Reproductive mechanisms of plains silver sagebrush Artemisia cana cana in southeastern Montana
by Todd Patrick Walton

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Range Science
Montana State University

Abstract:
A study was conducted during the years of 1982 and 1983 to investigate reproductive characteristics and mechanisms important in plains silver sagebrush (Artemisia cana Pursh ssp. cana). The study was conducted on the Fort Keogh Livestock and Range Research Laboratory at Miles City, Montana. In particular, studies examined: (1) seed dispersal from individual plants and among sites, (2) factors affecting germination, (3) emergence, growth and survival of seedlings under controlled and field conditions, and (4) whether the primary origin of individual plants was from seed or vegetative propagation.

Dispersal patterns were examined for a one-month period in the fall of 1982. Wind dispersal appeared to be the most influential factor in the dispersal of achenes from plains silver sagebrush for the area studied. A definite three-directional distribution of dispersed seed was found. Most seed was dispersed close to, or under, the shrub, but this depended on date and direction. No major differences in dispersal patterns were found among the three study sites. Plains silver sagebrush can germinate under a variety of environmental conditions, but certain situations did favor higher germination percentages. Stratification had no effect on germination success. Date of seed collection, light and dark regimes, temperature and water stress had important influences on germination success. Higher temperatures that had adverse effects on germination were favored in seedling growth. Seedling response was enhanced by addition of supplementary water and burial at 5 mm. Mortality was lowest from seedlings emerging from 15 and 25 mm. Despite large numbers of seeds that were planted, very few seedlings emerged in the field (1.2%), and of these only 11 percent survived the summer. The degree to which plains silver sagebrush relies on vegetative reproduction was established by root excavations. Plains silver sagebrush in almost all cases showed some degree of rhizomatous growth, even among small seedlings. Most excavated individuals turned out to be sprouts from an already established plant. No differences could be found among sites or between disturbed or undisturbed sites in terms of numbers of sprouts or seedlings. Drought was likely the most important influence on growth habits.

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by

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APPROVAL

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Todd Patrick Walton

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

A study was conducted during the years of 1982 and 1983 to investigate reproductive characteristics and mechanisms important in plains silver sagebrush (Artemisia cana Pursh ssp. cana). The study was conducted on the Fort Keogh Livestock and Range Research Laboratory at Miles City, Montana. In particular, studies examined: (1) seed dispersal from individual plants and among sites, (2) factors affecting germination, (3) emergence, growth and survival of seedlings under controlled and field conditions, and (4) whether the primary origin of individual plants was from seed or vegetative propagation.

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INTRODUCTION

An adequate understanding of how individual species influence plant-community dynamics is fundamental to successful management of rangelands. Members of the sagebrush genus (Artemisia L.) have long been regarded as having an important role in rangelands of North America. In the past, sagebrush species have generally been considered undesirable in rangeland operations due to their adverse impact on preferred forage species and livestock operations. Consequently, control measures were often recommended with high brush densities. Recently, with expanding knowledge, the sagebrush complex has been regarded as often providing valuable forage and cover for either livestock and/or wildlife. As such, it serves an important role in western ecosystems. However, the economic and management importance of sagebrush depends upon the specific taxon present (Beetle 1977).

Silver sagebrush (Artemisia cana Pursh[1]) occupies an estimated 13 million hectares (ha) in the 11 western United States (Beetle 1960). It ranks second to big sagebrush (Artemisia tridentata Nutt.) with respect to area occupied. In Montana there are about 7.8 million ha of big sagebrush and 5.2 million ha of silver sagebrush, while in Wyoming there are 9.1 million ha and 2.85 million ha respectively. The geographic range and ecological dominance of this shrub merits intensive research attention. However, this has not previously occurred. While big sagebrush has been studied extensively in recent

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1 Scientific nomenclature in this thesis follows Beetle 1960, Beetle and Young 1965, Shetler and Skog 1978.

years, biological information dealing with silver sagebrush is very limited. States such as Montana and Wyoming rely heavily on range and pasture forage for their livestock industry. Therefore, appreciation of silver sagebrush communities and their implications for management is important.

Plains silver sagebrush (Artemisia Pursh cana ssp. cana) is an important shrub in the Northern Great Plains. It is found on deep, lowland soils of floodplains and is generally considered to increase in response to cattle grazing. This sagebrush is an erect, freely branching shrub of up to 1.5 meters often found in dense stands. It sprouts vigorously after disturbances such as burning.

