Life history and reproductive strategies in Artemisia
by Stephen John Harvey

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Botany
Montana State University

Abstract:
Life histories of four Artemisia species were compared, with emphasis on characteristics important to land reclamation. The subject species included the herbaceous perennial A. ludoviciana, the suffrutescent A. frigida, and the shrubs A. cana cana A. tridentate tridentate, A. t. Vaseyana, and A. t. Wyomingensis.

The natural ranges and habitats were reviewed as indicators of areas where the taxa might be used in reclamation. Vegetative reproduction is absent in A. frigida, rare in A. tridentata, and common in A. cana and A. ludoviciana, and could probably be used successfully for revegetation in the last two species.

Since seed reproduction is important to all species, each step in a sexual life cycle was considered. Phenological studies showed that seed formed in September and early October and could be harvested in mid October and is naturally dispersed in late October and November. Wind dispersal distance varies among the shrubs, but the majority of the seeds fall within two shrub diameters of the shrub center; mucilaginous areas, especially prominent on shrubby species, probably contributes to long distance dispersal. Potential germination was in excess of 80 percent for all species. Standard methods of measuring germination considerably underestimate germination potential, perhaps due to autopathic inhibition and observations at non-optimal temperatures. Optimal planting depth was about two mm. Field emergence occurred throughout the April to June period and those individuals that were present after three months were likely to survive for at least three years. Initial mortality was higher in the non-shrubs, which have smaller seeds, than for the shrubs, which have larger seeds. Seedling development on mine spoils was poorer than on normal topsoils of adjacent areas. Insect predation and annual plant competition severely reduce seedling survival. After the initial rapid mortality, survivorship for the remainder of a population's existence was estimated for three species in areas of eastern Montana. Shrub size was correlated with shrub age (R2 = 0.65 to 0.92). Seed yields were best correlated with the number of inflorescences (r2 = 0.74 to 0.94). The species differed little in their sexual life cycles except in seed number, seed size, wind dispersal distance and the presence of mucilaginous areas on the seed presumed to contribute to long distance dispersal.

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by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

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Approved:

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ABSTRACT

Life histories of four *Artemisia* species were compared, with emphasis on characteristics important to land reclamation. The subject species included the herbaceous perennial *A. ludoviciana*, the suffrutescent *A. frigida*, and the shrubs *A. cana cana*, *A. tridentate tridentate*, *A. t. vaseyana*, and *A. t. wyomingensis*. The natural ranges and habitats were reviewed as indicators of areas where the taxa might be used in reclamation. Vegetative reproduction is absent in *A. frigida*, rare in *A. tridentata*, and common in *A. cana* and *A. ludoviciana*, and could probably be used successfully for revegetation in the last two species.

Since seed reproduction is important to all species, each step in a sexual life cycle was considered. Phenological studies showed that seed formed in September and early October and could be harvested in mid October and is naturally dispersed in late October and November. Wind dispersal distance varies among the shrubs, but the majority of the seeds fall within two shrub diameters of the shrub center; mucilaginous areas, especially prominent on shrubby species, probably contributes to long distance dispersal. Potential germination was in excess of 80 percent for all species. Standard methods of measuring germination considerably underestimate germination potential, perhaps due to autopathic inhibition and observations at non-optimal temperatures. Optimal planting depth was about two mm. Field emergence occurred throughout the April to June period and those individuals that were present after three months were likely to survive for at least three years. Initial mortality was higher in the non-shrubs, which have smaller seeds, than for the shrubs, which have larger seeds. Seedling development on mine spoils was poorer than on normal topsoils of adjacent areas. Insect predation and annual plant competition severely reduce seedling survival. After the initial rapid mortality, survivorship for the remainder of a population's existence was estimated for three species in areas of eastern Montana. Shrub size was correlated with shrub age (R^2 = 0.65 to 0.92). Seed yields were best correlated with the number of inflorescences (R^2 = 0.74 to 0.94). The species differed little in their sexual life cycles except in seed number, seed size, wind dispersal distance and the presence of mucilaginous areas on the seed presumed to contribute to long distance dispersal.

Chapter 1

INTRODUCTION

Artemisia dominated vegetation comprises 35 to 110 million hectares in western North America (Platt, 1959; Beetle, 1960). When land containing economically valuable, non-dominant *Artemisia* (such as *A. ludovociana* and *A. frigida*) is added, the figures probably double. Because of the historical use, and misuse, of these lands for economic gain (Young and Evans, 1979) and because of the large area dominated by members of this genus, interest in the biology of *Artemisia* was stimulated. Because the shrubby species, especially *A. tridentata*, dominate in many habitats (whereas the non-shrubby species are not dominants; e.g. Mueggler and Stewart, 1980), the shrub species have been studied in much greater detail.

Because of an interest in *Artemisia*, the paucity of non-shrub *Artemisia* data, an interest in comparing strategies of different, closely related life forms, and a need to determine some of the potential of *Artemisia* for revegetation of strip-mine spoils in eastern Montana, this study was initiated. This study set out to meet the objectives: 1) describe life histories of different life forms of *Artemisia*, 2) compare reproductive strategies of the different life forms, and 3) determine the capabilities of the selected species to establish from seed on the coal spoils of eastern Montana.

