



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

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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*, *A. tridentata*, *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.

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LIFE HISTORY AND REPRODUCTIVE STRATEGIES IN ARTEMISIA

by

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

of

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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. tridentata tridentata*, *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. ludoviciana* 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. ludoviciana*. 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

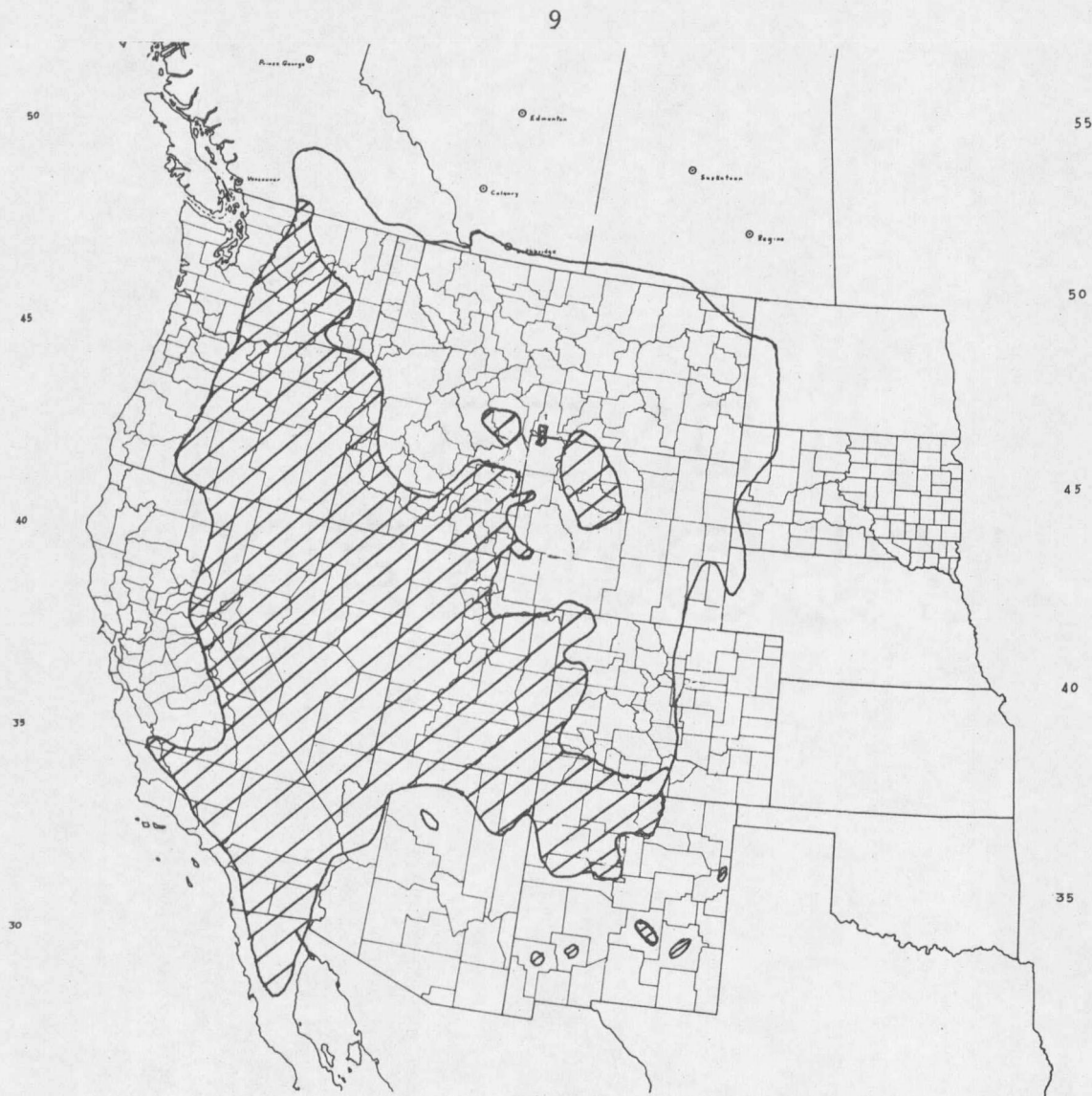


Figure 2.1 Distribution of Artemisia tridentata (entire circled area) subspecies tridentata (hatched area)

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 *Artemisia tridentata* (entire circled area) subspecies *vaseyana* (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 principally 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