It is important to understand factors contributing to reproductive success or failure in order to gain a better appreciation of plant population dynamics. This is probably best accomplished in conjunction with autecological studies of principal species that include research on phenology and production of field populations (Mott 1979). Due to plain silver sagebrush's extensive occurence in many Northern Great Plains plant communities, a study was undertaken to examine some of the variables involved in its success. The study was conducted over a two year period at the Fort Keogh Livestock and Range Research Laboratory at Miles City, Montana. It was designed to examine reproductive characteristics and mechanisms which are important in the success and maintenance of plains silver sagebrush.

Two study goals were addressed in the course of my research. They were: (1) to establish baseline information on plains silver sagebrush reproduction, and (2) to consider sexual and asexual means of reproduction with regard to the relative importance of each. More specific objectives were established within this context and examined in individual studies. This research work was designed to reach four objectives. These were: (1) to examine seed dispersal characteristics from individual plants, (2) to investigate factors affecting seed germination, (3) to evaluate emergence, early growth and survival of seedlings, and (4) to determine whether the primary origin of individual plants was from seed or vegetative propagation.

LITERATURE REVIEW

Introduction to Artemisia Taxonomy

A New World group of closely related sagebrush species comprise a North American endemic Section of the world-wide Genus Artemisia L. (300 species) and occur in varying amounts over about 109 million hectares (ha) in the 11 western United States (Beetle 1960). This Section, designated Tridentatae, likely evolved in North America during the late Tertiary or early Quaternary times from an ancestral species of Artemisia originating in Asia. Differentiation throughout the Cenozoic era probably occurred under the stimulus of arid cycles. Tridentatae is of mountain origin and Great Basin adaptation (Beetle 1960, Johnson 1978, McArthur and Plummer 1978). Members of Tridentatae are distinguished from Old World counterparts by woody stems and a lack of ray florets. In addition they share common characteristics within the Section, including: (1) dentate leaves, in general, covered with characteristic sericeous or canescent pubescence, (2) an aromatic odor caused by a variety of terpenes, and (3) campanulate heads arranged in modified panicles (Beetle 1977, McArthur and Plummer 1978, Tisdale and Hironaka 1981).

Characteristics and Taxonomy of Sagebrush

Several adaptive features have been associated with the Section Tridentatae and have resulted in its extensive distribution and persistence of many species in a variety of habitats. Physiological features such as ability to carry on photosynthesis at low temperatures, ability to germinate over a wide range of temperatures, extensive root system, and prominent secondary metabolic compounds may confer a competitive advantage for sagebrush (DePuit and Caldwell 1973, Caldwell 1978).

Evidence indicates that all species and subspecies of Tridentatae can be given the status of at least topographic and edaphic climax dominants. As such, each defines in its own way a different ecological area. Many of the factors which influence the distributional patterns in sagebrush are reflected in soil development combined with climatic or environmental characteristics (Hazlett and Hoffman 1975, Winward 1980, Froeming 1981). Several species such as silver sagebrush (Artemisia cana Pursh) and big sagebrush (Artemisia tridentata Nutt.) have achieved sufficiently wide distribution to have developed subspecies. Both have three subspecies. Big sagebrush is the most widespread and has received the most research attention. Silver sagebrush is second in distribution and is not well researched.

Two genetically differentiated groups in the Tridentatae Section are recognized. One group resprouts after disturbance (A. tripartita Rydb., A.cana and A. rigida (Nutt.) Gray), while the other group does not (A. tridentata, A. arbuscula Nutt., A. longiloba (Osterhout) Beetle, A. nova Nelson, A. biglovii Gray and A. pygmeae Gray).

Silver Sagebrush Taxonomy

The silver sagebrush complex is composed of three subspecies with allopatric distribution (Figure 1) and characteristic ecological