Two shrub species, one suffrutescent species, and one herbaceous perennial species were selected because of their presence over a wide geographical area and their value to agriculture, wildlife and revegetation. Nomenclature for the shrubs studied follows Beetle (1960) and Beetle and Young (1965), and for the non-shrubs follows Hitchcock, et al. (1955).

1. *Artemisia tridentata* Nutt. (shrub), includes three subspecies; *A. t. tridentata, A. t. vaseyana* (Rydb.) Beetle, and *A. t. wyomingensis* Beetle and Young.

2. *Artemisia cana* Pursh (shrub), includes three subspecies; *A. c. cana, A. c. viscidula* (Osterhout) Beetle, and *A. c. bolanderi* (Gray) Ward.

3. *Artemisia frigida* Willd. (suffrutescent).

4. *Artemisia ludoviciana* Nutt. subspecies *ludoviciana* (herbaceous perennial).

LITERATURE REVIEW

In the *Artemisia* bibliography compiled by me, R. Harniss and R. Murray (Harniss, et al., 1981), over 80 percent of the papers deal with *A. tridentata* and most of the remainder deal with other *Artemisia* species in association with *A. tridentata*, less than 5 percent deal with *A. cana* or *A. frigida*, and less than 1 percent involve *A. lucoviciana*. Because of the huge volume of literature (1,489 entries), I have chosen to review the work in outline form: two or more representative articles are presented for each topic heading. Because of their rarity, non-shrub articles are emphasized.

1. Taxonomy and cytogenetics. Hall and Clements, 1923; Ward, 1953; Beetle, 1960; Estes, 1968; Winward and Tisdale, 1977; McArthur and Plummer, 1978; McArthur, 1979.
2. Morphology and Anatomy. Diettert, 1937; Moss, 1940; Farnsworth and Hammond, 1968; Winward, 1970; McDonough, et al., 1975; Sturges, 1977.
3. Chemistry. Demarchi, 1968; Shafizadeh, et al., 1971; Hanks, et al., 1973; Kelsey, et al., 1976.
4. Physiology. Skiles, 1971; West and Mooney, 1972; Williams and Markley, 1973; DePuit and Caldwell, 1973; Campbell and Harris, 1977.
5. Distribution. Beetle, 1960; Winward, 1970; Morris et al., 1976.
6. History and Paleobotany. Axelrod and Ting, 1960; Wright, et al., 1973; Vale, 1975; Young and Evans, 1979.
7. Communities. Smith, 1969; Daubenmire, 1970; Lewis, 1971; Franklin and Dyrness, 1973; Sabinske and Knight, 1978; Mueggler and Stewart, 1980.
8. Production and Biomass. Pearson, 1965; McGinnies, 1967; Davis, et al., 1972; Rickard, et al., 1974; Uresk, et al., 1977; West, 1972.
9. Phenology. Criddle, 1927; Goodwin, 1956; Price, 1966; Fernandez and Caldwell, 1975; Kleinman, 1976; Sauer and Uresk, 1976.

10. Soils. Robertson, et al., 1966; Hyder, et al., 1966; Houston, 1961; Daubenmire, 1970; Ross and Hunter, 1976; Morris, et al., 1976; Mueggler and Stewart, 1980.

11. Climate. Beath, 1935; Pechanec, et al., 1937; Patten, 1963; Wambolt, 1970; Dirmhirn and Belt, 1971; Despain, 1973; Dina, et al., 1973; Mueggler and Stewart, 1980.

12. Watershed. Van Dersal, 1938; Woodward, 1943; Lusby, 1970; Salih, et al., 1973; Sturges, 1975.

13. Revegetation. Plummer, et al., 1968; Shown, et al., 1972; Hull, 1974; McArthur, et al., 1974; Monsen, 1975; Howard, et al., 1977.

14. Livestock Grazing.

    A. Cattle. Hurd and Pond, 1958; Marquiss and Lang, 1959.

    B. Horse. Olsen and Hansen, 1977; Hansen, et al., 1977.

    C. Sheep. Green, et al., 1951; Spang, 1954.

    D. Nutrition. Smoliak and Bezeau, 1967; Welch and McArthur, 1977.

15. Wildlife Use.

    A. Antelope. Bayless, 1969; Pyrah, 1970.

    B. Big Horn. Schallenberger, 1966; Todd, 1975.

    C. Birds. Klebenow and Gray, 1968; Schroder and Sturges, 1975.

    D. Deer. Smith, 1952; McKean, 1954; Greer, 1960.

    E. Elk. Anderson, 1953; Mackie, 1970; Ward, 1971.

    F. Moose. Harry, 1957; Knowlton, 1960.

G. Small Mammals. Mueggler, 1967; Frischknecht and Baker, 1972.

H. Insects. Pringle, 1960; Furniss and Barr, 1975.

16. Sagebrush Control.

A. Biological. Gates, 1964; Halford, et al., 1973.

B. Chemical. Cornelius and Graham, 1958; Johnson, 1958; Thilenius and Brown, 1974.

C. Fire. Graves and McMurphy, 1969; Britton and Ralphs, 1978.

D. Mechanical. Cook and Stodart, 1960; Plummer, et al., 1968.

Possibly the best single publication for an overview of the current literature and topics for future study is the Proceedings of The Sagebrush Ecosystem: A Symposium (1979), held by the College of Natural Resources, Utah State University, in April, 1978. The 24 contributed articles cover the entire range of subjects, from taxonomy, autecology and synecology, to management strategies and economics.

