to kill sagebrush in mixed stands without harming the bitterbrush. Results have been mixed. Blaisdell and Mueggler (1956b) in eastern Idaho obtained high rates of killing on big sagebrush with only minor damage to associated bitterbrush. Hyder and Sneva (1962) found a more critical situation under drier conditions in eastern Oregon. Damage to bitterbrush varied considerably with different treatments, but was least with light applications of 2,4-D made early in spring when new leaves of bitterbrush and sagebrush were first appearing. Mortality was highest for young bitterbrush plants under 30 cm (12 inch). Growth stage of bitterbrush, duration of favorable growing conditions after treatment, and age of the plants were the principal factors determining the effects of herbicide application.

Much less information is available for *P. glandulosa*. It is rated as a valuable browse species, though less palatable than *P. tridentata* (Sampson and Jespersen 1963). Its phenology is similar to that of the latter species. Desert bitterbrush sprouts readily after burning, and is valuable for restoration of seriously disturbed sites because of its sprouting ability and low soil fertility requirements (Blauer et al. 1975).

### *Amelanchier* (Serviceberry)

Two species, *A. alnifolia* (Saskatoon serviceberry) and *A. utahensis* (Utah serviceberry), occur in and adjacent to the sagebrush-grass region. *Amelanchier alnifolia* is a variable species, with five poorly defined varieties, three of which (vars. *alnifolia*, *humilis* and *cusickii*) occur in the area covered by this review (Hitchcock and Cronquist 1974). The varieties have rarely been recognized by investigators, so little is known of their ecological significance. In Idaho,

var. *alnifolia* seems to be widespread, while var. *humilis* is restricted to drier sites, and var. *cusickii* mainly to riparian situations.<sup>2</sup>

*Amelanchier alnifolia* occurs throughout western North America, and occupies a wide variety of habitats in the sagebrush-grass, mountain brush, pinyon/juniper and ponderosa pine regions (Hitchcock and Cronquist 1974, Blauer et al. 1975). *Amelanchier utahensis* has a more restricted range, occurring mainly in the Inter-mountain areas of Idaho, Oregon, Nevada, Utah and Colorado, also in New Mexico and northern Arizona (Yake and Brotherton 1979). It tends to occupy drier habitats than *A. alnifolia*. Both species are usually minor constituents of the communities in which they occur (Blauer et al. 1975).

The importance of *Amelanchier* lies in its wide distribution and high forage value. Both species are highly palatable to native herbivores, and are eaten readily by sheep and cattle (USDA Forest Service 1937, Hemmer 1975, Blauer et al. 1975). It is a deciduous shrub, attaining heights of 1 to 5 m (3-16 ft) depending on site quality and grazing pressure. It reproduces both by seed and vegetatively by root sprouting. Ages of 50 to 85 years are attained where the plant is climax, but less where the plant is seral as it often is in forest or woodland types (Hemmer 1975, Blauer et al. 1975).

The aerial portions of *Amelanchier* are easily destroyed by fire, but survival usually occurs through root sprouting (Stanton 1974). Light clipping or grazing stimulates growth, and full vigor can be maintained under a use rate of 60 percent in fall or winter. Clipping in spring and summer is more harmful, with a safe use rate of 40 to 50 percent indicated (Young and Payne 1948, Shepherd 1971).

Both species of *Amelanchier* occur sparingly in sagebrush-grass vegetation, mainly in communities dominated by *Artemisia tridentata* subsp. *vaseyana*, but are found also on rocky areas in more xeric sagebrush types.

### *Cercocarpus ledifolius* (Curlleaf mountain-mahogany)

*Cercocarpus ledifolius*, unlike *Amelanchier*, is rarely found growing in sagebrush-grass communities, but occurs in adjacent areas, often occupying a zone between sagebrush and coniferous vegetation. This species occurs throughout the Intermountain region from southern Oregon east through Montana and Wyoming, and south to Arizona and California. Two varieties, *ledifolius* and

*intercedens* are recognized (Hitchcock and Cronquist 1974), but no ecological differences between varieties are indicated in the literature.

*Cercocarpus ledifolius* is an erect evergreen shrub or small tree, attaining heights of 6 m (20 ft) on favorable sites. It reproduces primarily by seed, but sprouts to some extent from the base of the trunk after cutting, though rarely after fire. Seedlings are produced in considerable numbers, but mortality is high due to seasonal drought and grazing by rodents and rabbits (Scheldt 1969). Larger plants are utilized mainly by big game, especially deer to whom this species is highly palatable. Utilization by domestic livestock is light (Scheldt and Tisdale 1970, Duncan 1975, Blauer et al. 1975).

Curlleaf mahogany occurs mainly on rocky and immature soils. Fire tends to kill most existing plants, and restocking occurs mainly from seed. Susceptibility to fire may have kept *C. ledifolius* from occupying sites with deeper, less rocky soils (Dealy 1975). There is no evidence, however, of mass invasion into sites previously occupied by sagebrush-grass as in the case of *Juniperus occidentalis* (Burkhardt and Tisdale 1969, 1976).

The response of *C. ledifolius* to clipping or grazing differs from that of many other shrubs. Grazing of larger plants usually results in greatly diminished regrowth of the lower branches, and most of the potential forage is produced on the upper part of the plant, out of reach of grazing animals. Thompson (1970) reports that forage production from such plants can be greatly increased by topping, provided this is done in early spring or fall. Plants grazed heavily while still small assume a rounded form and appear to withstand browsing much like bitterbrush (Garrison 1953, Scheldt and Tisdale 1970, Blauer et al. 1975).

Curlleaf mahogany is affected by a number of insects, the most important being the mountain-mahogany looper (*Anacamptodes clivinaria*). Normal populations of this insect are small and cause little damage, but occasional outbreaks occur. A 3-year outbreak in southwestern Idaho killed 50 percent of the *Cercocarpus* plants in a 6000-acre stand (Furniss and Barr 1975).

### *Prunus* (Wild cherry)

Two species of *Prunus*, *P. emarginatus* (bittercherry) and *P. virginiana* var. *melanocarpa* (western chokecherry) occur in and adjacent to the sagebrush region. Both species range throughout most of western North America (Hitchcock and Cronquist 1974). They occur along with *Amelanchier*, *Purshia*, etc., in mixed stands in the mountain brush region, but also form relatively pure stands on limited areas. Within sagebrush-grass vegetation, *Prunus* usually occurs in the form of scattered plants, associated with the more mesic *Artemisia* communities (Roberts 1971).

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Neither species has received much study, although it is recognized that both are eaten readily by native herbivores and to a lesser extent by domestic livestock. The leaves and young shoots of *P. virginiana* are poisonous to livestock, due to containing a precursor of hydrocyanic acid. Technically, the plants are toxic throughout spring and summer, but due to relatively low palatability animals rarely eat enough to be affected. Wildlife seem to be immune (USDA Forest Service 1937).

Both species propagate by seed and vegetatively by root suckers, with the latter method most common. They sprout readily after cutting or burning (Roberts 1971, Wright et al. 1979). They can be seral in forest habitats, but stands in mountain brush areas appear to be relatively stable (Roberts 1971).

### *Symphoricarpos* (Snowberry)

Two species, *S. oreophilus* (mountain snowberry) and *S. albus* (common snowberry) have a wide range in western North America. *Symphoricarpos oreophilus* is more common in the sagebrush region, however, and occurs in several of the more mesic communities with *Artemisia tridentata* subsp. *vaseyana* (Schlatterer 1972, Hironaka and Fosberg 1979). It is also common in several communities of the mountain brush region (Schlatterer 1972).

*Symphoricarpos albus* appears to be marginal in the sagebrush region, occurring mainly in the northern portion, and more closely related to the Pacific Northwest bunchgrass vegetation where it occurs with *Festuca idahoensis* (Daubenmire 1970).