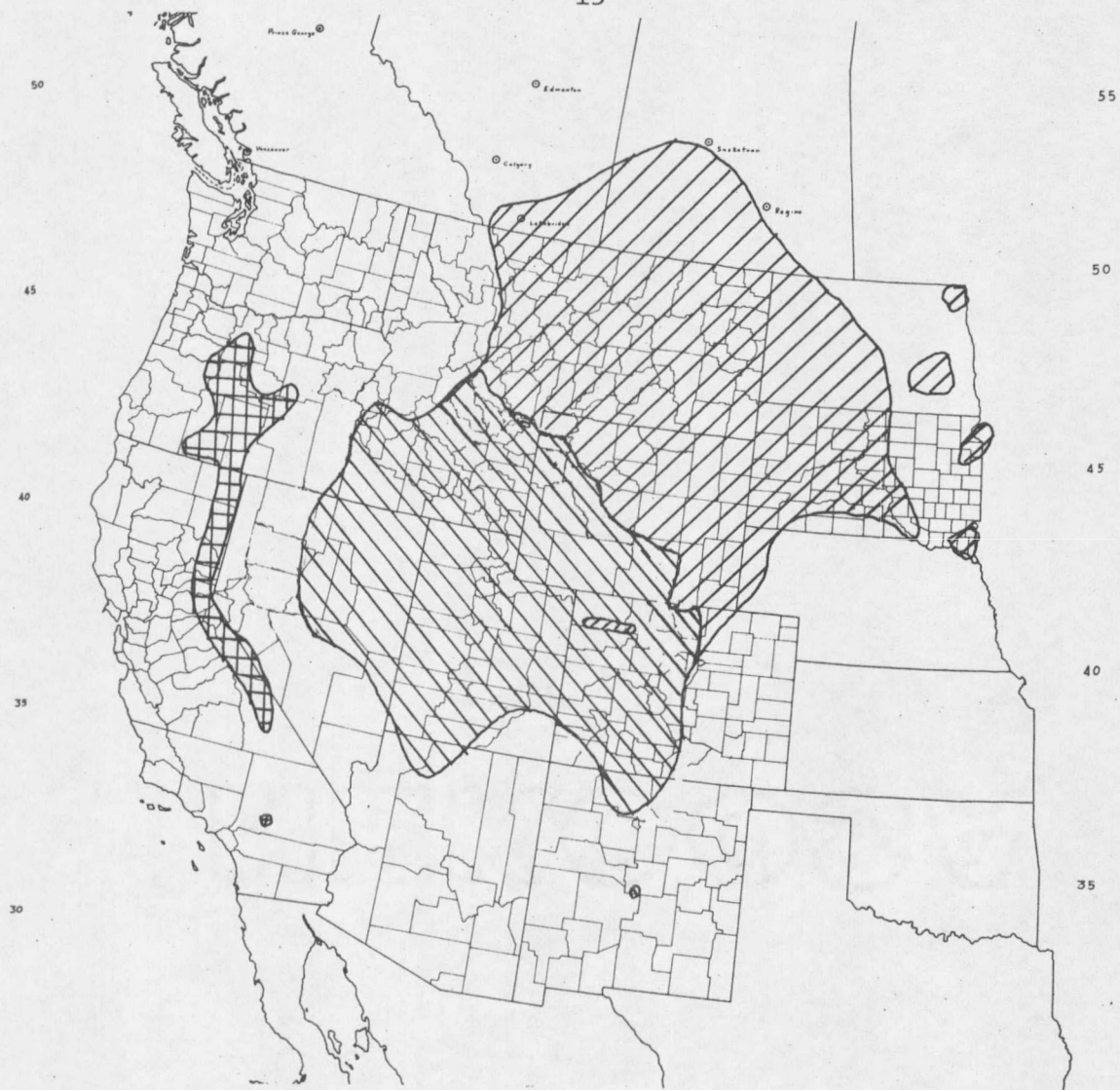


Figure 2.4 Distribution of Artemisia cana subspecies cana (right slanted hatching), subspecies viscidula (left slanted hatching) and subspecies bolanderi (cross hatching)

it root sprouts abundantly (see Chapter 8, Vegetative Reproduction). It often is found in mixed stands with *A. tridentata* (principally 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

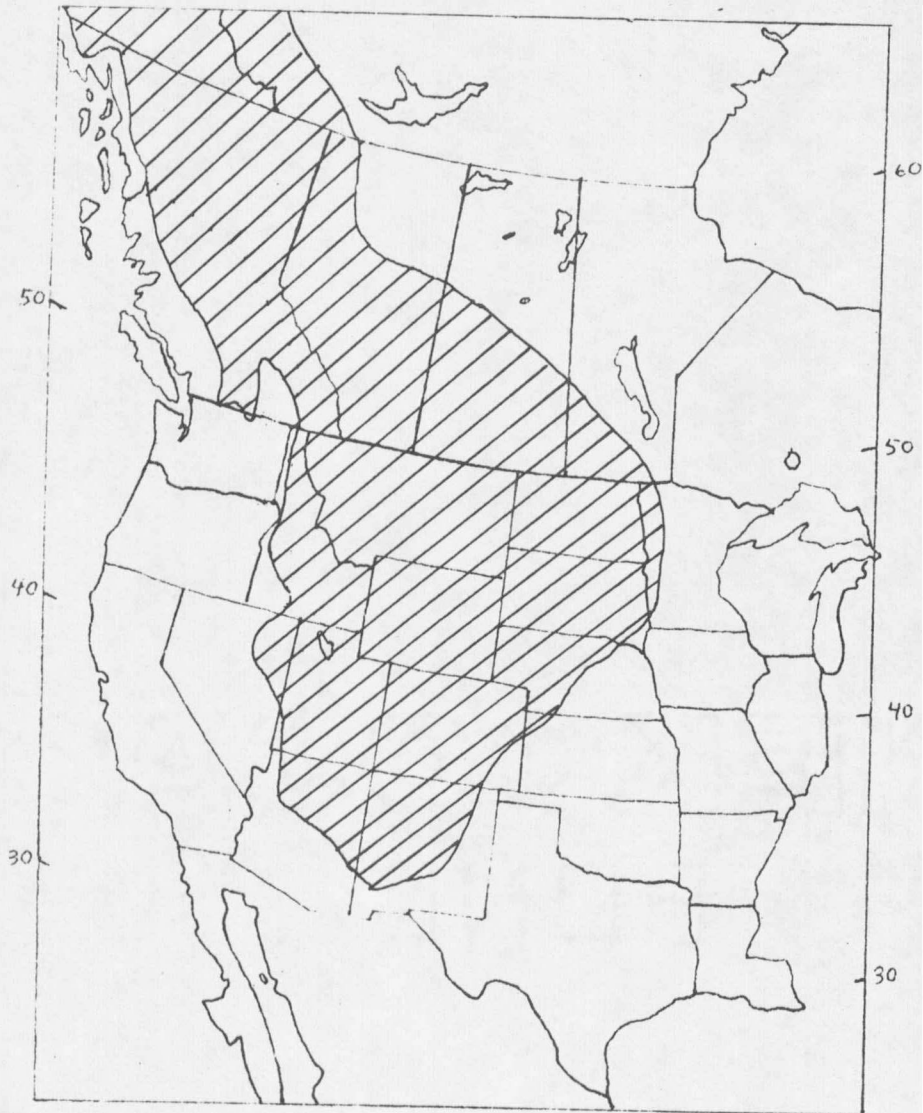


Figure 2.5 Distribution of *Artemisia frigida* in North America south of 60° north latitude

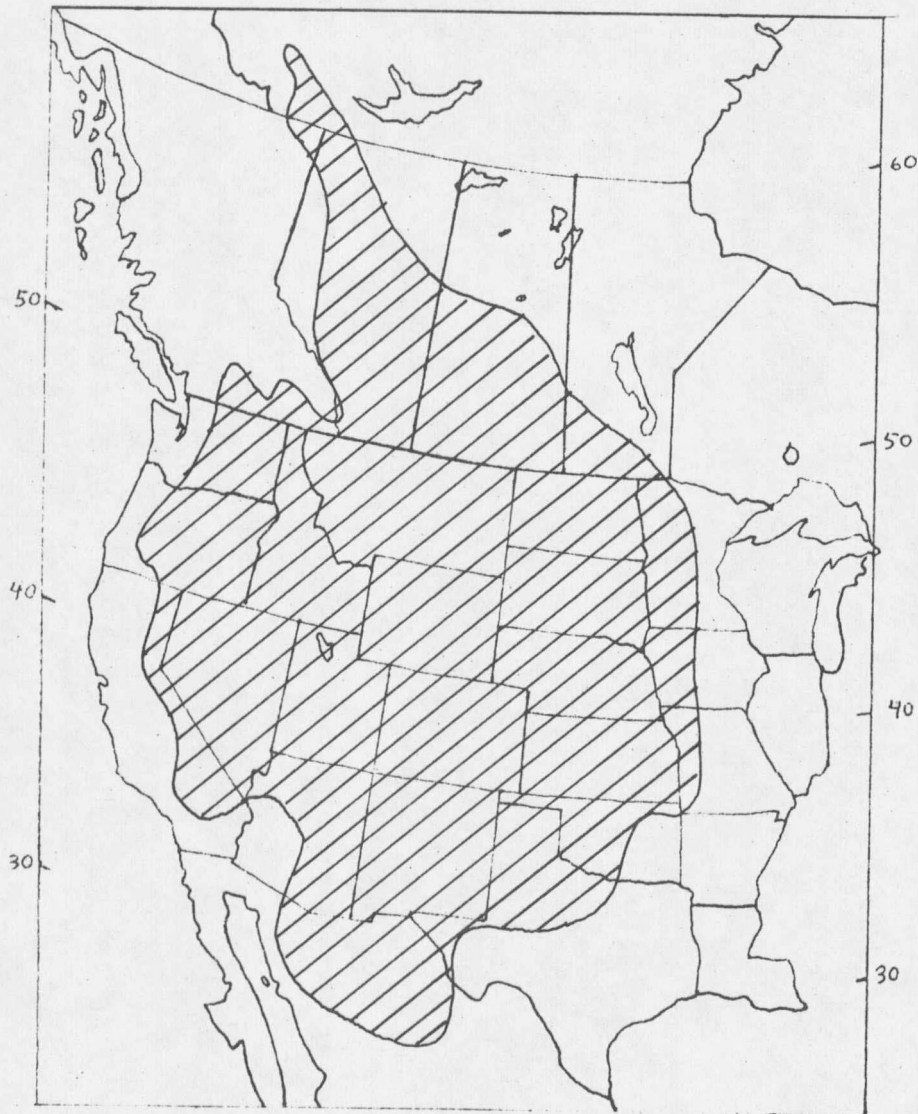


Figure 2.6 Distribution of Artemisia ludoviciana

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 integrate into *A. mishanxiana* (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).