Chapter 2

DISTRIBUTION

Introduction

Knowledge of the distribution of a taxon contributes to an understanding of the range and limits of the environment in which it may live (i.e. autecology); it may aid in understanding the derivation or causes of plant communities (i.e. synecology), floristic groups and provinces, and life forms (Gleason and Cronquist, 1964). The current distribution in space may also aid in understanding the distribution in time and the phylogenetic relationship to other taxa (McArthur, 1978 personal communication), and may also aid in the extrapolation of research results to areas outside the actual study area.

Distribution of *A. frigida* and *A. ludoviciana* have not been previously mapped. As more is learned about the nature of a species and the communities in which it exists, more detailed delineation of its distribution may be necessary. For example recent research suggests that the response of *A. tridentata* to habitat manipulation differs significantly among subspecies (Winward, 1970; Winward and Tisdale, 1977). A distribution map of all three subspecies of *A. tridentata* throughout its range has not been previously published. Beetle, 1960, described and mapped the various species and subspecies in the Tridentatae section of *Artemisia*. Since that time, additional subspecific taxa have been recognized and proposed (Winward, 1970; Winward and Tisdale, 1977; Beetle and Young, 1965), but distributions have been mapped in only two areas; southern Idaho by Winward (1970) and Montana by Morris, et al. (1976).

This chapter reports on the distribution of *A. tridentata* and its three subspecies, *A. cana* and its three subspecies, *A. frigida* (excluding northwest Canada, Alaska and Eurasia), and *A. ludoviciana*. No attempt was made to map the subspecies of the latter because of the author's unfamiliarity with the complex nature of the subspecific taxonomy. The maps are to be used as a general help in understanding the distribution of these species and should provide a starting place for more detailed mapping, such as published for southern Idaho and western Montana.

Methods

Montana distribution was determined by field observations, examination of herbarium specimens at Montana State University and University of Montana and from personal communication with Drs. R. Kelsey and M. Morris of the University of Montana. Dr. Kelsey kindly provided chemical confirmation of many specimens.

Distribution outside Montana was determined in part by field observations (Saskatchewan, western Wyoming, northcentral Utah), but largely through cooperation with curators of herbaria in Alberta, Arizona, British Columbia, Colorado, Kansas, Nebraska, Nevada, New Mexico, Oklahoma, Washington and Wyoming. Dr. A. H. Winward provided the distribution in Idaho and Oregon and Dr. E. D. McArthur provided help with the entire region. Additional data were obtained from state and regional floras, and from journal articles.

Results

Species of the genus *Artemisia* occur in all states and provinces of western North America, from Alaska to Mexico and the Great Plains to the Pacific Coast. Members of the genus are dominant in many plant communities from Baja, Mexico and northern New Mexico to southern British Columbia and Saskatchewan, Canada, and from the eastern slope of the Cascade and Sierra Nevada mountains to the east slope of the Rocky Mountains in Colorado and the Northern Great Plains of the western Dakotas.

Artemisia tridentata occurs from southern British Columbia, Alberta and Saskatchewan to central New Mexico, northern Arizona and northern Baja, Mexico. The western limit is the Cascade, Sierra and coastal southern California and northern Baja mountains. The eastern limit is the Rocky Mountains in the southern half of its range and the western Dakotas in the northern half of its range.

Subspecies *tridentata* (Basin Big Sagebrush) is distributed west of the Pacific-Atlantic divide (Figure 2.1) except for a few areas