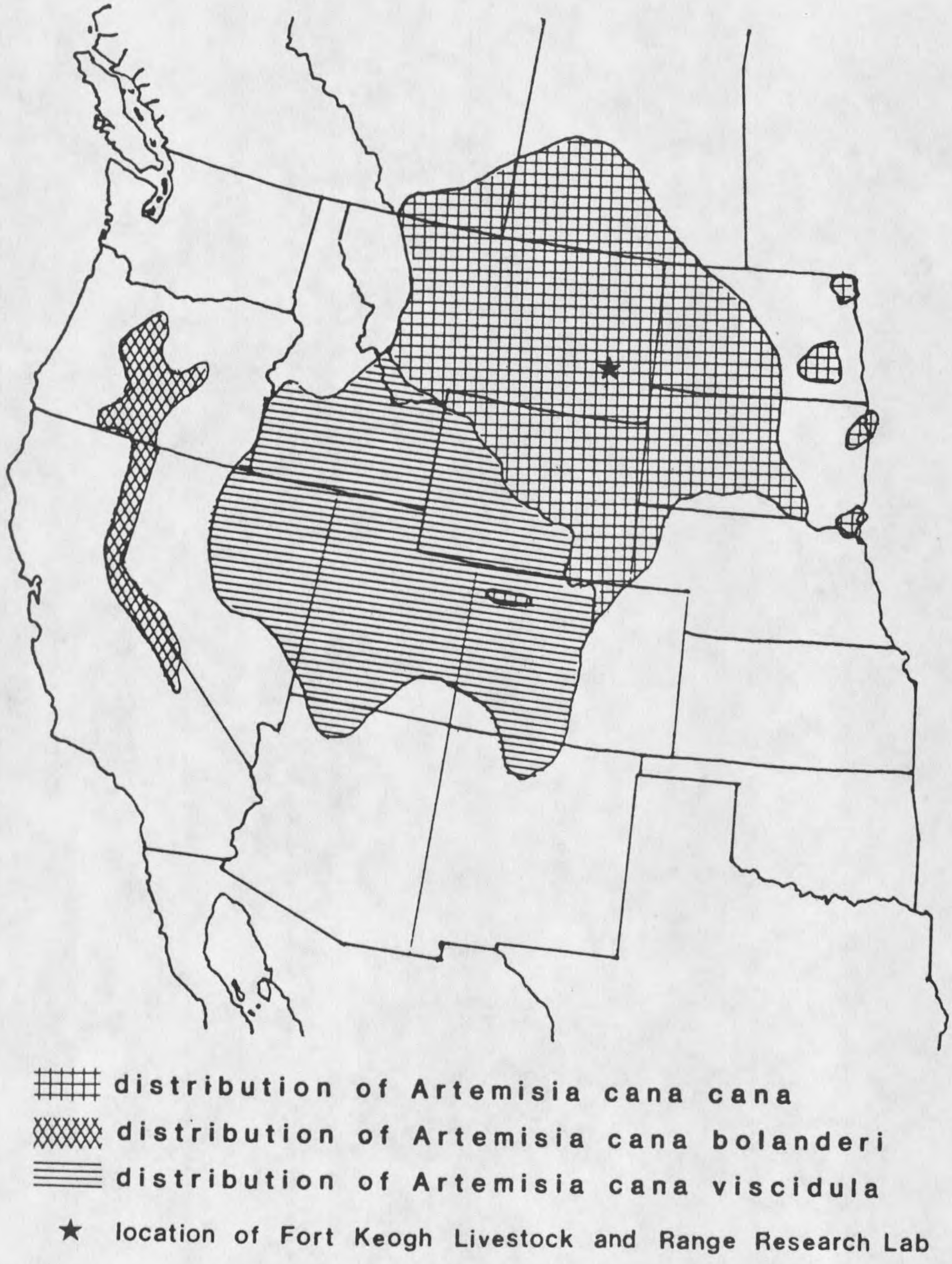

Figure 1. Distribution of the three subspecies of silver sagebrush in western North America (Harvey 1981).

niches (Beetle 1977). Subspecies are separated morphologically on the basis of leaf width, sesquiterpene content and geography (Morris et al. 1976).

Mountain silver sagebrush (A. cana ssp. viscidula (Osterhout) Beetle) is typified by its greenish, linear leaves, and it occurs on stream banks, meadows and depressions generally at higher elevations. It is often in close association with conifers in the Rocky Mountain region of the western states. Bolander silver sagebrush (A. cana ssp. bolanderi (Gray) Ward), in contrast, has linear, canescent leaves and grows on poorly drained soils in central Oregon and eastern California. Plains silver sagebrush (A. cana Pursh ssp. cana) is an erect, canescent, freely branching shrub of up to 1.5 m with large linear leaves. This taxon is found growing on well watered, deep soils throughout the Northern Great Plains, especially along streambottoms and drainageways, in sparse to dense stands. Wyoming big sagebrush (A. tridentata ssp. wyomingensis Beetle and Young) is the only other major shrubby sagebrush in the Northern Great Plains (Beetle 1977, Johnson 1978, Tisdale and Hironaka 1981).

Distribution of Plains Silver Sagebrush

Plains silver sagebrush occurs east of the continental divide (except for the Yampa River Valley, Colorado) in Wyoming and Montana north to southern Alberta and Saskatchewan and east to central North and South Dakota and northwest Nebraska. Several disjunct populations occur in the eastern Dakotas (Harvey 1981).