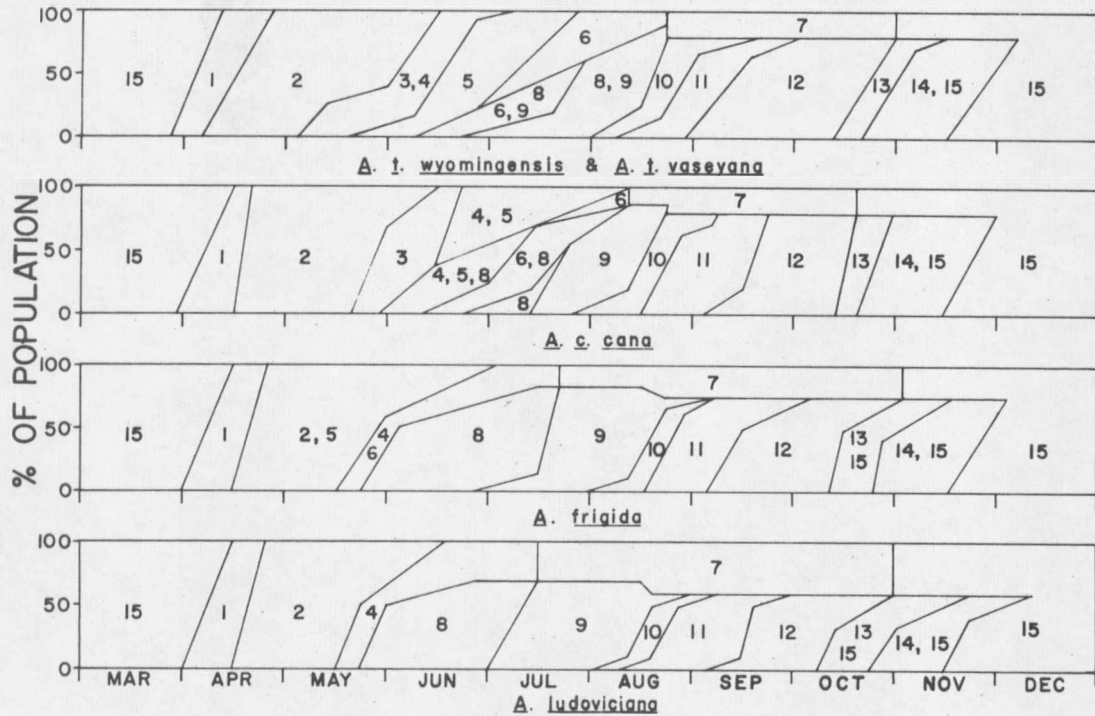
Methods

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, southcentral) 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 remarkably 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



PHENOLOGICAL STAGES

- | | |
|---|-------------------------------------|
| 1 APICAL BUD ENLARGEMENT | 8 FLORAL BRANCH ELONGATION |
| 2 APICAL TWIG ELONGATION
(EPHEMERAL LEAF DEVELOPMENT, ARTR) | 9 FLORAL BUDS ENLARGING |
| 3 LATERAL BRANCH BUD ENLARGEMENT | 10 ANTHER DEVELOPMENT (BUDS YELLOW) |
| 4 APICAL GROWTH CEASES (VEGETATIVE) | 11 ANTHESIS |
| 5 LATERAL BRANCH ELONGATION | 12 CYPSELLA DEVELOPMENT |
| 6 LATERAL GROWTH CEASES (VEGETATIVE)
(EPHEMERAL LEAF ABSCISSION, ARTR) | 13 DISSEMINATION INITIATED |
| 7 INCOMPLETE OR NO FLORAL DEVELOPMENT | 14 DISSEMINATION COMPLETED |
| | 15 WINTER DORMANCY |

Figure 3.1 Phenology of 4 *Artemisia* species. Lines separate the phenological stages listed above; Angle of the line is determined by the proportion of the in a given phenological stage

McDounough, et al. (1975). *A. c. cana* did not have these two distinct sets of leaves as did *A. tridentata*. Leaves produced on apical growth were of two sizes, the larger leaves being produced first. On xeric sites, the larger leaves began dying at the time of floral branch elongation, but on mesic sites (the dominant *A. c. cana* habitat), leaf death occurred during the latter part of the floral bud enlargement stage. All apical leaves had been shed by April and lateral leaves by mid-June of the following year. Leaf shedding in both species appears to be regulated by water availability. *A. c. cana* is usually found in more mesic habitats than *A. tridentata*, but where they occur together, *A. c. cana* is rooted deeper (personal observation) and, therefore, has probably not developed the need for a distinct set of ephemeral leaves to reduce the evapotranspirative surface.

Vegetative growth of the non-shrubs began at the same time as the shrubs, but ceased four weeks sooner, corresponding to the cessation of apical growth in the shrubs (Figure 3.1). Although the entire aboveground growth of *A. ludoviciana* could be considered floral growth for those stems that produce an inflorescence, for the purpose of this study, that portion of the growth below the inflorescence and equal to the height of stems not producing the inflorescences was considered vegetative growth. This was usually less than 15 cm high (compared to 100 cm for a robust inflorescence). Lateral growth is initiated on the rhizome below ground and was not observed. Lateral

growth was not apparent on *A. frigida*; branching results from apical growth of lateral buds of the previous year.

Anther development and flowering occurred in mid-August to early September and was simultaneous in all taxa (Figure 3.1) except *A. t. vaseyana*, which preceeded the others by seven days. While some plants of each species failed to produce floral growth, the shrubs had fewer plants with no flowers at all. Shrubs on the driest sites initiated floral branch growth but failed to mature the buds or matured only one or two heads of the inflorescence such that the number of inflorescences was markedly reduced. However, the non-shrubs of dry sites mostly failed to produce even aborted inflorescences or visible buds. Conversely, plants of each species on the most mesic sites (e.g. roadsides, runoff channels, depressions) produced more, longer and often profusely branched inflorescences.

The maturation of cypsellas appeared related to available moisture. Xeric sites produced fewer visible seeds and matured seeds 7 to 10 days earlier than mesic sites. This is consistent with the observations of Winward (1970). Dissemination occurred almost simultaneously for all of the species (Figure 3.1). The most viable seeds were dispersed in the first seven days, leaving aborted flowers and half-filled seeds to be dispersed over the next two to four weeks (also observed by Goodwin, 1956). Dissemination of filled and half-filled seeds were completed by mid-December.