Both species of *Symphoricarpos* are erect, deciduous shrubs which grow to heights of 50 to 150 cm (20-60 inch). Little has been published concerning their ecology. The only detailed study of a member of this genus is that by Pelton (1953) on *S. occidentalis* in Minnesota. Both *S. albus* and *S. oreophilus* reproduce by rhizomes as well as by seed. Both resprout after fire or cutting, but *S. oreophilus* is a weak sprouter and is harmed by fire (Blaisdell 1953, Wright et al. 1979). Both species are eaten fairly readily by deer, elk and sheep, but less by cattle (Sampson and Jespersen 1963). Morris et al. (1962) rate *S. oreophilus* highest in grazing value of the four species of *Symphoricarpos* which occur in Montana, including *S. albus*.

### *Agropyron spicatum* (Bluebunch wheatgrass)

This is the most abundant and widespread perennial grass of the sagebrush region and the most important economically. Relatively little variability of a morphological nature has been reported in this species. Hitchcock and Cronquist (1974) recognize two varieties, *spicatum* and *pubescens*, but regard these as little more than geographical races distinguished only by differences in pubescence of the

vegetative parts. The presence or absence of awns on the lemmas has been given taxonomic status in the past, the awnless form having been called *A. inerme* (Hitchcock and Chase 1951) or *A. spicatum* var. *inerme*. Due to the variability of this character, and to the lack of other morphological differences (Daubenmire 1939, Chapman and Perry 1973), most authorities now consider both awned and awnless plants to form one taxon, *A. spicatum*. Ecological significance may be associated with the awn character, however, for Passey and Hugie (1963c) found that in southern Idaho awnless populations were confined to the more mesic sites, while awned plants occupied drier areas. In most of British Columbia awnless plants dominate under all situations (Tisdale 1947).

*Agropyron spicatum* has a wide geographic and ecological range, and occurs throughout western North America east of the Cascades and Pacific coastal mountains. It is an important constituent of the Pacific Northwest bunchgrass, mountain shrub, pinyon/juniper and ponderosa pine regions along with the sagebrush vegetation. It is a long-lived perennial which usually forms distinct bunches, but populations with short rhizomes occur in the more mesic habitats. This characteristic is found in the sagebrush region (Passey and Hugie 1963a) and appears to be heritable (Daubenmire 1960). The existence of other forms of ecotypic variation is suggested by its occurrence over a wide range of habitats. DeWitt (1969) found striking differences in rate of seedling root growth in populations of *A. spicatum* from 51 source locations in nine western states and two Canadian provinces. There were also significant differences among sources in growth response at different soil temperatures. Further study will probably reveal additional genealogical variability, which enables this species to thrive in so great a variety of habitats.

*Agropyron spicatum* reproduces by seed, and seed production varies greatly by years depending primarily on precipitation. Harris (1967) reported a germination rate of 53 percent in the laboratory and 16 percent under field conditions in southeastern Washington. Germination occurred in the fall, but it is likely that some seeds can remain dormant over winter and germinate in the spring. The seedlings are slow growing in their first year and appear less vigorous than those of competing species such as the annual *Bromus tectorum*. Harris (1967, 1970, 1977) found that although *A. spicatum* and *B. tectorum* plants germinated at the same time in the fall, root growth of the brome was much greater over winter. As a result, the annual was able to compete better for soil moisture during the following growing season.

Once established, *A. spicatum* is a highly drought tolerant, long lived species, well adapted to the various habitats occupied. In areas where significant fall rains occur, new leaf growth in that season may attain heights of

12 to 25 cm (5-10 inch) (Harris 1967, Evans and Tisdale 1972). Growth resumes in early spring and proceeds rapidly while soil moisture is abundant. Blaisdell (1958) found that vegetative growth of *A. spicatum* was generally completed by the end of May. Flowering occurred in late June and seed was ripe and shedding by late July, but plants were not fully dried until mid-August. Growth development was a few weeks earlier at lower elevations (Evans and Tisdale 1972, Daubenmire 1972), but in all cases *A. spicatum* fully utilized the period of the year when soil moisture was available.

The root system of *A. spicatum* is characterized by primary roots which grow to depths of 1 to 1.5 m (3-5 ft) depending on soil conditions, and by adventitious roots which spread laterally from the root crown for distances of 20 to 30 cm (8-12 inch) before turning downward (Hanson and Stoddart 1940, Harris 1967). Thus a single root system occupies a considerable volume of soil from surface to maximum root depth.

*Agropyron spicatum* occurs under an exceptionally wide range of climatic and soil conditions. The precipitation range is from about 18 to 76 cm (7-30 inch) annually, with temperatures varying greatly due to an altitudinal range of 150 to 2400 m (500-8000 ft) or more. Soils vary greatly in texture, depth, etc., but tolerance to soil salinity is low (Dewey 1960, Daubenmire 1970).

The primary biotic factors affecting *A. spicatum* are herbage removal by animals and damage by fire. The effects of the former have been studied extensively (Stoddart 1946, Blaisdell and Pechanec 1949, Wilson et al. 1966). These workers found that *A. spicatum* is highly sensitive to clipping especially in the late sheath or head emerging stages. Reserve carbohydrates are at their lowest point during these stages, and opportunities for regrowth are small in areas of summer drought. Herbage production of *A. spicatum* is severely reduced by even 1 year of such treatment and repetition for 2 or 3 consecutive years kills most plants. Mueggler (1975) found that the recovery of *A. spicatum* plants whose vigor had been reduced by clipping was a slow process, requiring as much as 6 years to regain normal vigor. *Agropyron spicatum* is more tolerant to the effects of fire than to those of clipping. Blaisdell (1953) and Mueggler and Blaisdell (1958) found that burning of sagebrush-grass stands reduced the yield of this grass for the first year after burning, but yields were increased by the third year. Pechanec et al. (1965) and Wright et al. (1979) reported that fires in late summer or fall when *A. spicatum* is mature were less damaging than fires earlier in the season. Uresk et al. (1976) found an increase in leaf and culm production the first year following a late summer fire. Conrad and Poulton (1966) found significant reduction in basal area but no mortality following a fire in mid-summer. Plants in the ungrazed portion of the site were damaged more than grazed plants, presumably due to greater intensity of fire where more fuel was available.

### *Festuca idahoensis* (Idaho fescue)

This species is important in the sagebrush-grass region due to its wide range, abundance and good forage value. The only subspecific units recognized are var. *oregona* which occurs in subalpine to alpine areas from Washington to California, and var. *idahoensis* which occurs over the range of the species. No ecological significance has been established for these varieties. Dwarfed plants at high elevations in the Rocky Mountains are sometimes confused with *F. ovina* (Mueggler and Stewart 1980).

*Festuca idahoensis* occurs in a wide variety of habitats, and is an important species in the Pacific Northwest bunchgrass, mountain shrub, pinyon/juniper and ponderosa pine regions as well as the sagebrush-grass. In the latter, it is abundant mainly in the moister and/or cooler portions of the region, occurring to elevations of 2730 m (9000 ft) (Hironaka and Fosberg 1979). It is commonly associated with *A. tridentata* subsp. *tridentata* and *vaseyana*; and with *A. tripartita* and *A. arbuscula*. This grass is moderately drought resistant, but less tolerant of high summer temperatures than *A. spicatum* (Hironaka 1963, Daubenmire 1972, Hironaka and Fosberg 1979).

Ecotypic variation in *F. idahoensis* has been shown by Tisdale (1959, 1961), who studied 18 populations collected from a wide range of habitats. Heritable differences in survival, phenology, height, culm and seed production were found among these populations when grown under uniform conditions.

Idaho fescue is a perennial bunchgrass which propagates strictly from seed. Culms are abundant under favorable conditions and apparent seed production is high, but the percentage of filled caryopses is usually no more than fifty. Laboratory germination of filled seeds exceeded 50 percent for most populations, and ranged from 30 to 94 percent (Tisdale 1959). The seasonal growth development of *F. idahoensis* is similar to that of *A. spicatum* with which it is often associated. Vegetative growth begins in the fall when moisture and temperature conditions are suitable and resumes in early spring. Dates of flowering, seed ripening and shedding are 1 to 2 weeks earlier than in *A. spicatum* (Mueggler 1972a).