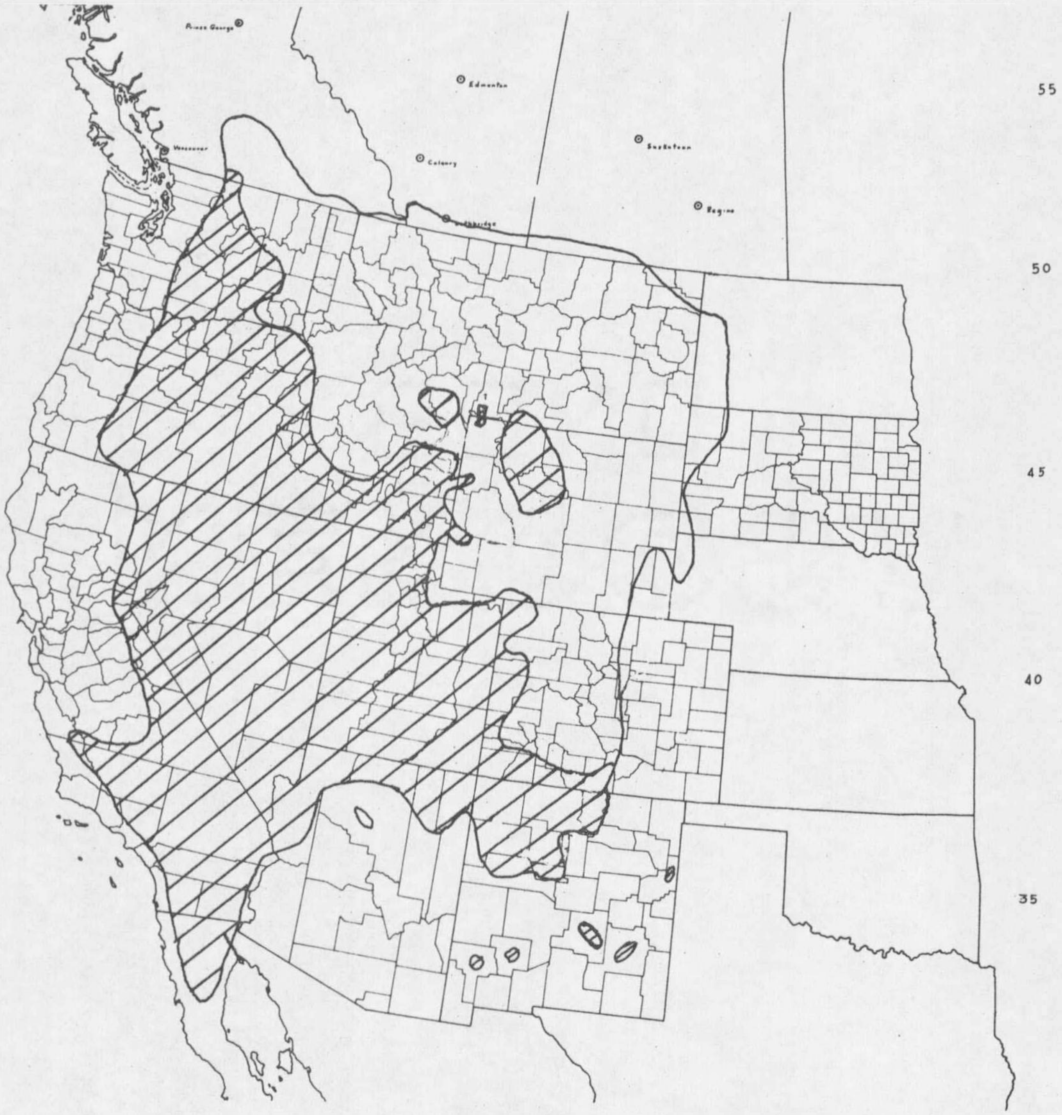

Figure 2.1 Distribution of <u>Artemisia</u> <u>tridentata</u> (entire circled area) subspecies <u>tridentata</u> (hatched area)

just east of the divide in Montana and Wyoming (Madison, Park and Carbon counties, Montana and Yellowstone National Park, Big Horn Basin, Wind River Basin, Wyoming). In the extreme southwest, it occurs at elevations as low as 150 meters (Beetle, 1960), but in the central Great Basin and Colorado Plateau regions it is found on mountain slopes from 1500 to 2100 meters. West, et al. (1975) report that *A. t. tridentata* does not occur in the woodlands of the southern Great Basin. It is found at progressively lower elevations as one travels north, until it is found on the lower mountain slopes and valley bottoms in the northern Great Basin. In the Snake River plains, Columbia Basin and Northern Rocky Mountains, it prefers alluvial benches or coarse textured, well drained slopes from 750 meters to 2100 meters in elevation (personal observation and Winward, 1970).

Subspecies *vaseyana* (Mountain Big Sagebrush), Figure 2.2, is similar in range to subspecies *tridentata*, but is absent from the most southern portions of the species range and extends east of the continental divide in Montana and Wyoming. In the northerly parts of its range, *vaseyana* occurs from the lower mountain valleys to the mountain slopes and ridges as high as 3000 meters (Beetle, 1960; Winward, 1970). In the southerly portion of its range, it is restricted to the higher mountain ranges of the Great Basin, Colorado Plateau and southern Rocky Mountains. In Montana, it is not found

Figure 2.2 Distribution of <u>Artemisia</u> <u>tridentata</u> (entire circled area) subspecies <u>vaseyana</u> (hatched area)

east of the Rocky Mountain foothills in the north, nor east of the Little Belt, Big Snowy, Castle, Crazy or Beartooth Mountains. The *A. tridentata* occurring in habitat types described by Mueggler and Steward (1980) is almost solely subspecies *vaseyana* (see *wyomingensis* below), and is the principle subspecies in the *Pinus flexilis*, *P. ponderosa* and *Pseudotsuga menziesii* described by Pfister, et al., 1977 (*P. ponderosa/Andropogon* ssp. and *P. ponderosa/Prunus virginiana* habitat types contain only subspecies *wyomingensis*).