Winter dormancy as used in this description includes pre- and post-dormancy quiescence. The true dormancy period occurs somewhere between December and early February since stem cuttings collected in late October and mid-February both rooted in the greenhouse. Aboveground growth of xeric site plants ceased as early as mid-June in the shrubs and mid-May in the non-shrubs.

Geographical variation of stage initiation varies with the year. Vegetative development in Montana began earlier in Utah (1974 and 1975) and Washington (1974) by three weeks and flowering and dissemination were later by the same amount (personal observation and Campbell and Harris, 1975). In 1976, the vegetative events were only one week earlier and flowering only one week later in Utah than in Montana. In northern Utah, West and Fareed (1973) reported pre-flowering stages 4 to 6 weeks earlier than I observed in Montana during 1974, 1975 or 1976. In Montana, *A. t. vaseyana* spring stages were two weeks earlier in the extreme northwest portion of the state than in the remainder of the state.

Artemisia growing above 1800 meters elevation initiated the early phenological stages 2 to 3 weeks later and initiated floral bud enlargement, anther development, anthesis and dissemination two weeks earlier than at lower elevations. This is consistent with Winward's (1970) observations in Idaho. These observations suggest that the early and late phenological stages are influenced by temperature

(higher elevations have a shorter frost-free period).

Insects also influenced the progression of phenological events in local areas. Aphids are common on the inflorescences of the shrubby species and on some plants retarded or aborted floral development (especially often and severe in *A. c. cana*). Aphid infestation was most severe in 1975 and in some areas of eastern Montana, entire stands were essentially devoid of flowers. Grasshoppers also infested eastern Montana rangelands in 1975 and damaged both shrub species by eating the leaves and floral buds of the inflorescence. Entire stands of *A. c. cana* were found stripped of inflorescence vegetation. In 1976, however, only minor damage was observed.

Summary

All five *Artemisia* taxa exhibited very similar phenological stage initiation. Post dormancy activity began with apical bud swelling in the first week of April, followed within two weeks by apical twig elongation. Vegetative growth in the non-shrubs ceased by mid-June but continued for an additional four weeks in the shrubs. Inflorescence initiation occurred in late May to early June and reached full length by mid-July. Anther development occurred in mid to late August, followed by flowering in mid September. Dissemination was initiated in late October and the most viable seed dispersed within seven days.

Above 1800 meters, spring phenology is later and fall stages earlier by two weeks. Phenological stages in Utah and Washington are initiated earlier in the spring and later in the fall than in Montana. Idaho appears to be similar to Montana.

The early stages appear to be influenced mostly by temperature and the middle and late stages influenced by both temperature and water. Campbell and Harris (1975) found cessation of vegetative and initiation of reproductive growth to be correlated with a drop in turgor pressure. Insect predation may halt the progression of phenological stages of reproduction.

Chapter 4

GERMINATION

Introduction

Interest in the conditions which favor *Artemisia* germination has been stimulated by the use of various species as forage and cover for livestock and wildlife, and for erosion control (McArthur, et al., 1975), and by the desire to control stand density in areas where plants of the genus are considered undesirable competitors of livestock forage plants (Pechanec, et al., 1965).

This chapter reports on: 1) studies of germination made both in the laboratory and the field, 2) studies of temperature effects on germination, 3) possible causes of variability in previously reported germination results, and 4) the effect of planting depth on seedling emergence.

Methods

Seed collection - Seeds for 1974 germination and planting tests were obtained from the Department of Animal and Range Science, Montana State University. These seeds were collected during the 1972 season from an undetermined Montana location and stored at room temperature. I collected seeds for all other tests and plantings during October 1974 and 1975 from numerous locations across southern Montana.

Extraction and Cleaning of Seed - To collect seeds, entire inflorescences were clipped, placed in bags, and air-dried for one week at room temperature. The floral branches were hand stripped and the strippings rolled through a graded series of seed screens to a final mesh size of 2mm X 4 mm. The material not passed through the screens contained no viable seed. That portion passing through the screens contained a mixture of seed and dried floral parts. This material was fed into an Antlers Custom Manufacturing model CS-1 head thrasher and both the seed fraction and the chaff fraction were retained and stored at room temperature in sealed glass bottles. At the time of seed use, the remaining extraneous debris and aborted seeds were removed by hand with a teasing needle.

Germination Tests: Petri Dish - The seeds were germinated in 9 cm glass petri dishes on two layers of Whatman No. 3 filter paper (W & R Balston, Ltd.) wetted to saturation with distilled water. The dishes were stacked 5 high in an open metal box stored at room temperature ($20^{\circ} \pm 1^{\circ}\text{C}$) with a 10 hour photoperiod (1200 lumens/m^2). The dishes were inspected and systematically rotated daily for each two week observation period. This period was determined to be sufficient from two 30 day trial tests. This test was modified from Goodwin (1956) and McDonough and Harniss (1974a).

Because fungal growth became prominent in the petri dishes (except in *A. ludoviciana*) and may have reduced germination, the

tests were repeated using seed powdered with a fungicide, Arasam 75 (tetramethylthiuramdisulfide). Five replications each of treated and untreated seed (50 seeds/replication) were used for each seed lot.

Autopathy was tested using seed from 1975 in a modification of the above method (Klarich and Weaver, 1973). A 1 cm open petri dish containing 0.1 gm of crushed leaves or crushed seed was placed within the large petri dish containing the seeds for germination analysis. These seeds were then exposed to the odor of the crushed material. Three replications each of crushed leaves, crushed seeds, and an empty 1 cm dish were tested. Each taxon was tested only against itself (ie. *A. frigida* seed was tested with crushed *A. frigida* leaves and seeds).

Germination Tests: Temperature Gradient Bar - Germination at constant temperatures ranging from 6° to 30° C was tested with a temperature gradient bar (modified from Barbour and Racine, 1967).

The temperature gradient bar (Fig. 4.1) was constructed of three 8 mm thick plastic coated aluminum plates, each 15 cm wide and 90 cm long, with each end resting on two 2.5 cm square aluminum tubes. The tubes at one end circulated 0° C isopropyl alcohol, cooled and pumped by a Brinkman Instruments Lauda K-2/R controlled temperature circulator. The tubes at the other end circulated distilled water heated to 35° by a National Appliance Company model 2725 water bath and pumped with