The results of clipping *F. idahoensis* plants show the same general response as for *A. spicatum*, the degree of injury depending on both time and intensity of clipping (Pond 1960, Mueggler 1972b, 1975). The fescue was less sensitive to the effects of clipping, however, and recovered vigor more rapidly, requiring about 3 years from low to full vigor compared with 6 years for *A. spicatum*. Pond (1960) showed that the detrimental effects of grazing Idaho fescue were greater in stands growing on granitic soils than for those on sedimentary soils. Both authors found leaf height to be a reliable index of vigor for this species.

Idaho fescue is less tolerant to fire than many grasses, including *A. spicatum*. Blaisdell (1953) and Mueggler and Blaisdell (1958) found that Idaho fescue was among the most severely injured species in stands of sagebrush-grass subjected to burning. Yields of fescue had not fully recovered in 12 to 15 years in some cases. Doubtless part of this injurious effect was due to competition from other herbaceous species which increased in 2 or 3 years after burning. Conrad and Poulton (1966) recorded a mortality of 25 percent and reduction of basal area of 50 percent for Idaho fescue 1 year after a mid-summer fire. Comparable damage to *A. spicatum* was only 1 and 29 percent. Burning is least damaging to *F. idahoensis* in spring or fall under conditions of adequate soil moisture (Wright et al. 1979).

### *Poa sandbergii* (Sandberg bluegrass)

This species is abundant and widespread in the sagebrush-grass region, but because of its low stature and short season of growth is less important than the larger bunchgrasses discussed previously. *Poa sandbergii*, erroneously called *P. secunda* for many years, occurs widely in western North America, including the Great Plains. It is a highly variable species, but no taxonomic subdivisions have been established for it (Hitchcock and Cronquist 1974). Ecotypic variation occurs, but data on this aspect are extremely limited. Daubenmire (1970) reports instances of two or more populations which differ in morphology and phenology occurring in the same habitat. Hironaka and Tisdale (1973) studied two populations, one from a relatively mesic sagebrush-grass habitat and one from a drier site. These populations differed in phenology and stature when grown in a common environment, but also showed great intra-population variability.

*Poa sandbergii* is a low-growing perennial bunchgrass which is notable for early growth and short season of vegetative activity. Blaisdell (1958) found that this species began growth about 1 week earlier in the spring than *A. spicatum* and other associated grasses, flowered and ripened seed 3 weeks earlier, and became dried 5 weeks earlier. Laude (1953) and Hironaka and Tisdale (1972) found that summer dormancy is induced by a long photoperiod and high temperatures, not by lack of soil moisture. Fall leaf growth occurs in many habitats. Reproduction is entirely by seed, which is produced in significant amounts most years. Germination of 50 percent was obtained by Hironaka and Tisdale (1972) following an after-ripening period of about 3 months.

No data on the effects of clipping on *P. sandbergii* have been found in the literature. The effects of fire are better documented (Blaisdell 1953, Wright and Klemmedson 1965, Daubenmire 1975b). In these studies *P. sandbergii* was damaged little by fire and usually increased during the next few years.

*Poa sandbergii* is found in a large number of habitat types in the sagebrush-grass region, but is best represented in the drier portions of the region (Hironaka and Fosberg 1979).

### *Stipa* (Needlegrass)

Four or five species of *Stipa*, depending on taxonomic interpretation, occur commonly in the sagebrush-grass vegetation. *Stipa comata* (needle-and-thread) and *S. thurberiana* (Thurber needlegrass) are common in the drier parts of the region. *Stipa occidentalis* (western needlegrass), *S. columbiana* (Columbia needlegrass), and *S. lettermanii* (Letterman needlegrass) occur in cooler, moister areas. All are native perennial bunchgrasses.

*Stipa comata* is characterized by long awns and a sharp callus on the seed. Two varieties are recognized, var. *comata* with the terminal section of the awn flexuous and curved and var. *intermedia* in which this awn segment is firm and nearly straight (Hitchcock and Cronquist 1974, Cronquist et al. 1977). Identification of *S. comata* to variety has been uncommon in ecological literature, but the references available indicate that var. *comata* is the most common, with var. *intermedia* restricted to relatively moist sites (Hironaka and Fosberg 1979). *Stipa comata* is dominant in the mixed prairie of the Great Plains, and is the most common needlegrass of the sagebrush region (USDA Forest Service 1937, Cronquist et al. 1977).

The most complete data on phenology are those of Blaisdell (1958). He found that spring growth began in early April at the same time as that of *Agropyron spicatum*. Subsequent development was faster, with seed ripening and shedding in early and late July respectively, nearly 3 weeks earlier than for *A. spicatum*. The fully dried stage for *S. comata* was reached in early August. Reproduction is entirely by seed; dissemination is aided by ready attachment to coats of animals.

*Stipa comata* is fairly susceptible to heavy grazing (USDA Forest Service 1937), although its tolerance may be increased by natural selection for a more prostrate growth form (Peterson 1962). Wright (1967) found that it was damaged more by clipping at the time of seed dispersal than was *Sitanion hystrix*, apparently because the foliage of *Stipa* was still green and photosynthetically active, while that of *Sitanion* was dry and dormant. A similar difference in reaction occurred with respect to fire in summer (Wright and Klemmedson 1965, Wright 1971).

*Stipa comata* is a dominant in several habitat types of the sagebrush region, in association with all three subspecies of *Artemisia tridentata* (Tueller and Blackburn 1974, Hironaka and Fosberg 1979). Only the variety *intermedia* occurs with *A. tridentata vaseyana* (Winward 1970). In these situations where *S. comata* is the climax dominant, the sites are edaphically distinct. The soils are coarse

textured (sandy loam to loamy sand) and fairly deep. This relationship has been reported from other parts of the sagebrush region (Daubenmire 1970, Parsons et al. 1971).

*Stipa comata* acts as a decreaser under heavy grazing on sandy sites, but it may behave as an increaser on areas of comparable climate but finer textured soils (Tueller and Blackburn 1974, Hironaka and Fosberg 1979, Mueggler and Stewart 1980).

*Stipa thurberiana* is distinguished by shorter glumes, lemmas and awns than *S. comata*, and by the plumose hairs on the awns. Although widely distributed in the sagebrush region (Cronquist et al. 1977), this grass occurs mainly as a lesser associate of species such as *Agropyron spicatum*, and is recorded as a dominant in only one habitat type with *Artemisia tridentata wyomingensis* (Hironaka and Fosberg 1979).

Literature on the ecology of *S. thurberiana* is sparse. The phenology appears similar to that of *S. comata* (authors' observations). The species is palatable to livestock, (Uresk and Rickard 1976) and responds to heavy grazing as a decreaser, recovering slowly on sites where it has been depleted (Hironaka and Tisdale 1963, Tisdale et al. 1969). Reaction to 2 years of spring use of 50 percent utilization included a 21 percent reduction in leaf length but no decline in basal area such as was experienced by *Agropyron spicatum* (Rickard et al. 1975). *Stipa thurberiana* is readily damaged by fire during the summer season (Uresk et al. 1976, 1980) and behaves much like *S. comata* in being vulnerable to fire before the plants become fully dormant (Wright and Klemmedson 1965).

The habitat factors involved in sites dominated by *S. thurberiana* include climate with annual precipitation of about 25 cm (10 inch) and coarse-silty soils with deep poorly defined horizons, low content of organic matter in the "A" horizon, and a lime-silica hardpan at 37 to 50 cm (15-20 inch) (Hironaka and Fosberg 1979). The species occurs in lesser amounts on a wider range of soils, including shallow, fine-textured sites where it grows with *Artemisia longiloba* (Tisdale et al. 1965).