Subspecies *wyomingensis* (Wyoming Big Sagebrush) is found on large areas both east and west of the continental divide (Figure 2.3). In the Great Basin it occurs mainly in the southern portion in the driest, warmest kinds of woodland sites (McArthur and Pope, 1975) and is lacking in the northern portion and on the central Nevada mountain ranges. In Idaho and Oregon, subspecies *wyomingensis* prefers generally shallow soils in the drier, hotter portions of the area at elevations from 750 to 2000 meters (Winward, 1970, and 1977 personal communication). In Oregon, it covers more area than any other species or subspecies of *Artemisia*. In Montana and Wyoming, subspecies *wyomingensis* is principally found east of the continental divide foothills. In Wyoming, however, it occurs west of the divide in the Green River drainage. In Montana, it occurs principly east of the foothills of the Rocky Mountains and the outlying Little Belt, Castle and Crazy Mountain ranges; however, it also extends into southwestern Montana

Figure 2.3 Distribution of Artemisia tridentata (entire circled area) subspecies wyomingensis (hatched area)

in parts of Beaverhead, Madison, Jefferson, Meagher and Park Counties, and west of the continental divide in Silverbow County. I often saw hybridization with subspecies *vaseyana* along this narrow corridor, especially from White Sulphur Springs, Meagher County, to Gardner, Park County (also R. Kelsey, 1975 personal communication). In the corridor area, subspecies *wyomingensis* is present only in the driest of the grassland and shrubland habitat types described by Mueggler and Stewart (1980), and is the only subspecies in eastern Montana in the habitat types of Pfister, et al. (1977). It prefers fine textured soils in areas with 300 to 400 mm of precipitation at elevations from 750 to 2000 meters.

Artemisia cana, Figure 2.4, occurs generally from southern Alberta and Saskatchewan to South Dakota and southwest to northern New Mexico and Arizona, west to eastcentral California and north to central Oregon and southern Idaho. Three essentially allopatric, subspecies are recognized (Beetle, 1960).

Subspecies *cana* (Silver Sagebrush) occurs east of the continental divide (except for Yampa River valley, Colorado) in Wyoming and Montana north to southern Alberta and Saskatchewan and east to the western Dakotas and northwest Saskatchewan and east to central North and South Dakota and northwest Nebraska. Several disjunct populations occur in the eastern Dakotas. This subspecies prefers a variety of soils on alluvial benches and ephemeral water courses below 1550 meters, where