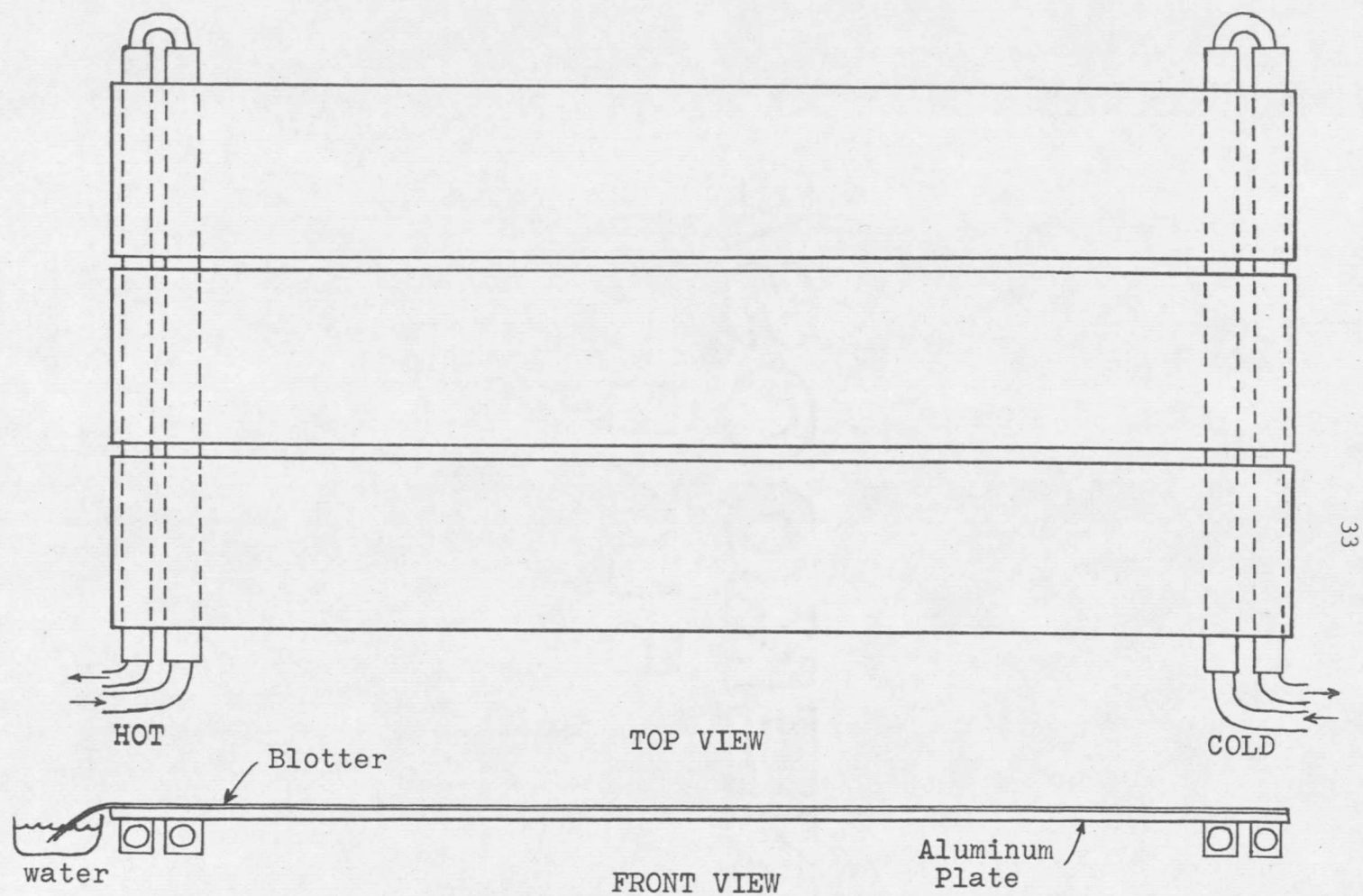


Figure 4.1 Temperature gradient bar schematic diagram

a centrifugal-type immersible pump (Little Giant Pump Company, Oklahoma City). Both the plates and the tubes were insulated from below by 5 cm of styrofoam.

Each plate was covered with Anchor Paper Company Steel Blue Blotter. The blotter projected beyond the 30° C end of the plate and into a distilled water bath to maintain a constant moisture level. A box style cover of 8 mm clear plexiglass was constructed to create 3 chambers, each 7.5 cm high and the length and width of one aluminum bar. A 10 hour photoperiod was maintained with a 200 watt clear bulb 60 cm above the bar surface (1000 lumens/m² at the bar).

The resulting temperature gradient was a linear 0.3° C per cm, and the temperature at any one location was maintained $\pm$ 0.5° C. Twenty seeds of each species were placed in a row at each desired temperature and checked daily for the first four days, then every other day to 14 days. Germination was considered to occur when either radical growth or cotyledon emergence was observed. Twenty-four replications were made for seed collected in 1974, except for *A. t. vaseyana* where only ten replications were conducted. Ten replications were made for seed collected in 1975.

Germination Tests: Greenhouse Soil and Planting Depth - Seeds were planted on the surface and at 2.5 mm, 5.0 mm, and 7.5 mm depths in

two soil types (silty loam and loamy sand) in the greenhouse and sub-irrigated daily to maintain a saturated soil moisture. Eight replications in each soil type were made in January and February, 1976. Seed from 1975 was used for these tests. The soil temperature was $15^{\circ} \pm 1^{\circ} \text{ C}$ during both tests.

Germination Tests: Field Planting - Three locations were chosen in Montana for field tests. Site 1 was located at the Montana State University Horticultural Experiment Farm in Bozeman (southwestern Montana). Sites 2 and 3 were 5% north and south slopes respectively, located at the Western Energy Mine, 6.5 kilometers south of Colstrip (southeastern Montana). Soils were as follows: site 1, Pachic Cryoboroll silt loam; sites 2 and 3, Ustic Torreforthent sandy loam. Table 4.1 lists weather data for the sites.

The test sites were prepared by disking and hand raking. A randomized complete block design with eight blocks per site was used for all plantings. Two blocks at site 2 were eliminated in 1975 due to erosion. One thousand seeds per species per block were sown in rows by hand and covered with approximately 2 mm of soil. Germination was indicated by emergence. The data was analyzed using analysis of variance and least significant difference (LSD) tests.

In 1974, planting was done in June, with a sprinkling system used to provide adequate water. Plantings for 1975 and 1976 were made

Table 4.1 Temperature and precipitation data characterizing study sites at Bozeman and Colstrip, Montana; U.S.D.A. Weather Bureau 1974, 1975, 1976

Montana State University, Bozeman								
Temperature ($^{\circ}\text{C}$)					Precipitation (cm)			
	Norm	1974 ^a	1975	1976	Norm	1974 ^a	1975	1976
Jan	-6.2	0.3	1.2	3.2	2.34	-1.27	1.68	-0.81
Feb	-3.2	3.2	-2.7	2.3	1.65	-0.56	1.17	-0.33
Mar	-1.2	1.5	-0.4	-0.7	3.66	0.69	-0.91	-1.04
Apr	5.5	2.2	-4.9	0.8	4.47	0.23	-0.03	3.99
May	10.4	-1.4	-2.2	2.6	6.78	0.84	5.61	-1.83
Jun	14.2	3.7	-0.8	0.4	8.18	-5.74	0.61	1.98
Jul	19.1	2.0	1.6	0.9	3.30	-2.08	1.50	0.86
Aug	18.3	-1.0	-1.5	-0.4	3.48	3.25	-0.61	-1.47
Sep	12.9	0.2	0.3	1.7	4.47	-0.76	-0.23	3.89
Nov	7.7	1.6	-0.2	-0.2	3.71	0.36	7.19	0.79
Dec	0.3	1.4	-1.1		3.20	-1.50	0.18	
Year	6.2	+1.17	-0.7		47.40	-6.07	+16.84	

Colstrip, Montana								
	Norm	1974 ^a	1975	1976	Norm	1974 ^a	1975	1976
Jan	-6.1	-0.6	3.5	4.6	1.42	-1.22	-0.54	-0.33
Feb	-3.0	4.7	-3.4	3.9	1.42	0.91	-0.36	0.10
Mar	0.1	2.8	-0.4	0.7	1.88	-0.58	1.45	-0.97
Apr	7.1	2.2	-2.8	1.7	4.72	3.02	1.62	0.69
May	12.4	-1.5	-0.7	1.9	6.27	3.10	2.01	0.91
Jun	17.1	2.6	-0.4	0.8	8.41	-5.74	-1.99	0.56
Jul	21.9	1.9	0.3	2.9	3.00	2.01	0.89	-2.34
Aug	21.2	-4.0	0.7	0.8	3.53	-0.69	0.23	-2.90
Sep	15.4	-1.5	1.1	3.2	3.51	-0.64	-0.10	-1.78
Nov	1.3	1.4	-0.4		1.70	0.38	-0.64	
Dec	-2.9	3.0	4.4		1.60	-0.86	-0.94	
Year	7.9	+1.0	+0.2		40.11	+6.60	+5.87	

a) The numbers under year headings represent deviations from the norm.

in November of the preceeding year.