*Stipa occidentalis*, *S. columbiana*, and *S. lettermanii* are species associated with the higher, cooler portions of the sagebrush region, but are widely distributed within these portions (Hitchcock and Cronquist 1974, Cronquist et al. 1977). *Stipa occidentalis* and *S. columbiana* belong to a highly variable complex taxonomically. Cronquist et al. (1977) recognize both as valid species, but Hitchcock and Cronquist (1974) treat *S. columbiana* as var. *minor* of *S. occidentalis*. The plants of this group and *S. lettermanii* are similar in many respects and distinguished mainly by differences in the structure of the seed callus, length, and pubescence of awns and other floral characters. *Stipa lettermanii* commonly extends to higher elevations, and subalpine forms of it are commonly shorter and more slender than those of the *S. occidentalis* group.

All three species occur in several habitat types of the sagebrush region, usually in association with *A. tridentata vaseyana* or *A. vaseyana spiciformis* and often with *Symphoricarpos oreophilus* also. These grasses occur commonly, but not as climax dominants and in most cases they act as increasers with heavy grazing (Schlatterer 1972, Hironaka and Fosberg 1979).

### *Sitanion hystrix* (Squirreltail)

This perennial bunchgrass is common in the drier parts of the sagebrush-grass region. It is important mainly as a seral species of fair forage value which exceeds climax grasses such as *A. spicatum* in ability to increase rapidly in depleted stands once grazing pressures are reduced (Hironaka and Tisdale 1963, 1972).

*Sitanion hystrix* is widely distributed in the western United States and far western Canada. It is recognized as a variable species and its taxonomic treatment has differed among authorities. Wilson (1963) described two varieties, *hystrix* and *californicum*. Variety *hystrix* was considered to occupy the drier parts of the species range; *californicum*, a taller, later developing variety, occurred in the less arid portions. Hitchcock and Cronquist (1974) recognized three varieties, *brevifolia*, *hordeoides* and *hystrix*, and included var. *californicum* in variety *hystrix*. Cronquist et al. (1977) recognized var. *californicum* and described it as "mid-elevation to arctic-alpine" compared with lower elevation habitats for the other varieties.

Hironaka and Tisdale (1972, 1973) found differences in phenology, stature and productivity between two populations, one from a dry sagebrush-grass habitat and the other from a less arid area. These populations were identified as vars. *hystrix* and *californicum*, respectively, according to Wilson's (1963) classification. Clary (1975) found significant differences in phenology and production among 12 populations collected from seven states in the west and southwest, but failed to classify his material to varietal level.

The phenology of *S. hystrix* has received little study. In southwestern Idaho an experimental field planting provided a comparison between an early developing and a late developing population (Hironaka and Tisdale 1972). In the earlier population, leaf growth was well started by the first of April, the sheath stage occurred by early May, flowering by the end of May, seed ripe by late June and shedding by early July. The later population started leaf growth almost as early but developed less rapidly, so that subsequent growth stages were all about 2 weeks later. By mid-July the plants of the earlier variety had dried and gone into summer dormancy, the usual condition for this species in the drier parts of the sagebrush-grass region (Wright and Klemmedson 1965). This is a shorter growth period than that of *A. spicatum* and only 1 to 2 weeks longer than that of *P. sandbergii*. Seed is produced in abundance most

years, and germination occurs rapidly and at high rates under a wide temperature range (Young and Evans 1977).

In the field, seed of *S. hystrix* germinated in the fall when moisture conditions were favorable, otherwise this occurred in the spring. Seedlings which started in fall resumed growth in March, and grew rapidly until soil moisture became deficient in mid-summer (Hironaka and Sindelar 1973). This early and vigorous aerial growth, plus the ability of the root system to continue growth at low temperatures during winter enables *S. hystrix* to compete successfully with aggressive annuals such as *Bromus tectorum* and *Taeniatherum asperum* (medusahead). *Sitanion hystrix* greatly exceeds *A. spicatum* and other climax grasses of the sagebrush-grass region in reproductive ability under these conditions (Hironaka and Sindelar 1975). This ability, plus the ready dispersal of the seed heads by wind, make it a successful species for increasing on depleted ranges (Hironaka and Tisdale 1963, Hironaka and Sindelar 1973). Although it has only moderate longevity (5-7 years) this grass is able to maintain a stand over a long period of years due to its strong reproductive ability.

Wright (1967) found that *S. hystrix* was affected most by clipping in the sheath and flowering stages, and much less by clipping in later growth stages. This species is little damaged by burning. No mortality and only moderate reduction in basal area occurred in plants burned in July, even less damage occurred from burning in August when the plants were fully dried (Wright and Klemmedson 1965).

### ***Bromus tectorum* (Cheatgrass, Downy brome)**

Although this grass is introduced, and an annual, it has become so widespread and abundant that it now ranks among the major herbaceous species of the sagebrush-grass region. Two reviews of information on cheatgrass are available (Ibrahim 1957, Klemmedson and Smith 1964). *Bromus tectorum* is a well defined species, and no subspecific categories are recognized (Hitchcock and Cronquist 1974). A southern European species, it was introduced into North America in the latter part of the 19th Century and has spread until it occurs over the whole western part of the continent. It has become dominant on millions of acres in the sagebrush-grass and Pacific Northwest bunch-grass regions due to disturbance by cultivation, fire or excessive grazing (Stewart and Hull 1949, Klemmedson and Smith 1964). Ecotypic variation in *B. tectorum* noted by Hulbert (1955) included differences in phenology and winter survival, but no comprehensive study of intraspecific variability has been reported. *Bromus tectorum* occupies a wide range of habitats within the sagebrush-grass region and occurs in most of the habitat types described to date. It tends to be extremely persistent, especially in drier sagebrush-grass communities (Daubenmire 1975b, Cline et al. 1977b).

Cheatgrass usually acts as a winter annual, the seed germinating in early fall when moisture becomes available. Germination can also occur in the spring, but the plants so produced are usually less numerous and vigorous and emergence is slow (Hull and Hansen 1974). Fall germinated plants resume activity in early spring when they grow and develop rapidly. Flowering occurs in early May, seed is ripe by early June and the plants are fully dried in 1 or 2 more weeks (Klemmedson and Smith 1964). These dates are about 6 weeks earlier than corresponding stages in *Agropyron spicatum*. Height growth and standing crop are highly variable from year to year, much more than with perennial grasses (Hull and Pechanec 1947, Murray 1971).

The seeds become viable shortly after maturity and germinate at high rates (up to 95 percent) in a week under favorable moisture conditions (Hulbert 1955, Hull and Hansen 1974). *Bromus tectorum* is a prolific seed producer and generally produces ample seed to maintain stands even in unfavorable years.

Seedling establishment is favored by presence of plant litter and rough microtopography (Evans and Young 1970, 1972). The root system develops rapidly and has remarkable ability to continue growth under low temperatures. It continues to develop over winter while aerial growth is dormant (Harris 1967, 1970). The roots reach depths of 1 m (39 inch) or more, with laterals extending as much as 30 cm (12 inch) (Hulbert 1955, Hironaka 1961). Total soil moisture utilization is lower, however, than for comparable sites dominated by *Artemisia tridentata* and *A. spicatum* (Cline et al. 1977a).

Cheatgrass is palatable in its earlier growth stages. It appears to be less affected by clipping than many of the associated perennial grasses. Flemming et al. (1942) and Hulbert (1955) found that plants clipped in the sheath or flowering stages produced new inflorescences in a few weeks, although herbage production was much reduced.

Due to its early and complete drying and fine structure, *B. tectorum* is extremely flammable, and the danger of fire is increased enormously on areas dominated by it (Klemmedson and Smith 1964). The majority of wildfires in the sagebrush-grass region occur on areas where cheatgrass is abundant. Since the seeds of this species are usually shed before the fire, reduction of the stand in the following year is generally not great (Billings 1951, Wright et al. 1979). Fires in June were found to cause significant reduction in subsequent stands (Stewart and Hull 1949), but fires are much less frequent so early in the season. The amount of unburned organic matter remaining on the soil is a good index of the potential population following fire (Young et al. 1976).