Silver sagebrush was first collected by Lewis and Clark on the bluffs of the Missouri River (Nuttall 1841) and typical habitats include loamy to sandy, well drained soils of uplands, and alluvial flats and terraces of valley bottoms. It is further distinguished as growing in dense or open stands along streams and valleys that are subject to erosion, flooding and deposition. Hence, stratification and heterogeneity are conspicuous in the alluvial profiles (Thatcher 1959, Hazlett and Hoffman 1975, Johnson 1978). Thatcher (1959) noted that only one of the four sagebrush species he studied, plains silver sagebrush, grew on soils influenced by high water tables. Johnson (1978) reported that only silver sagebrush and western wheatgrass (*Agropyron smithii* Rydb.) thrived in areas of frequent flooding.

Ecology and Characteristics of Sagebrush

Winward (1980) notes that questions continually arise as to (1) how much sagebrush is required for wildlife, (2) the ecological status of the plant, and (3) whether control is desirable. Each sagebrush taxon has unique biological features that influence management decisions. Moreover, most of the region dominated by sagebrush in the western states is stable, meaning that species presence has not changed appreciably since the time of settlement. However, some areas have shown a substantial increase in sagebrush density due to heavy livestock grazing (Tisdale and Hironaka 1981). Under these circumstances, implementation of control practices may be desirable.

Control Methods and Results

Methods of control that have been used on sagebrush include herbicidal, mechanical, biological or burning treatments. Alternate possibilities of altering sagebrush communities have included fertilizer treatments and genetic selection of improved plant materials. However, what control work on silver sagebrush that has been done, in southeastern Montana, is reported in White and Currie (1983).

Species of sagebrush which do not layer or sprout in nature are relatively easy to control by various methods. Heavy kill has been reported with 2,4-D on big sagebrush (Blaisdell and Mueggler 1956, Cornelius and Graham 1958). Mechanical and burning treatments are also effective in reducing big sagebrush (Johnson and Payne 1968). Wright et al. (1979) have noted that fire has probably played an historic role in keeping brush density low in sagebrush/grass communities. It was estimated that fires occured every 32-70 years in these communities.

White (personal comm.) has studied herbicidal, mechanical and burning treatments on plains silver sagebrush in southeastern Montana and has found that fall burning can lead to good control (White and Currie 1983). Blaisdell and Mueggler (1956) indicated that silver sagebrush shows much greater resistance to 2,4-D than other sagebrushes. The sprouting nature of shrubs such as silver and threetip sagebrush (A. tripartita) makes control efforts more difficult. It has also contributed to higher plant density when animal use is high and/or fire frequency has been reduced. In threetip sagebrush populations in Oregon, Winward (1980) believed control efforts may be the only way to keep shrub densities low enough to allow for healthy stands of herbaceous species. He reported that light grazing and even nonuse will fail to restore stable herbaceous composition. Mountain silver sagebrush density increased less rapidly in response to maintenance of a good herbaceous cover than did threetip sagebrush.

Defoliation of browse species appeared to reduce carbohydrate reserves to about the same extent regardless of control treatment date (Donart and Cook 1970). Sturges (1977a) reported that fall moisture was reduced by 19 percent in a big sagebrush stand with gains noted at 91-183 cm depth. However, moisture depletion was greater on sprayed sites in the top 61 cm because grass density increased when sagebrush was controlled. This response was observed where soils were sufficiently deep so that grass roots were above sagebrush roots.

Biological control has gained recent attention and Gates (1964) has indicated that a leaf-defoliating moth (Aroga websterii) has been one of the most promising in this regard because it prefers sagebrush species. Besides this moth, some other insects have been reported as destructive to sagebrush. These include Trirhabda pilosa and various species of grasshoppers (Harvey 1981, Tisdale and Hironaka 1981). Voles (Microtus spp.), a rodent on rangelands, have caused extensive damage on big and silver sagebrush populations as well as other plant species (Mueggler 1966, Tisdale and Hironaka 1981). In southeast Montana, they were present in sufficient numbers in 1983 to girdle and topkill many shrubs on both my study area and in nearby pastures.

Rodents do not seem to take the seed as food however, possibly due to terpenoids present (Everett, Meeuwig and Stevens 1978).

Sagebrush plants that survive control treatments have been found to be the most important factor in shrub reinvasion (Johnson and Payne 1968). Generally, reestablishment occurred during the first few years after treatment and ultimately was also due to plants growing to seed bearing size (Bartolome and Heady 1978). Control treatments might also allow other species such as green rabbitbrush (Chrysothamnus viscidiflorus (Hook.) Nutt.) to exploit new sites where competition has been eliminated (Young and Evans 1972). Control of plains silver sagebrush was significant in reducing shrub competition and increasing desirable forage. When mechanical treatments were examined in this context, cutting date and original plant size were found to be important in determining subsequent sprouting and regrowth (White personal communication). Phenology and moisture stress also affected mortality.