Germination in native plant communities (*A. tridentata*/*Stipa comata* and *Bouteloua gracilis*/*Stipa comata*) was attempted, but the inability to distinguish the emerging *Artemisia* from other emerging species rendered the data too unreliable for use,

A. t. vaseyana was not used in field planting because its distribution is restricted to the western half of the state in Montana and is therefore not found in the vicinity of Colstrip; *A. t. wyomingensis* is found in all the southern counties of Montana and occurred naturally near all the planting sites; and therefore was selected as the only subspecies of *A. tridentata* to be planted.

Results and Discussion

Laboratory and Greenhouse Germination

The highest average germination for all species was obtained on the temperature gradient bar. The lowest average germination occurred in the petri dishes, except of *A. ludoviciana* which had its lowest in the soil tests. There were no differences between the two subspecies of *A. tridentata* in any of the germination tests (Table 4.2). Germination rates (expressed as the time to reach one-half the final germination) were generally fastest on the gradient bar and slowest in the soil tests.

Germination rates were faster for all species when a fungicide

Table 4.2 A comparison of Artemisia laboratory germination percentage and rates on filter paper in petri dishes, on filter paper on a temperature gradient bar and in soil in a greenhouse

	Petri Dish Tests		Soil Test ^b	Temperature Tests		
	Untreated	Treated ^a		15°C	20°C	Optimum ^e
<u>A. t. vaseyana</u>	47/6 ^c	47/3	76/9	94/3	85/3	9 /3
<u>A. t. wyomingensis</u>	49/6	46/3	75/9	95/3	86/3	96/3
<u>A. c. cana</u>	51/6	64/4	75/9	97/3	93/3	97/3
<u>A. frigida</u>	25/6	45/5	69/9	72/3	36/4	81/3
<u>A. ludoviciana</u>	95/4	95/3	69/9	56/4	87/3	90/3

a) Treated with a fungicide, Arasam 75

b) Planted 2.5 mm deep

c) % germination / germination rate^d

d) Expressed as no. days to reach $\frac{1}{2}$ final germination

e) Optimum temperatures are 12, 12, 14, 12 and 22 °C, respectively, for A. t. vaseyana, A. t. wyomingensis, A. c. cana, A. frigida and A. ludoviciana

was applied, but percentage of seeds germinating was significantly increased only in *A. frigida*. The best germination for *A. ludoviciana* occurred in the petri tests, but the other species had their lowest germination here (Table 4.2).

Autopathy was investigated because the fungicide treatment did not increase germination for *A. tridentata* or *A. c. cana* and because *A. t. vaseyana* has been shown to inhibit germination in other species (Klarich and Weaver, 1973). The 'odor' of crushed leaves from its own taxon reduced the germination in *A. t. vaseyana*, *A. t. wyomingensis*, *A. c. cana* and *A. frigida* by $49.9 \pm 7.5\%$, $41.7 \pm 8.3\%$, $43.4 \pm 9.3\%$, and $44.1 \pm 10.8\%$ ($\bar{x} \pm SD$; $P < .01$, $n = 5$) respectively; the 'odor' of seed from its own taxon reduced germination $35.4 \pm 6.2\%$, $33.4 \pm 7.4\%$, $35.1 \pm 8.5\%$, and $24.1 \pm 6.7\%$ respectively. Fungicide treated seed provided the control germinations. *A. ludoviciana* vapors did not significantly reduce its germination ($8.9 \pm 7.3\%$, and $8.3 \pm 5.2\%$ for leaves and seed, respectively). Hoffman and Hazlett (1977) found that aqueous extracts as well as vapors of *Artemisia* leaves reduce germination in *A. tridentata* and *A. cana*. Though not all the difference between the low petri and the high gradient bar germinations are explained by these results, much of it is. Since the petri test confines the germinating seeds to a smaller volume of air and a smaller filter paper area per seed than does the gradient bar, the concentration of volatile substances in the air and the aqueous

substances in the water will be higher in the petri dish tests and, therefore, the inhibitory effect will be higher as well (see Hoffman and Hazlett). Part of the remaining difference between the tests is probably due to temperature and is discussed later in this chapter.

Germination in a soil medium (Table 4.2) was better than in the petri dishes for all taxa except *A. ludoviciana*, which had its lowest average germination in the soil test (this is also probably due to temperature). All soil germinations were lower than the optimum results from the gradient bar and the germination rates were the slowest of any of the tests. This is at least partially due to using emergence from a planting depth of 2.5 mm rather than emergence of the radical from the seed as an indication of germination. There were no significant differences between soil types.

Several authors have reported that in sagebrush-grass range treated for eradication of sagebrush, there are good years and bad years for reestablishment (Pechanec, 1945; Mueggler, 1956; Johnson, 1958; Daubenmire, 1970). The literature about laboratory germination of *Artemisia* is confined to a single species, *A. tridentata*, and early investigators did not recognize any subspecies.

Considerable variation in germination results has been reported in the literature. Van Dersal (1938) and Stoddard and Smith (1943) reported 35% and 52% respectively, but failed to give the conditions under which the tests were conducted. Payne (1957) reported on

collections from several states, with a wide range of germination results. Shepherd (1937), Goodwin (1956), and Weldon et al. (1959) tested the effects of light, temperature, water and scarification on *A. tridentata* germination; conflicting results are reported. Beetle (1960) and Winward (1970) suggested these conflicting results might be due to differences in seed germinability of individual plants or differences among subspecies. The three subspecies of *A. tridentata* were tested in a series of studies by McDonough and Harniss (1974a, 1974b, 1975, and Harniss and McDonough, 1976). They reported differences between subspecies in the same year, between individual plants of a subspecies in the same year, and in subspecies *tridentata*, differences between years.

In the studies reported here, differences between individuals were averaged out by collecting seed from several plants at each collection location and combining them into a common seed lot. No significant ($P < .05$) differences were found between locations or years for any of the *Artemisia* taxa, and no differences were found between the subspecies *vaseyana* or the subspecies *wyomingensis* or *A. tridentata* in Montana. *A. t. tridentata* was not tested in this study.

The germination results reported by other authors compare more favorably with the results of the petri tests reported here than with the gradient bar results. This is expected, since most of the authors reported using petri tests of similar design. The low

germination in the petri tests reported here and in the literature is probably due to autopathy and temperature. Further studies of autopathy should be conducted, using a more open system such as the temperature gradient bar, to determine if the relatively common petri test method is valid as an indicator of the viability of a seed crop.