*Bromus tectorum* is sensitive to several herbicides, especially when these are applied before or just after seedling emergence (Evans et al. 1970a).

## COMMUNITY CHARACTERISTICS

Consideration of community characteristics of the sagebrush region could be interpreted to include an enormous range of information. The present treatment is focused on the natural vegetational aspects of the ecosystems concerned, including their reaction to major disturbance factors, cultivation, fire and grazing. No attempt has been made to cover fully topics such as range manipulation, reseeding, wildlife-livestock relationships or hydrologic relations.

### Extent and Stability

The sagebrush-grass ranks as one of the major vegetation regions of western North America and occupies large areas in eastern Oregon and Washington, southern Idaho, northern California, Utah, Nevada, western Montana, Wyoming and Colorado. Smaller outliers of this type occur in northern Arizona and New Mexico, and in southwestern Canada (British Columbia, Alberta and Saskatchewan).

Estimates of the total area occupied have varied greatly, reflecting differences in criteria used and also the lack of a comprehensive survey. An early and widely quoted estimate of 38 M ha (95 M acres) made by the USDA Forest Service is obviously low. Beetle's (1960) estimate of 109 M ha (270 M acres) seems high, and apparently was based on total distribution of the sagebrush species rather than the area in which they occurred (or have occurred) as dominants. The figure of 58 M ha (143 M acres) derived by Branson et al. (1967) from Kuchler's (1964) vegetation map may be closer to the actual area, although West (1979) calculated 69 M ha (170 M acres) for just the Great Basin and Colorado Plateau sections. Kuchler's (1964) delineation of the sagebrush region necessarily represents a compilation of estimates from various sources. A new source now available in the form of satellite imagery should provide a more accurate figure than has been available previously (Hironaka et al. 1976).

In addition to differences concerning the extent of the sagebrush region, there has been disagreement concerning the extent to which its boundaries may have been changed since European settlement. Several authorities including Clements and Clements (1939) and Shantz and Zon (1924) considered that much of the area currently occupied by sagebrush-dominated vegetation was grassland at the time of white settlement. The sagebrush invasion was considered to have been most marked in the northern part of the Intermountain region. For example, Shantz and Zon (1924) in their map of vegetation types show an extensive belt of grassland extending around the southern end of the central mountain mass in Idaho and separating the sagebrush-grass from forest communities. This view of the sagebrush-grass region is still evident in the literature (Weaver and Clements 1938, Stoddart and Smith 1955, Stoddart et al. 1975, Barbour et al. 1980). It was supported by several researchers including Cottam and Stewart

(1940), Stoddart (1941), Cooper (1953), Christensen and Johnson (1964), and Hull and Hull (1974). These studies showed that sagebrush can invade grassland stands on sites where the water table has been lowered by abusive land use. They also indicated that plant communities resembling Pacific Northwest bunchgrass may occur in the foothills of northern Utah. In the latter instance the issue seems partly one of definition, for Christensen's (1963) description of "undisturbed bunchgrass communities" lists *Artemisia tridentata* as second only to *Agropyron spicatum* in foliage cover and constancy.

Basic to the idea of massive sagebrush invasion of grasslands was the well-known fact that most species of sagebrush are considerably less palatable to domestic livestock than are the grasses associated with them (USDA Forest Service 1936). The high susceptibility of most sagebrush species to fire was overlooked or minimized, as was the fact that a sagebrush-grass stand can be converted, at least temporarily, into one that closely resembles true grassland.

In recent years, more intensive studies have led to a different view, namely that the sagebrush-grass region is ecologically stable and that its boundaries closely resemble those which existed at the beginning of settlement by European peoples. This idea is supported by historical records and by studies of existing vegetation. The historical record, contained in the reports of early explorers and travelers (Townsend 1834, Fremont 1845, Watson 1871, Merriam 1890, Wislizenus 1912), portrays the dominance of sagebrush over vast areas of the Intermountain West (Tisdale et al. 1969). Vale's (1975b) review of historical references also supports the view that the boundaries of the sagebrush region were about the same in those early days as they are now. Egger (1941), from his studies of primary succession on volcanic deposits in southern Idaho, concluded that the regional climax vegetation was sagebrush-grass.

More recent field research has supplied evidence from quantitative studies of sagebrush-grass vegetation, undertaken by a number of investigators beginning in the 1950's. Study of sites relatively undisturbed by fire, abusive grazing or cultivation, and comparison of these with adjacent disturbed stands have been a basic technique. Research on the soils of the region and their relation to vegetation has also brought new understanding (Anderson 1956, Fosberg and Hironaka 1964, Passey and Hugie 1963a). Publications resulting from vegetational studies of this type include those of Poulton (1955), Blaisdell (1958), Eckert (1958), Marquiss and Lang (1959), Thatcher (1959), Passey and Hugie (1962b), Tisdale et al. (1965, 1969), Daubenmire (1970), Harniss and West (1973), Zamora and Tueller (1973), Young et al. (1977), Hironaka and Fosberg (1979), and Mueggler and Stewart (1980). This research has documented the nature and variety of sagebrush-grass vegetation and indicates that invasion of sagebrush into other plant communities has been relatively uncommon. The opposite kind of change is reported by Poulton (1955) who found

areas in northeastern Oregon where repeated burning had reduced the apparent extent of *Artemisia*-dominated vegetation. It seems likely that reports of "grasslands" in areas now considered part of the sagebrush-grass region were based on similar situations produced by frequent burning and even mowing for hay in the early days of white settlement. Evidence of invasion into sagebrush-grass vegetation in post-settlement time has been reported by several investigators. Most widespread has been the increase of junipers, especially Utah juniper (*Juniperus osteosperma*) (Christensen and Johnson 1964, Blackburn and Tueller 1970); and western juniper (*J. occidentalis*), (Burkhardt and Tisdale 1969). Other invaders reported include white fir (*Abies concolor*) in California (Vale 1975b). Causal factors suggested include overgrazing (Christensen and Johnson 1964, Vale 1975b) and reduction in burning since white settlement (Burkhardt and Tisdale 1976).

In western Montana, however, on the tension zone between the sagebrush-grass and Plains grasslands there seems to be evidence for invasion of sagebrush. Morris et al. (1976) considered many stands dominated by *A. tridentata* subsp. *vaseyana*, and *A. tridentata* subsp. *wyomingensis* to be seral. Overgrazed areas and abandoned fields were the principal areas of sagebrush invasion. Obviously there is need for further study of the successional relationships of sagebrush species, particularly along the borders of the sagebrush region.

### Diversity in the Sagebrush-Grass Region

The great variety of vegetation evident today in the sagebrush-grass region is the result of two major influences, natural differences in habitat and disturbances produced by white settlement.

Natural habitat differences within the region are great, ranging from near-desert to subalpine climates and including a wide variety of physiographic and soil types (Tisdale et al. 1969, Hironaka and Fosberg 1979, K. L. Johnson 1979, West 1979). Environmental diversity has resulted in comparable variety in vegetation, notably through the evolution of species, subspecies and varieties of sagebrush adapted to specific habitats (Beetle 1960, Winward and Tisdale 1977, McArthur 1979, McArthur et al. 1979). The result has been the development of a large number of steady state communities, each dominated by a single taxon of sagebrush. These communities differ greatly in their understory vegetation, which usually includes one or more perennial bunchgrasses: *Agropyron spicatum*, *Festuca idahoensis*, *Poa sandbergii*, *Stipa thurberiana*, *S. comata*, or *Oryzopsis hymenoides*. Communities of this kind have been described by many workers including Blackburn et al. (1968, 1969) in Nevada, Thatcher (1959) and Brodahl (1977) in Wyoming, Mueggler and Stewart (1980) in Montana, Tisdale et al. (1965, 1969), Schlatterer (1972) and Hironaka and Fosberg (1979) in Idaho, Eckert (1958) and Tueller (1962) in Oregon, Daubenmire (1970)

in Washington, Passey and Hugie (1962b, 1963a), Hugie et al. (1974) in Idaho, Nevada and Utah. The nature of the habitats involved is discussed earlier in this review, under the autecology of individual species.