Many shrubs, including silver sagebrush, are desirable in reclamation of disturbed lands for catching snow and furnishing forage or cover for livestock and wildlife. However, silver sagebrush consistently had the least growth of five shrubs transplanted as seedlings on topsoil and overburden in Wyoming (Howard et al. 1977). To improve on these characteristics, Welch and McArthur (1979) have suggested that sagebrush can probably be genetically improved to become a more valuable forage resource. This is because of a richly variable germ plasm.

Forage Considerations

All sagebrushes have some importance as forage (Beetle 1960), but it has been established that there are significant differences in animal preference among taxa. Most research on this subject has been concerned with big sagebrush, low sagebrush (A. arbuscula) and black sagebrush (A. nova). Limited studies with silver sagebrush have been done. Genetic variation between sagebrush species and subspecies influenced animal preference more than environmental variation within the taxon (Sheehy and Winward 1981). Studies relating to grazing use of plains silver sagebrush have shown that it is a relatively important plant for winter use by some wildlife species such as elk (Cervus canadensis), mule deer (Odocoileus hemionus) and antelope (Antilocapra americana) (Dietz et al. 1962, Mackie 1970, Kufeld 1973, Dusek 1975, Beetle 1977, Scholl et al. 1977, Wilson 1977, Sheehy and Winward 1981). It will be used by livestock only if there is little else available (Mackie 1970, Kufeld 1973, Dusek 1975, Branson and Miller 1981, Sheehy and Winward 1981, Roath and Krueger 1982).

Wildlife Forage Considerations

Beetle (1977) reported that plains silver sagebrush was less palatable than Wyoming big sagebrush, but stated that it was readily taken by elk and deer in winter. Sheehy and Winward (1981) showed that Bolander silver sagebrush was highly preferred by mule deer. Scholl et al. (1977) reported that mountain silver sagebrush was moderately palatable to mule deer. Two studies in the Missouri Breaks of Montana demonstrated that use of plains silver sagebrush by mule deer and elk was extensive (Mackie 1970, Kufeld 1973). Heaviest use was observed on bottomlands, but moderate use was observed throughout the area studied. Mackie based his conclusions on observations of frequency of shrub use and rumen content from dead animals. Plains silver sagebrush was found in 50 percent of the collected mule deer rumens and in 22 percent of the elk rumens. Although these numbers differ, elk were observed to use the shrub as frequently as the deer. Antelope in Wyoming used silver sagebrush predominantly during late fall, winter and early spring (Wilson 1977). Dietz et al. (1962) reported that use of sagebrush was dependent on what other plant species were available. Sagebrush was regarded as more palatable when other plants were available. Mule deer in low condition refused to eat sagebrush alone. Deer were seldom observed in a silver sagebrush type during winter in central Montana, and diets contained less than 10 percent of the shrub in all seasons (Dusek 1975). This was noted even though use of this type doubled from early to late summer in association with a corresponding decrease in use of the big sagebrush areas. White (personal comm.) considers silver sagebrush of limited forage value. He has observed use by rabbits and voles, but only occasional use by mule deer. More frequent use by deer seemed to be restricted to winter periods when deer populations were high.

Livestock Forage Considerations

Reported livestock use of silver sagebrush presents a conflicting and unclear picture. Mackie (1970) and Kufeld (1973) reported no use by cattle on plains silver sagebrush in the Missouri Breaks. Although

Dusek (1975) reported that cattle spent 64 percent of their time in silver sagebrush communities from June to September, no use of the plant was observed. Season of cattle use and degree of shrub utilization were related to palatability and availability of herbaceous vegetation. However, shrub utilization was not excessive and had no long term effects on abundance or vigor in Oregon. The only shrubs which were obviously avoided by livestock were shrubby cinquefoil (Potentilla fruticosa L.) and mountain silver sagebrush (Roath and Krueger 1982). Sheehy and Winward (1981) showed some sheep utilization of Bolander silver sagebrush in Oregon, but preference was low. In northeastern Montana, Branson and Miller (1981) reported that plains silver sagebrush, in particular, increased greatly in density when rested from cattle. This was attributed to two factors. First, plains silver sagebrush was more palatable than most shrubs in the area and showed rapid recovery from reduced grazing. Secondly, silver sagebrush was located on level floodplains, adjacent to streams where it was readily accessable to livestock and vulnerable to heavy use.