Temperature Effects on Germination

The shrubby taxa (*A. t. vaseyana*, Figs. 4.2, 4.7; *A. t. wyomingensis*, Figs. 4.3, 4.7; *A. c. cana*, Figs. 4.4, 4.7) have optimum germination over a greater range of temperature, 12° - 18° C, than the suffrutescent (*A. frigida*, Figs. 4.5, 4.7) which has the coolest optimum, 10° - 14° C, or the herb (*A. ludoviciana*, Figs. 4.6, 4.7) which has the warmest optimum, 20° - 23° C. No differences between years or collection locations for any species or between *A. t. vaseyana* and *A. t. wyomingensis* were found. Germination rates (half-times) were slower for temperatures both above and below the optimum for each species. Germination tests conducted for 30 days (versus 14 days) significantly improved the final germination only at 6° C; + 10% for *A. tridentata* and *A. cana*, + 25% for *A. frigida*, and + 3% for *A. ludoviciana* (Figs. 4.2 - 4.6).

The optimum temperatures reported by McDonough and Harniss (1974a) for *A. tridentata* germination compare well with my findings though the former tested germination only at 10°, 20°, and 30° C. They reported

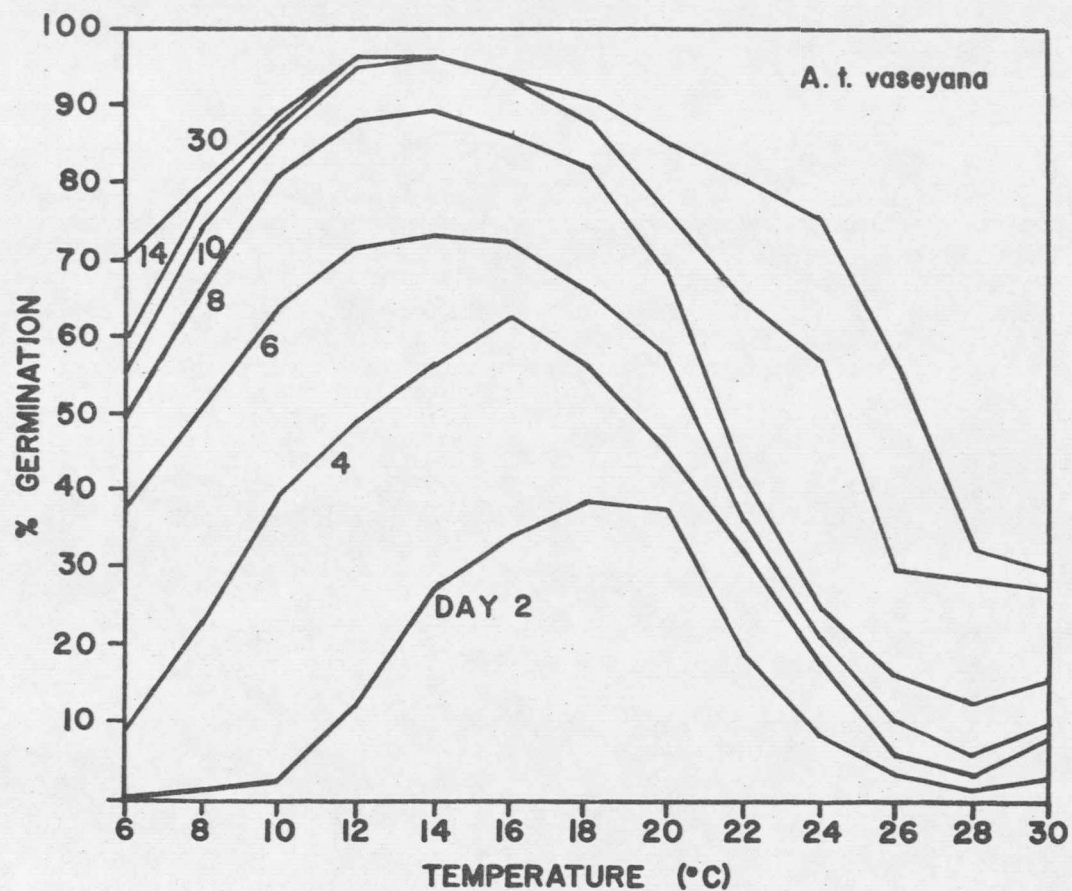


Figure 4.2 *A. t. vaseyana* germination (%) after 30 days on a temperature gradient bar at temperatures from 6° C to 30° C

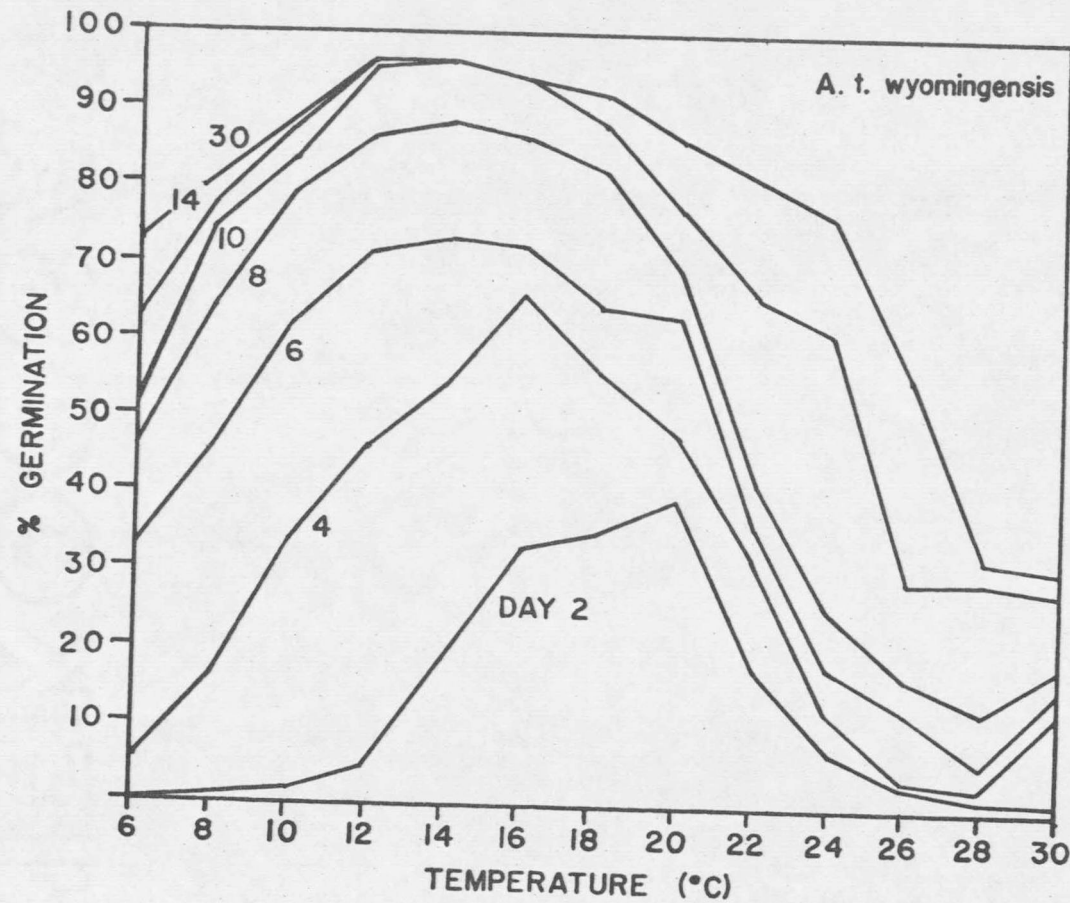


Figure 4.3 *A. t. wyomingensis* germination (%) after 30 days on a temperature gradient bar at temperatures from 6° C to 30° C