### Classification

Classification of sagebrush-grass vegetation has been a relatively recent endeavor because of lack of basic synecological knowledge (Billings 1952). This was evident in the early classification of range types for the purpose of inventory and mapping. While no attempt was made to subdivide the sagebrush range type, three major range types were recognized from the shadscale zone (Interagency Range Survey Committee 1937). This no doubt was the result of early research on salt desert shrub communities (Kearney et al. 1914, Shantz 1925, White 1932, Flowers 1934, Shantz and Piemeisel 1940). Later, the sagebrush type was subdivided on the basis of growth form, i.e., big and low sagebrush (USDA Forest Service 1969).

The range site classification developed by Dyksterhuis (1949) was adopted agency-wide by the USDA Soil Conservation Service (Shiflet 1973) and in recent years by the USDI Bureau of Land Management (1979). This classification scheme is restricted to nonforest landscapes. Although the basis of this classification is the climax or potential vegetation, much emphasis is placed on site productivity in the climax state, and digression in productivity of the climax species is used as an index to the condition of the vegetation. Nomenclature of range site classification is descriptive of site and not vegetation, however.

Although many field guides of climax vegetation of the sagebrush-grass type were produced by the USDA Soil Conservation Service, the lack of basic synecological information prevented uniform interpretation and application of the range site classification. To overcome this obstacle, a special soil-vegetation team was assigned to identify, classify and describe climax sagebrush-grass communities and their soils (Passey and Hugie 1962a, 1962b, 1963a, 1963b, Hugie et al. 1964, Passey et al. 1964, Hugie et al. 1974). Much of today's range site classification of sagebrush-grass vegetation is based on their findings.

The use of climax vegetation is also the basis of the habitat type classification developed by Daubenmire (1952). Although this classification was developed for forest vegetation, it soon became evident that it was equally applicable to nonforest types. The habitat type classification is a land classification that utilizes the climax vegetation as an expression of the total effective environment. It is defined as the aggregate area that supports or until recent time supported a particular plant association (climax plant community, *sensu* Daubenmire 1952) and is capable of again supporting the same plant association.

Classifications that pertain to the sagebrush-grass vegetation based on the habitat type concept, although not adhering strictly to the discrete community concept (Daubenmire 1966), have been developed for a number of areas in the Pacific Northwest (Eckert 1957, Culver 1964, Smith 1969, Hall 1967, Daubenmire 1970, McLean 1970, Winward 1970, Zamora and Tueller 1973, Lewis 1975, Brodahl 1977, Young et al. 1977, Hironaka 1979, Hironaka and Fosberg 1979, Erhard 1980, Mueggler and Stewart 1980). Tisdale's (1947) work was a forerunner to the development of the habitat type classification.

Recognition of subspecies within *Artemisia tridentata* (Beetle 1960, Beetle and Young 1965) was a major contribution in development of sound habitat type classification for sagebrush-grass vegetation. Prior to the recognition of subspecies of *Artemisia tridentata*, the species was credited with a distributional range from 800 to 10,000 ft in elevation within an 8- to 22-inch precipitation zone. This made it extremely difficult to explain the presence of the same habitat type over such a wide range of environmental conditions.

The habitat type is generally named after the unique combination of dominants or characteristic species in the overstory and understory, distinguishing it from other habitat types. This is not the case with the naming of range sites.

Because the range site and habitat type classification systems are both based on climax vegetation, the two systems are related. The habitat type classification emphasizes the similarity of climax species composition over the landscape, placing variability as secondary in importance. The range site classification considers the importance of productivity equal to species composition. Thus, two stands of essentially the same climax composition may be assigned to different range sites, if their productivity is deemed significantly different. The habitat type may include more than a single range site, whereas the contrary is not true. The range site may be likened to a "phase" of a habitat type. The difficulty with the "phase" subdivision is that it has not been specifically defined. It is generally understood to be a variant of the habitat type and is often identified by the presence or absence of one or few diagnostic species (Hall 1967, Culver 1964, Daubenmire 1970, Pfister et al. 1977, Mueggler and Stewart 1980) and/or soil differences.

A classification of climax communities (habitat type or range sites) is essential as a reference base, but is of limited value by itself because relatively few examples of climax stands remain in most sagebrush communities. What is needed is a classification of disturbed communities associated with each habitat type for maximum utility. If the habitat type and its attendant seral communities were known, this would provide the basic framework of a sound, usable information storage and retrieval system for land management purposes (Hironaka and Fosberg 1979,

Huschle and Hironaka 1980). Information on seral communities within their respective habitat types could be accumulated and retrieved in terms of response to management, hazards, improvement, etc., in relation to management objectives. It would be a continuing activity with new information added or updated and accessed by community type within habitat type. A scheme of this sort would greatly extend use of vegetational classification information.

## Effects of Disturbance

Superimposed on the natural diversity of sagebrush-grass vegetation are changes produced by disturbances resulting from cultivation, fire, herbicides, excessive grazing, insect attacks, etc. The combined effects of disturbance and natural variability have brought about great changes in botanical composition and productivity of the native communities.

Since the beginning of European settlement, the abundance of many native species has been drastically reduced, and a number of alien species, mostly annuals, have invaded the region (Tisdale et al. 1969, Young and Evans 1970, 1973; Young et al. 1972, 1979). The vegetation of the region appears to have been altered more in the past 100 years than in the previous thousand (Davis et al. 1977).

Changes resulting from the action of disturbance factors have received considerable study, but due to the variability of these factors, and their frequent interaction, interpretation of results is often difficult. A further difficulty arises from the fact that the plant communities under study have often been described inadequately, and not identified to habitat type (Poulton and Tisdale 1961). The various types of disturbance are considered here in terms of their relative effects in changing the composition and decreasing the stability of the natural sagebrush-grass vegetation.

## CULTIVATION

Cultivation is the most drastic of these disturbances, and when continued it eliminates native vegetation completely. Lands once cultivated may later be abandoned, and secondary succession allowed to operate. The principal studies of this process in the sagebrush-grass region are those of Piemeisel (1938, 1945, 1951) in south central Idaho. He traced the succession from annual forbs to domination by *Bromus tectorum* and then to the gradual recovery of perennials, chiefly *Artemisia tridentata wyomingensis* and *Sitanion hystrix*. Hironaka and Tisdale (1963) continued this research and documented the slow return of the two climax grasses, *Stipa thurberiana* and *Poa sandbergii*. The latter species increased in peripheral fashion on the site, indicating limited means of seed dispersal. With *Stipa thurberiana* the difficulty lay in seedling establishment in competition with *Bromus tectorum*, a

situation similar to that reported for *Agropyron spicatum* (Harris 1967). Apparently the complete recovery of a cultivated area is likely to require a half century or more, at least in the xeric type noted above. A minimum of 40 years is required for reestablishment of sagebrush communities on abandoned crop land in eastern Wyoming (K. L. Johnson 1979).

## FIRE

Fire, in contrast to cultivation, is a highly selective agent in sagebrush vegetation. The common species of sagebrush, with the exception of *Artemisia cana* and *A. tripartita*, are readily killed by fire, while many of the understory species and some associated shrubs are relatively resistant. The result of burning a sagebrush-grass community in good range condition is to greatly decrease the amount of sagebrush and to increase most of the understory species plus *Chrysothamnus* and a few other shrubs (Blaisdell 1953, Mueggler and Blaisdell 1958). The effect on understory species is not uniform, for these authors showed that *Agropyron spicatum*, *A. dasystachyum* and other coarse grasses were relatively unharmed by burning, while finer species including *Festuca idahoensis* and some species of *Poa* showed a reduction of yield 12 to 15 years after burning. A long-term (30-year) evaluation of this study by Harniss and Murray (1973) showed that sagebrush (*A. tridentata vaseyana*) had increased to pre-burn cover, while *Chrysothamnus viscidiflorus*, which increased after burning, had returned to its low, pre-burn population. Yields of the coarser grasses had declined from their post-burn maximum, but were still as high as before the burn. Idaho fescue and other fine grasses, along with the fire sensitive forbs, had finally returned to pre-burn levels.