Sagebrush Chemistry

Interest in the chemical properties of sagebrush in relation to taxonomic refinement into species and subspecies has led to speculations as to why certain taxa are preferred by animals. Mineral and nutrient content can be shown to coincide with the use of sagebrush by season. This may be primarily due to availability and not illustrate a cause and effect relationship. Gough and Erdman (1980) found significant differences in concentrations of 30 elements in

Wyoming big sagebrush by season. The highest concentrations of the major elements (Ca, Cu, Mg, P, K, S) were in June and July and the lowest were in the winter. The inverse was found with two groups of minor elements (Al, Cr, An, Ar, Ba, Cd, Fe, Pb, Na, Co, Mn). In general, high crude protein and low crude fiber contents are found in winter and often related to increased preference during that season.

The variation in secondary metabolic compounds among the taxa may strongly influence palatability. Secondary chemicals may be modifiers of foraging behavior and are likely influences on selectivity. Black sagebrush has been found to precondition sheep for the action of Tetradymia toxins in photosensitism (Johnson 1982). The sagebrush genus has three groups of secondary compounds. These include phenolics, volatile oils and sesquiterpene lactones. The first group, which includes flavenoids and coumerins, are flourescent under UV light and were first used to separate subspecies of certain taxa (Winward and Tisdale 1969). Color extracts have been linked with palatability to mule deer (Stevens and McArthur 1974), with silver sagebrush being fairly palatable and in the same category as Wyoming big sagebrush. The light blue color found in extracts of silver sagebrush denotes a medium preference whereas the darker blue of mountain big sagebrush extracts (Artemisia tridentata ssp. vaseyana (Rydb.) Beetle) indicates higher animal preference. The presence of coumerin derivatives and their glycosides are also correlated with this darker blue (Shafizedeh and Melnikoff 1970). This concept has not been consistently verified under wide ranging circumstances.

Sesquiterpene lactones are also being studied as taxonomic markers and may be related to preference. Specific compounds in this group have been identified (Bhadane and Shafizedeh 1975), but it is not known which have a role to preference. Plains silver sagebrush chromotographic patterns are very close to the non-preferred subspecies, basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) (Kelsey et al. 1976).

Ecological Aspects of Sagebrush

Grazing Impacts

Shrub communities may be exceptionally stable in the absence of external perturbation (Harper 1977). Therefore, community composition may depend more upon the nature of previous disturbances and the flora that developed immediately thereafter than upon successional development.

In one big sagebrush/grass community in Idaho, shrubs and perennial grasses doubled after 25 years of no livestock grazing (Anderson and Holte 1981). Selective grazing by cattle in spring encouraged growth of sagebrush, but sheep grazing in late autumn on communities with low shrub densities prevented an increase in density of big sagebrush. At higher shrub densities, the sheep lost weight and failed to control sagebrush. After six years sagebrush increased in both size and potential seed production in this situation (Frischnecht and Harris 1973).

Soil Relationships

Soil characteristics have been examined to evaluate relationships with sagebrush distribution. Silver sagebrush prefers well drained, alluvial, coarser textured soils in bottomlands. More detailed soil and vegetation relationships in silver sagebrush communities have been reported. Lower levels of P, K, N, organic matter and cation exchange capacity were reported in silver sagebrush soils than adjacent big sagebrush soils (Hazlett and Hoffman 1975). This was probably due to more mature soil development in the big sagebrush community. Cunningham (1971) reported that moderate to high levels of extractable magnesium in the 12-24 inch layer was important to the presence and success of silver sagebrush. This was associated with imperfect soil drainage and a shallow root system in the plant. Optimum habitat seemed to include a moist upper six inches of soil along with coarse materials in the soil profile. Sturges (1977b) states that water-use zones shift outward and downward in the soil from the big sagebrush plants as the growing season advances. Sturges (1977b) and Caldwell (1978) both characterize big sagebrush as having a prominent taproot with sufficient lateral spread and root density to capture summer precipitation. Deeper roots are present which allow utilization of deeper water reserves and moisture recharge. Similar research has not been done with silver sagebrush.

Allelopathy

Allelopathy is one area that is extensively covered in the literature on Artemisia. This wealth of information is probably due, in part, to interest in why this genus is so successful. Allelopathy is a prominent feature found in Artemisia throughout the world, and much of the foreign research focuses on it.