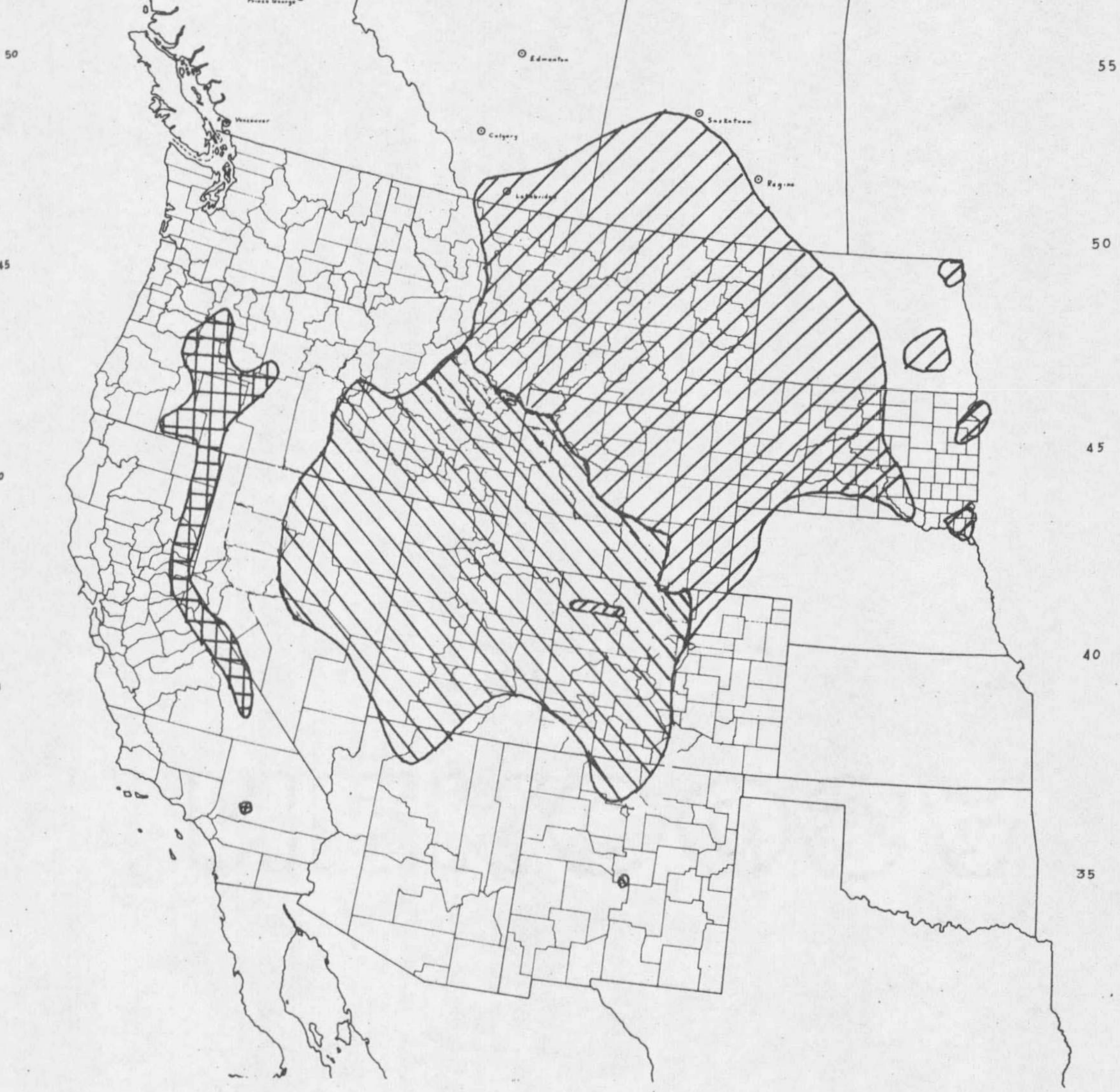

Figure 2.4 Distribution of Artemisia cana subspecies cana (right slanted hatching), subspecies viscidula (left slanted hatching) and subspecies bolanderi (cross hatching)

it root sprouts abundantly (see Chapter 8, Vegetative Reproduction). It often is found in mixed stands with *A. tridentata* (principly subspecies *wyomingensis*) and, in western Montana, it occasionally occurs in *Festuca idahoensis/Agropyron smithii* and *F. idahoensis/A. spicatum* grassland habitat types (Mueggler and Stewart, 1980) and in *A. tridentata (vaseyana)/F. idahoensis* shrubland habitat type. Graham (1978) has described an *A. cana/F. idahoensis* community type in Yellowstone National Park.

Subspecies *viscidula* (Mountain Silver Sagebrush) is restricted in distribution to rangelands west of the continental divide (except Beaverhead County, Montana) from southern Idaho and southwestern Wyoming south to northern New Mexico and Arizona. It occurs along mountain streams and on open, wet mountain slopes above 1500 meters (in the Great Basin it is above 2100 meters). In Montana, it occurs only in the southern Big Hole valley and the Red Rock River drainage south of Dillon, Beaverhead County; subspecies *cana* does not occur in the same area (Morris, et al., 1976).

Subspecies *bolanderi* (Bolanders Silver Sagebrush) is restricted to the central basins of Oregon and south along the California border to Inyo County, California. An isolated population also occurs in the San Bernadino Mountains (Beetle, 1960). Alkaline habitats are preferred.

Artemisia frigida (Fringed Sagewort) occurs in the Kirghiz Steppe of Kazakhstan (Russia) to the Kuznetsk Basin (Southern Siberian Lowlands) and the Trans Baikal region of Russia to the Gobi Desert in southern Mongolia. In North America, it occurs from Alaska and western Northwest Territories south along the Rocky Mountains to southern British Columbia, northern Arizona and New Mexico, and east to the Great Plains of Colorado, central Nebraska, western Minnesota, central Saskatchewan, and Alberta (Figure 2.5). It is also found in some of the higher ranges of the eastern Great Basin.

In Eurasia, *A. frigida* increases with grazing and is used as an indicator of steppe condition (Nemtsov, 1963; Savchenko, 1972, 1973); it colonizes mine spoils in southern Siberia (Tarchevskii and Chibrik, 1970). In North America, it is common in mixed prairie and mountain grassland from central Alberta south, as well as in shrublands and open, dry forests from eastern Montana to the southern Rocky Mountains and the higher ranges of the Great Basin. It has been considered an increaser under grazing pressure (Johnson, 1956; Marquiss and Lang, 1959; Smoliak, 1974; Currie, 1976; Ross and Hunter, 1976). In Montana, *A. frigida* occurs in all but the wettest grassland and shrubland habitat types of Mueggler and Stewart (1980) as well as the dry forest types of Pfister, et al. (1976).

Artemisia ludoviciana (Louisiana Sagewort) is widely distributed in North America (Figure 2.6), occurring from the foothills of the Rocky Mountains in northwest Alberta and the Northwest Territories