The above case illustrates the results of fire on a relatively pristine stand which was grazed carefully after fire. Similar results probably followed from fires in pre-settlement days, although we do not know much about the incidence of fire in this period. The fact that most sagebrush species are sensitive to fire and that the early explorers found sagebrush abundant in the region (Tisdale et al. 1969, Vale 1975a) suggests that fire was infrequent. On the other hand, Burkhardt and Tisdale (1976) have shown that fire in the sagebrush-grass of the Owyhee foothills in Idaho kept western juniper (*Juniperus occidentalis*) confined to relatively bare, rocky sites until white settlement reduced burning. It is likely that fire was uncommon in the drier sagebrush types but more frequent in the more mesic communities where the fuel supply would be greater. Houston (1973) estimated that fire frequency in *Artemisia vaseyana* communities in Yellowstone National Park was 20 to 25 years. Referring to drier parts of the sagebrush region, Wright et al. (1979) theorize that the probable fire frequency would be about 50 years. Griffiths (1902) reported many range fires set by "nomadic sheepmen" in high elevation sagebrush ranges in northern Nevada and southeastern Oregon.

The effects of fire since white settlement must be considered along with those of heavy grazing. The latter was prevalent over most of the region from the late 1800s to the 1930s or later, and greatly influenced the effects of fire. The combination of fire and overgrazing greatly reduced the population of both sagebrush and the understory species of grasses and the more palatable forbs. The affected areas were thus opened to invasion by various aggressive, less palatable species, especially the introduced *Bromus tectorum* (Pickford 1932, Stewart and Hull 1949). This annual grass is highly flammable, and its presence greatly increased the incidence of wildfire in the sagebrush region (Klemmedson and Smith 1964). The result has been the domination of several million acres of the region by *B. tectorum*, with *Chrysothamnus* the only remaining shrub in most cases. Plant succession on depleted sites may be seriously affected if significant soil erosion occurs following fire (Hinds and Sauer 1975).

## GRAZING

The effects of grazing on sagebrush vegetation are primarily those produced by introduced livestock. The post-Pleistocene population of native ungulates was limited, with the American bison and pronghorn antelope the only common large ungulates. Total wildlife grazing pressure appears to have been light compared with that which occurred on the Great Plains grasslands (Merriam 1926, Butler 1976). The sagebrush region was not adapted for concentrations of large herbivores such as occurred with European settlement.

Since most of the herbaceous species are more palatable than sagebrush, especially during the growing season, the former were reduced while the shrubs flourished. The result was a dense and vigorous stand of sagebrush with a relatively sparse understory of annuals and unpalatable perennials (Ellison 1960, Tisdale et al. 1969). Historically, this condition was reached fairly early (Kennedy and Doten 1901), and by the 1930s, federal range personnel estimated that 84 percent of the region was severely depleted (USDA Forest Service 1936). The accuracy of this figure is questionable in light of the state of ecological knowledge at the time, but there seems no doubt that major changes had occurred due to grazing (Cottam and Stewart 1940).

The reaction of any particular area of sagebrush range to grazing will vary with a number of factors, including intensity and season of use, kind of livestock and type of vegetation. In eastern Idaho, heavy spring grazing by sheep reduced the yield of palatable grasses and forbs and increased that of sagebrush. Heavy grazing in the fall had an opposite effect, improving the herbaceous cover at the expense of the sagebrush (Mueggler 1950, Laycock 1967, 1970). In eastern Oregon, Hyder and Sawyer (1951) found that continuous grazing by cattle at a moderate rate was better for the forage species than rotational grazing. The latter was conducted as a two-field system in which each field was exposed to heavy spring use two years out of six.

The "spring" season included almost the entire growing season for this type of vegetation and provided no opportunity for regrowth after heavy use. The effects of more realistic and flexible grazing systems, including rest-rotation (Hormay and Talbot 1961) have not yet been documented for sagebrush-grass vegetation, but observation indicates that these are often superior to continuous grazing. Badly depleted sagebrush ranges require measures other than changes in grazing or rest, however, if rehabilitation is to be achieved in a reasonably short time (Young et al. 1979).

An important phase of the grazing influence in the sagebrush region is the actual amount of use of the sagebrush species themselves. It is generally recognized that sagebrush provides important habitat for many species of wildlife, although only a few such as the sage grouse (*Centrocercus urophasianus*) and pygmy rabbit (*Brachylagus idahoensis*) are wholly dependent on it (Patterson 1952, Green and Flinders 1980). In the case of the currently common large ungulates of the region, mainly mule deer (*Odocoileus hemionus*) and pronghorn antelope (*Antilocapra americana*), sagebrush is recognized as an important source of browse, especially in winter (Taylor 1972, McAdoo and Klebenow 1979, Nagy 1979). Use of sagebrush by domestic livestock is considered to be less than for wildlife, but *A. nova* is important for sheep on winter ranges (Hutchings 1954) and sheep in southeastern Idaho used considerable amounts of *A. tridentata* and *A. tripartita* under conditions of heavy stocking in the fall (Laycock 1967).

Questions of palatability and nutritive value naturally arise in view of such relatively limited use of an abundant food source. A number of feeding studies, as well as observations under less controlled situations have provided some data but results have varied and there is need for further information. Earlier feeding trials indicated that mule deer preference for sagebrush (*A. tridentata* and *A. nova*) was not high and that they ate it more readily and fared better nutritionally when a mixed ration was available containing species besides sagebrush (Smith 1950, Smith and Hubbard 1954, Dietz et al. 1962). It has been commonly assumed that low palatability of sagebrush is related to the high content of volatile oils found in these species (Powell 1970), but the evidence is not clearcut. Sheehy (1975) and Scholl et al. (1977) found little relationship between deer preference and presence in sagebrush of eight major volatile compounds. Otherwise, sagebrush rates well as winter browse, with a higher protein content than most associated shrubs and fair digestibility (Dietz et al. 1962, Gibbs 1978). Some investigations have suggested that the volatile oils of sagebrush may inhibit digestion by antimicrobial activity in the rumen (Nagy et al. 1964, Nagy 1979, Oh et al. 1968). Other trials, however, show no such effect (Welch and McArthur 1979). Johnson et al. (1976) reported toxic effects in sheep when *Artemisia tridentata* was suddenly fed in large amounts (.75 lb daily), but no harmful effects when the initial dosage was small (.25 lb) and increased gradually.

Whatever the causal factor, it appears that the palatability of sagebrush varied by species, subspecies, local populations and even individual plants (Nagy 1979, Welch and McArthur 1979). Recent studies which recognize the significance of identification to subspecies and also consider population variability have been helpful in determining such differences. Sheehy (1975) tested the relative palatability of seven sagebrush taxa to mule deer and domestic sheep. The deer took sagebrush more readily than did the sheep; the latter required initial withholding of other feed to get them started on sagebrush. The deer showed definite preferences, however, with *A. arbuscula*, *A. tridentata vaseyana* and *A. cana bolanderi* in the top group; *A. tridentata tridentata* and *A. tridentata wyomingensis* second; and *A. nova* the least preferred. Sheep showed substantially different preference with *A. arbuscula* first; *A. nova* second; *A. tridentata vaseyana* and *A. cana bolanderi* third; and *A. tridentata tridentata* and *A. tridentata wyomingensis* last. Differences in preference with populations of sagebrush taxa have also been shown (Smith 1950, Hanks et al. 1973, 1975, Welch and McArthur 1979). Comparable detailed tests with cattle are not available but observations on the range indicate considerable differences among sagebrush taxa with at least some populations of *A. tridentata wyomingensis* utilized more than other subspecies of *A. tridentata* (Winward 1970, Brunner 1972). It is apparent that more investigation into the palatability and nutritive value of sagebrush is needed. It also may be possible to develop strains more palatable than those occurring naturally (Plummer 1974, Welch and McArthur 1979).