Allelopathic substances from Artemisia rhizomes and leaves have universally decreased respiration or inhibited germination of grass seeds (Chirca and Fabian 1973, Friedman et al. 1977, Hoffman and Hazlett 1977, Weaver and Klovich 1977, Groves and Anderson 1981, Hussain and Khanum 1982). In India, Melkania et al. (1982) attributed the allelopathic potential of Artemisia vulgaris L. to certain hydrophilic metabolites. In Japan, Numata et al. (1975) found a biologically active agent (caffeic acid) in the roots of mugwort (Artemisia princeps Pampan.). Inhibition of grass germinaton has been the most commonly reported response, but in some cases stimulation of growth has been recorded by Hoffman and Hazlett (1977), Weaver and Klovich (1977) and Chirca and Fabian (1973). Hale (1982) noted that leachates from A. vulgaris L. also increased growth of the fungus Pythium myriotylum. Harvey (1981) observed autopathy in some sagebrush species in Montana, plains silver sagebrush included.

Reproductive Characteristics

Seed Dispersal

One of the primary features of any reproductive strategy is the number of propagules that are produced and dispersed. In this respect, efficiency of seed dispersal by wind and reproductive capacity are associated. Sagebrush species are generally low in dispersal efficiency and seed production capacity is high (Bostock and Benton

1979). Seed dispersal is one of the most important factors promoting gene flow in plant populations. In most plant species, including sagebrush, dispersal seems to be incidental, especially during storms, and is not based on any special morphological structure. Dispersal is one way that plants can keep their descendents separated in space, and it provides each new plant with its own site where it has greater potential to compete with other plants (van der Pijl 1982). Dispersal strategy is complex and represents a compromise between conflicting demands, such as avenues of energy expenditure. Consequently, establishment might be more important in some species than dispersal for achieving reproductive success.

Dispersal can play a critical role in determining population size. Because seeds of most plants are dispersed close to the parent, seed density falls off steeply as distance from the parent increases (Harper 1977, Cook 1980). This is the case with sagebrush (Beetle 1960, Friedman and Orshan 1975, Harvey 1981, Tisdale and Hironaka 1981). Seed dispersal in arid communities is described as falling into two classes (Mott 1979). They are: (1) widespread dispersal, often of large numbers of seeds, enabling exploitation of a number of potential sites, and (2) utilization of a favorable habitat facilitated by minimal movement of seed from the parent plant. Under desert conditions, this second strategy is thought to improve the chances of seedling establishment since adjacent sites have already proved to be suitable for growth and development of parent plants (Friedman and Orshan 1975). The patterns of achene dispersal, seedling emergence, appearence of cotyledons and seedling mortality of _A. herba-alba_ Asso were related to distance from the parent plant. Eighty five percent of the achenes of this species fell under the existing shrub canopy. Although dispersal is important, only a few dispersal patterns are noted by Cook (1980) as being published.

Dispersal can be by wind, water or animals in sagebrush (Tisdale and Hironaka 1981) with varying importance given to each by different authors. Harvey (1981) states long distance dispersal by silver sagebrush is probably due to mucilaginous seeds attaching to animals. Beetle (1960) declares that water is undoubtedly a more important dispersal agent than wind. Anemochory (wind dispersal) is representative of Asteraceae (Compositae) and seems to be of greatest importance (Harper 1977, Bostock and Benton 1979, Evans and Young 1982). Seedlings of basin big sagebrush have been found up to 33 meters away from the nearest possible source plant. Since sagebrush seeds have limited morphological mechanisms for distant wind-borne dispersal, the range of the plant is probably extended in contiguous bands around the periphery of established stands (Daubenmire 1975). Although rodents play an active role in seed dispersal of many herbaceous species, no sagebrush seed was reportedly dispersed by rodents (LaTourette et al. 1971).

Achenes of certain sagebrush species, including silver sagebrush, develop a transparent gelatinous envelope around the seed upon contact with water (Clor et al. 1974, Harvey 1981, van der Pijl 1982). This seems an important method for attaching to soil particles, which thereby enhances germination conditions by protecting the delicate embryo from dessication and mechanical injury (Clor et al. 1974, van der Pijl 1982). The mucilaginous seed coat has also been regarded as a dispersal agent (Harvey 1981, van der Pijl 1982), and in general the drier the climate the more myxospermy (mucilaginous coating) present.

Phenological development in sagebrush results in most seed being shed during late fall and winter, although a few remain throughout the winter (Beetle 1960, Harvey 1981, Tisdale and Hironaka 1981). Most viable seed is dispersed during the first seven days, although aborted flowers and half-filled seeds are commonly dispersed over the next two to four weeks (Goodwin 1956). Tisdale and Hironaka (1981) have stated that up to 300,000 achenes per plant can be produced in big sagebrush, but Harvey (1981) reported a maximum production of only 54,000 achenes in silver sagebrush.