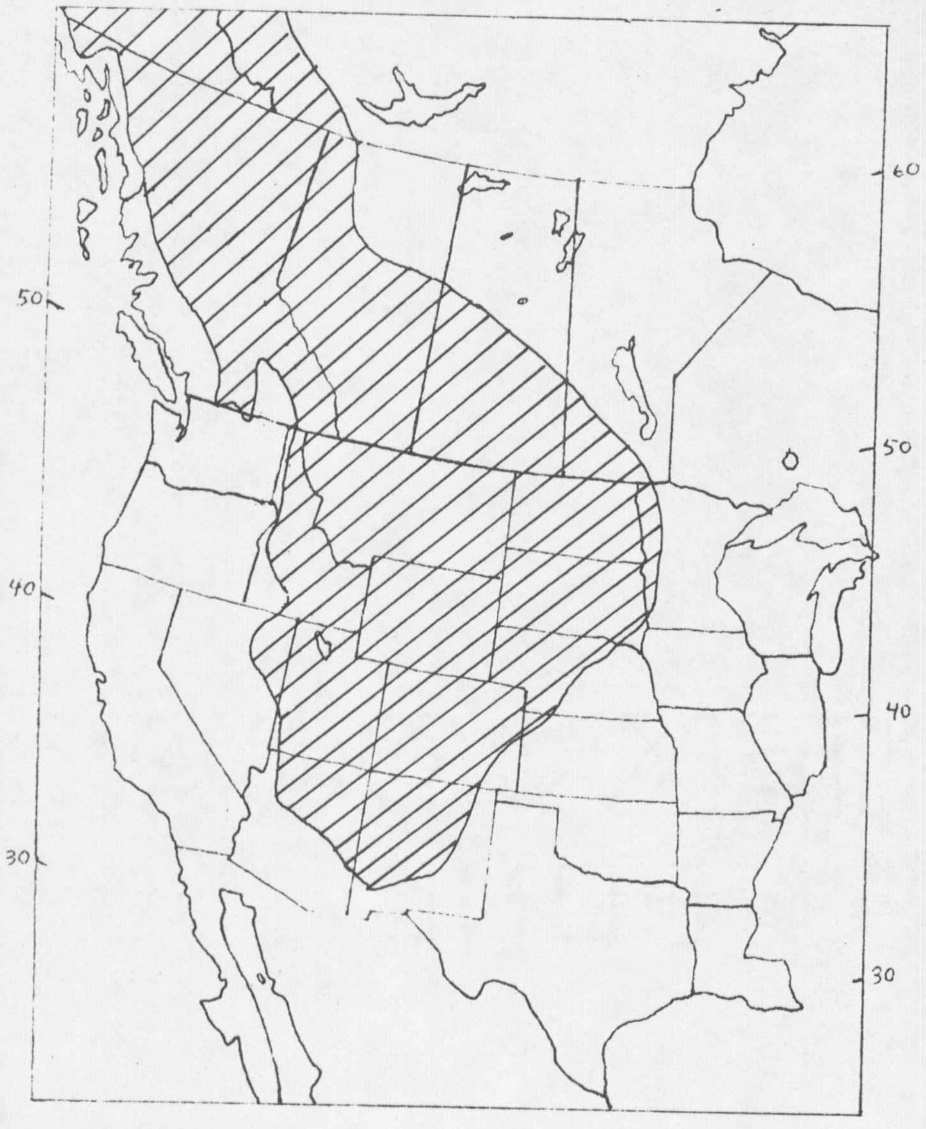

Figure 2.5 Distribution of Artemisia frigida in North America south of 60° north latitude