In total, it appears that use of sagebrush by wildlife and livestock combined is light, with localized exceptions, and is made mainly during the winter season. Thus, the impact of grazing on sagebrush is minimal, especially in relation to that of most associated herbaceous species.

Another possible effect of the high content of terpenoids (Kelsey et al. 1976) or other secondary compounds in sagebrush is that of inhibiting the germination and growth of other plant species. Aqueous extracts and volatile exudates of sagebrush leaves have been shown to inhibit germination and seedling growth of several associated species (Schlatterer and Tisdale 1969, Klarich and Weaver 1973, Weaver and Klarich 1977, Hoffman and Hazlett 1977). These results have all been obtained under greenhouse or laboratory conditions, however, and definite proof of such effects under field conditions has not been shown. Field observation indicates strong competitive ability against most herbaceous species, especially when the stand of sagebrush has become more dense and vigorous than normal. This effect may be due largely to the efficient root system of sagebrush and its ability to utilize moisture over a longer season than that of most herbaceous species. In any event, allelopathic influences remain a possibility and merit further field oriented research (Caldwell 1979).

The relationship of sagebrush to the herbaceous component of communities in this region has not received

much detailed study. The use of fire, herbicides, etc., is based on the premise that strong competition does exist and that herbaceous species will benefit from a reduction in the shrub stand (Blaisdell 1953, Blaisdell and Mueggler 1956b, and many others). In most of these cases, however, the natural balance between shrubs and herbaceous species had already been disturbed and the shrub cover had become much greater than in the pristine condition. Most direct studies of competition have been in connection with range reseeding and have involved sagebrush and introduced grass species, especially crested wheatgrass (*Agropyron desertorum*) and related species (Robertson 1947, Hull and Klomp 1974, Rittenhouse and Sneva 1976). These studies showed a negative relationship between the stand of sagebrush and the establishment and yield of seeded species. Blaisdell (1949) showed that degree of competition between seedlings and young plants of sagebrush and perennial grasses depended largely on their relative ages. The older the stand of sagebrush, the less chance there was for successful establishment and production of grass. Both the introduced crested wheatgrass and the native bluebunch wheatgrass responded in this manner. Tisdale et al. (1969) showed a negative relationship between Wyoming big sagebrush cover and native grass cover and yield on a stand dominated by *Sitanion hystrix* instead of the climax dominant, *Stipa thurberiana*. Daubenmire (1970) stresses the complementary nature of sagebrush and herbaceous root systems and patterns of activity in the sagebrush region of Washington, but offers no experimental evidence regarding the degree of competition. Evidently, there is need for further investigation of the shrub-herb relationship in sagebrush vegetation.

The reaction of grass species of the region to grazing was discussed earlier. Briefly, the climax grasses, *Agropyron spicatum*, *Festuca idahoensis*, *Stipa thurberiana*, and often *S. comata* are recognized as decreaseers under heavy use. *Poa sandbergii* and *Sitanion hystrix* act as increaseers, but also decline with prolonged overuse (Tisdale et al. 1969, Mueggler and Stewart 1980). Recovery from a depleted condition can occur, but tends to be very slow when a dense cover of sagebrush is present. Use by wildlife, especially rodents and rabbits may be sufficient to prevent recovery of perennial grasses and palatable forbs even when livestock grazing is excluded (Piemeisel 1945). Even on ranges in better condition, rabbits (*Sylvilagus* and *Lepus* spp.) can be an important influence on the herbaceous vegetation during periods of peak populations (M. Johnson 1979, McAdoo and Klebenow 1979). Use of herbaceous species by native ungulates, especially mule deer, is generally heaviest in the spring (Kufeld et al. 1973, Willms et al. 1979), and can also be an inhibiting factor on range recovery.

The extent of changes brought about by heavy grazing, fire, etc., have led some investigators to consider these changes as irreversible, and the pre-settlement sagebrush ecosystem to be essentially extinct (Young et al. 1979). This conclusion seems premature at least and fails

to take into account large areas in the region where native perennials still dominate the understory and where sagebrush density has not become extreme. The need for rapid improvement of many of the most depleted areas does not negate the fact that natural improvement can occur. Improvement is likely to be slow, however, especially on drier sites and in the lower range condition classes (McLean and Tisdale 1972). Robertson (1971) has reported changes on a depleted area in Nevada ungrazed for 30 years. The cover of *Stipa thurberiana* increased sevenfold; *Agropyron spicatum* reestablished itself on favored spots; *Sitanion hystrix* nearly trebled in amount; and perennial forbs increased by 85 percent during this period. Piemeisel (1938, 1951) and Hironaka and Tisdale (1963) have documented comparable changes over a 25-year period in southern Idaho. More rational grazing management in the future plus a reduction in grazing pressure made possible by forage produced by artificial rehabilitation of the most depleted stands could bring about natural improvement in much of the vast sagebrush region.

### HERBICIDES

The application of herbicides represents another selective disturbance of sagebrush-grass vegetation, since the chemicals used are designed to kill most species of sagebrush and to leave the associated perennial grasses unharmed. The effects are somewhat like those of fire, except that the herbicides tend to damage all broad-leaved plants, including palatable shrubs and forbs.

The shrub, *Amelanchier alnifolia*, and forbs such as *Balsamorhiza sagittata*, *Astragalus* spp., *Helianthella uniflora* and *Mertensia oblongifolia* were severely damaged in a study in eastern Idaho (Blaisdell and Mueggler 1956b), but *Purshia tridentata* was little affected. Much more damage to the latter species was found in trials in eastern Oregon (Hyder and Sneva 1962). Miller et al. (1980) report a twofold increase in perennial grass density and yield in stands of mountain big sagebrush treated with 2, 4-D butyl ester. *Agropyron spicatum* responded better than *Festuca idahoensis*, and reduction in forb cover was largely confined to one species, *Lupinus caudatus*.

Herbicide application aimed at partial control of undesirable shrubs and less damage to desirable shrubs and forbs presents one approach, but may lead to increases in shrub density (Evans et al. 1979). Timing of treatment and care in selecting suitable sites are major considerations in the proper use of herbicides on sagebrush-grass vegetation in which significant amounts of desirable shrubs or forbs remain. On areas which have been badly depleted and the understory changed to one of *Bromus tectorum* and other annual weeds, methods of treatment involving the use of paraquat and atrazine have been developed. Paraquat is used to kill annuals just prior to reseeding with perennial forage species, while atrazine is used to create a chemical fallow for a year preceding reseeding (Evans et al. 1979, Eckert et al. 1974).

Although the use of herbicides on sagebrush vegetation has been chiefly on *Artemisia tridentata*, Eckert et al. (1972) and Eckert and Evans (1968) showed that similar responses could be obtained in stands of *A. arbuscula*. The principal increase in herbaceous species was among the perennial grasses, with *Poa sandbergii* showing the greatest initial response. Best results were obtained on sites of high potential and in fair range condition.

Fewer studies have been made of the long-term effects of herbicidal treatment. Johnson (1969) in Wyoming found that increased herbage production after spraying big sagebrush lasted only 6 years. Recovery of sagebrush was essentially complete in 14 years on grazed areas and nearly so in 17 years on ungrazed plots. Sneva

(1972) in southeastern Oregon reported that herbage production increased more than twice following herbicidal treatment of a big sagebrush-grass range. Recovery of sagebrush was slow during the first decade following treatment, but was approaching pre-treatment amounts in 17 years. Thilenius and Brown (1974) in western Wyoming found increased herbage production to be short-lived, with yields returning to pre-treatment levels in 50 years or less, although big sagebrush cover at this time was still less than half the pre-treatment amount.

Factors influencing rate of sagebrush reestablishment apparently include initial percent mortality, grazing management and local climate, especially the effect of summer drought on establishment of sagebrush seedlings.

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