Germination Factors

Interest in germination characteristics of sagebrush is two fold. First, efforts to use sagebrush to provide forage or cover for livestock, wildlife and erosion control depend upon this knowledge. Secondly, there is often a desire to reduce stand density in areas where plants become too abundant and compete with forage plants (Pechanec et al. 1965, McArthur et al. 1974, Harvey 1981).

The combination of habitat conditions that favor seedling establishment has been referred to as a safesite (Cook 1980). In this environment, the water and nutrient resources and stimuli immediately surrounding a seed determines whether it will germinate (Harper 1977). Germination on a specific seedbed is also controlled by inherent characteristics of seeds, or in some cases, through modification of the physical environment by the seed itself (Evans and Young 1982). Heterogeneity in the microenvironment and the extreme subtlety of germination requirements can determine the number and variety of seedlings that are recruited into the plant population from the seedbank. High density stress can adversely affect seedling success. Another important element, herbivory, tends to diversify range plant communities. Herbivory influences locally different microenvironments for seedling establishment and subsequent growth of plants, and therefore initiates regeneration cycles on a small scale within the community.

One aspect of sagebrush communities is that very few sagebrush seeds germinate (Evernari et al. 1971, Hazlett and Hoffman 1975, Cook 1980, Harvey 1981). This occurs despite the great seed production typical of sagebrush plants. Several factors can contribute to this phenomenon including: soil matric potential with its effect on wetted contact between seed and soil (Collis-George and Hector 1966), early death of seedlings (Eddleman 1979), seasonal climatic conditions and plant age (Nosova 1973, Evans and Young 1982), soil moisture relationships and litter (Beetle 1960).

Achenes of sagebrush in general do not exhibit specific germination requirements. Therefore, they are usually considered non-dormant (McDonough and Harniss 1975, Caldwell 1978) and do not persist for long periods in the soil (Young and Evans 1975). However, if seeds are subjected to ideal laboratory conditions, germination can be as high as 90 percent (Harvey 1981). Important factors to examine, with respect to germination requirements, include cold treatments (stratification), temperature, light, water stress and maturity of the seed.

Stratification

Stratification has been defined as a cold treatment which breaks seed dormancy. It is important in many species. Bewley and Black (1982) state that it is most beneficial if seeds are hydrated. The amount of prechilling that is needed to enhance germination is quite variable among species and can range from a few days to several months (Young and Evans 1979, Bewley and Black 1982). It can also be unnecessary. Stidham et al. (1980) state that most shrubs require a prechill to achieve maximum germination, and they identified big sagebrush in this category without regard to subspecies. Krueger and Shaner (1982) reported prostrate spurge (Euphorbia supina Raf.) increased its germination by 70-80 percent with stratification, but Krasikova (1978) showed seeds of annual composites (Artemisia vulgaris L. included) were not affected by stratification. Because seeds of sagebrush species have been classified as nondormant, it might be hypothesized that such seeds would not benefit from prechilling. The only exception to this speculation has been mountain big sagebrush (McDonough and Harniss 1974, 1975, Caldwell 1978). Stratification can also affect germination responses to environmental variables. In arrowleaf balsamroot (Balsamorhiza sagittata (Pursh) Nutt.), stratification lowered the optimum temperature for germination (Young and Evans 1979), and in a similar fashion, prechill significantly lessened the effect of water stress on germination of mountain big sagebrush seeds (McDonough and Harniss 1975).

Temperature Effects

The effects of temperature on seed germination have been studied extensively in many species. Temperature regimes are frequently involved in seasonal control of dormancy especially in response to interactions with light. An optimum temperature becomes apparent when seeds germinate over a wide range. In addition, most seeds germinate better under constant rather than fluctuating temperature regimes (Bewley and Black 1982, Evans and Young 1982). Bewley and Black (1982) also note that rate of germination is of great value in characterizing seed responses to temperature, although there is often considerable variability due to genetic differences. This genetic heterogeneity is demonstrated through subpopulations of seed from a plant population. These subpopulations germinate under different temperature regimes and rates change with these temperatures. All subspecies of big sagebrush are noted to speed up germination from 18 to 2 days as a function of increasing temperatures (McDonough and Harniss 1975). Sagebrush seeds germinate over a wide range of temperatures, but optimum temperatures are usually well-defined (Weldon et al. 1959, Clor et al. 1974, Caldwell 1978, Krasikova 1978, Sabo et al. 1979, Wilson 1982). In silver sagebrush, the optimum seems to be about 14 C (Harvey 1981).

Light and Dark Effects

The light requirement of seeds has also been studied widely. To a large extent, light seems to play an interactive role with other