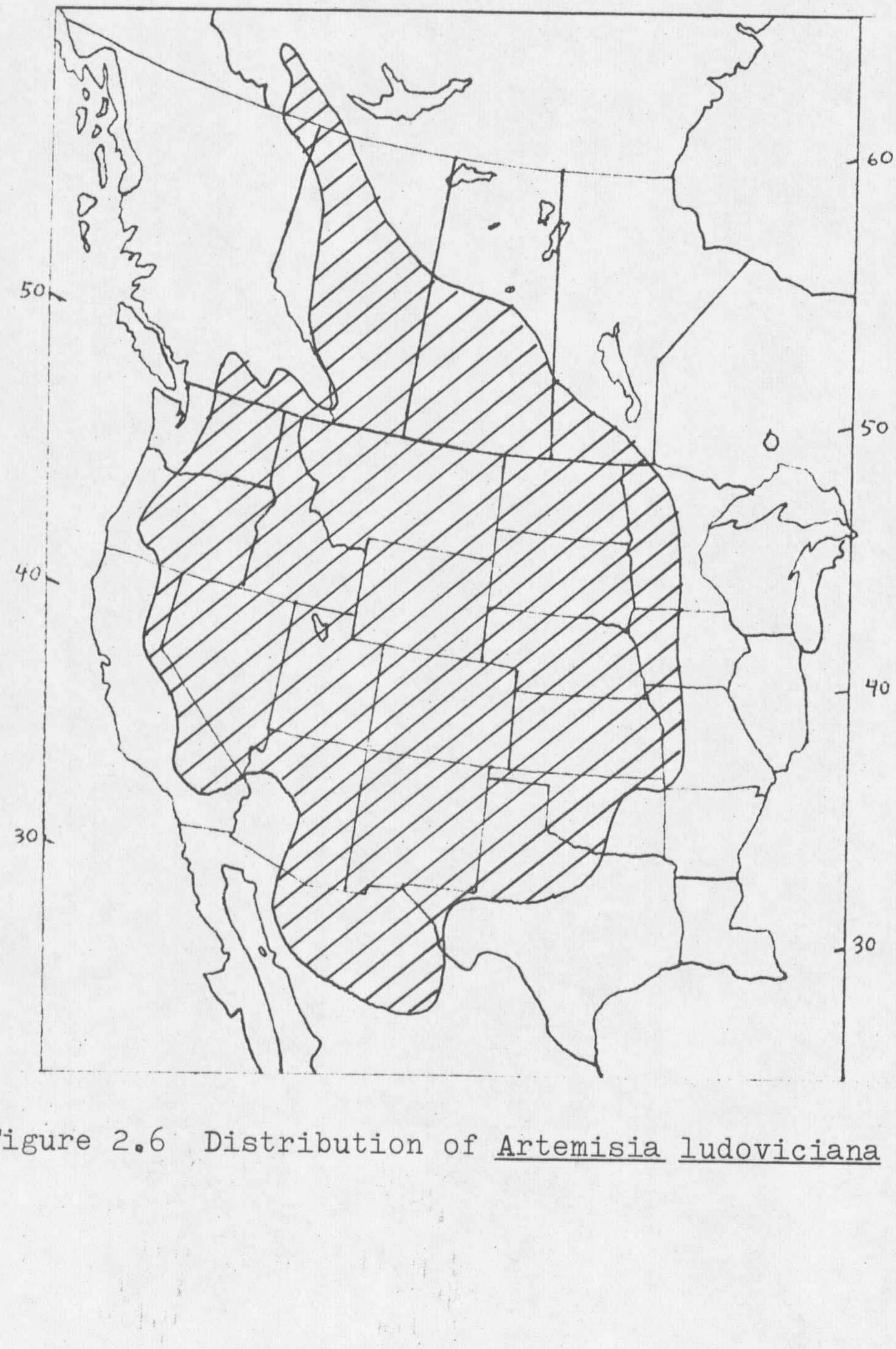

Figure 2.6 Distribution of Artemisia ludoviciana

south through the plains of Alberta, Saskatchewan, Minnesota, Iowa and Missouri, and west and south to northern Texas, Mexico, California, Oregon and Washington. I made no attempt to map the subspecies; at least eight are recognized. This species is occasional in dry to wet grasslands, shrublands and open forests as high as 2750 meters where it may hybridize or integrade into *A. mishauxiana* (Hitchcock, et al., 1955). In Montana it occurs in the dry to moist grasslands, shrublands and open forests throughout the state, and is a common roadside plant. As yet, there is little published information on this species, but some references relate to wildlife use (e.g. Urness, et al., 1977). Estes (1968) did a taxonomic study in the Pacific Northwest, Farnsworth (1975) found nitrogen fixing root nodules, and its use in revegetation has been proven effective by Monsen (1975).

Chapter 3

PHENOLOGY

Introduction

The seasonal development of a plant population provides valuable information about the average periods of activity (Larcher, 1973). Although seasonal development is genetically determined, the activity is set in motion by environmental factors such as light, heat and moisture (Daubenmire, 1968). Seasonal development may also be halted by the presence or absence of those same environmental factors. Phenological descriptions provide clues to the relative importance of the factors. This chapter reports on the phenological stages of four *Artemisia* species and the possible environmental influences on those stages.

The majority of the published data on *Artemisia* phenology considers only the species *A. tridentata*, and the observations are usually general in nature, with several phenological events considered collectively as a unit. Nevertheless, they do serve to establish the yearly and geographical variation in the initiation of easily recognizable stages. Some papers report on the phenology of the entire community containing *Artemisia* (Criddle, 1927; Stevens, 1956; Budd and Campbell, 1959; Kleinman, 1976). Others report on phenology as related to chemical composition (e.g., Cook and Harris, 1950;

Robertson and Cords, 1956; Hyder, et al., 1962; Robocker, et al., 1965).

Methods

Ten individuals of each of four species were selected at each of six sites across southern Montana to observe the phenological stages. For the species *A. tridentata*, subspecies *vaseyana* was measured at three sites (Bozeman and Springhill, southwest; Greycliff, south central) and subspecies *wyomingensis* was measured at three sites (Columbus, southcentral; Custer and Colstrip, southeast). At each location, several small branches on each selected shrub were marked with colored thread for observation of apical, lateral and floral branch growth. Individual leaves on the shrubs were marked with India ink to observe leaf abscission and drop. The non-shrubs were studied at all six sites. For *A. frigida*, the whole plant was tagged for observation. Single stems of *A. ludoviciana* were marked for observation and portions of the clone excavated in the spring to determine the onset of apical growth. Additional data were recorded about the surrounding population at these six sites and subsidiary sites in Montana, Idaho and Utah. The percent of the population in a given phenological stage was estimated at each locale (modified after West and Wein, 1971).

Results and Discussion

The date of initiation of a phenological stage in Montana was remarkedly similar in all five taxa (for elevations below 1800 meters; phenology above 1800 meters will be discussed at the end of this section). Except for extreme northwest Montana, initiation of any stage in any taxon usually occurred within seven days of each other. Of course, some variation in stage initiation occurred between years, locales, stands in a locale and even sites within a stand, and, in extreme cases, as much as 30 days separated the extremes across the state (less than 5 percent of the total state population).

Figure 3.1 summarizes observations over a three year period of observation. Post dormancy activity began with apical bud swelling in the first week of April; twig elongation followed within two weeks. Vegetative growth of the shrub species lasted longer than in the non-shrubs because of the additional lateral growth. Though *A. frigida* exhibits branching, no growth on lateral buds of the current year was apparent. Lateral growth in the shrub species began when apical growth ceased. In *A. tridentata*, leaves produced on buds that have overwintered are ephemeral and begin shedding when the persistent leaves, formed from lateral buds in the axils of ephemeral leaves, become mature. For a more detailed description of the development and morphology of these two types of leaves, see Goodwin (1956) and