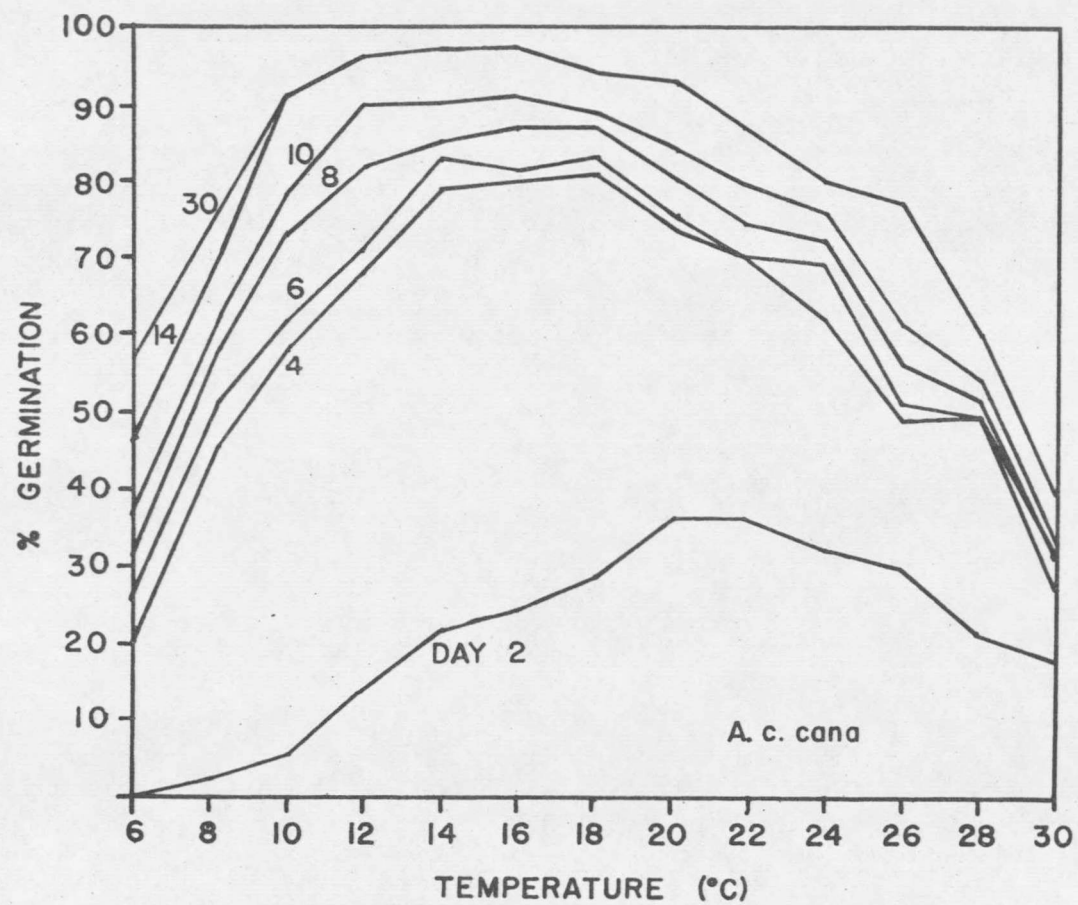


Figure 4.4 *A. c. cana* germination (%) after 30 days on a temperature gradient bar at temperatures from 6° C to 30° C

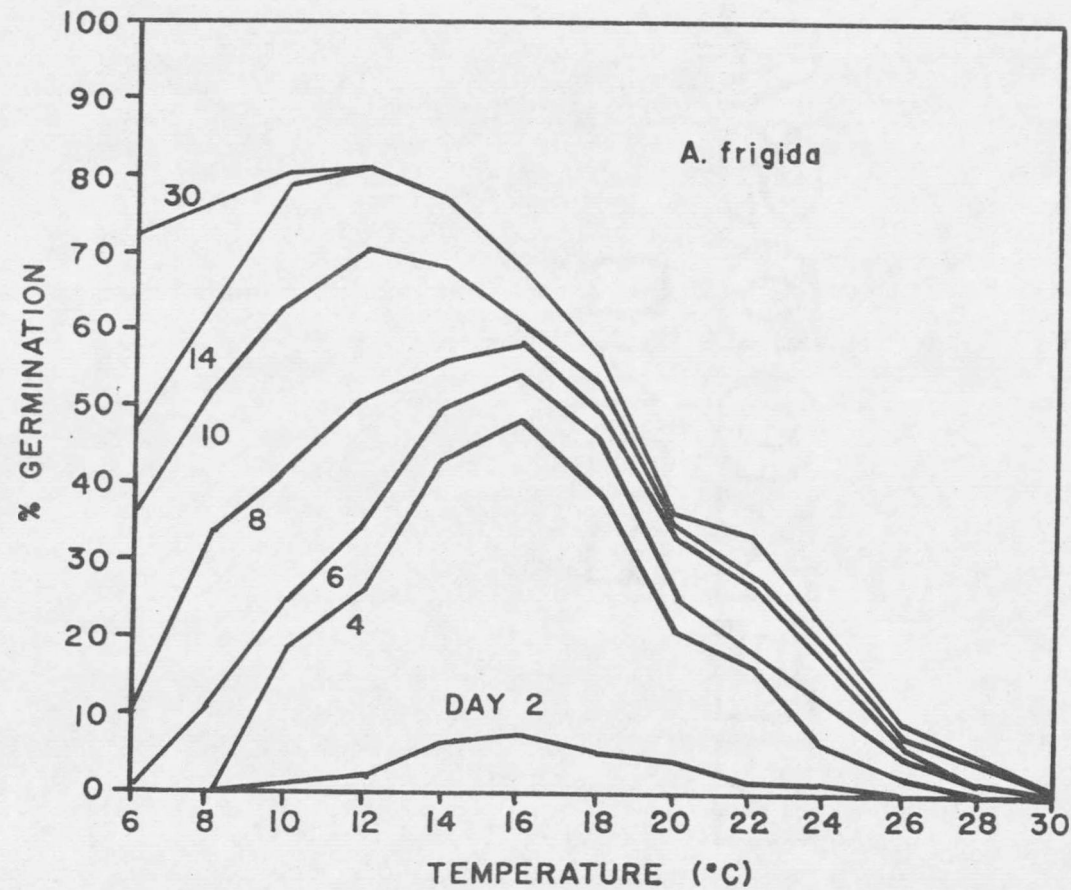


Figure 4.5 *A. frigida* germination (%) after 30 days on a temperature gradient bar at temperatures from 6° C to 30° C

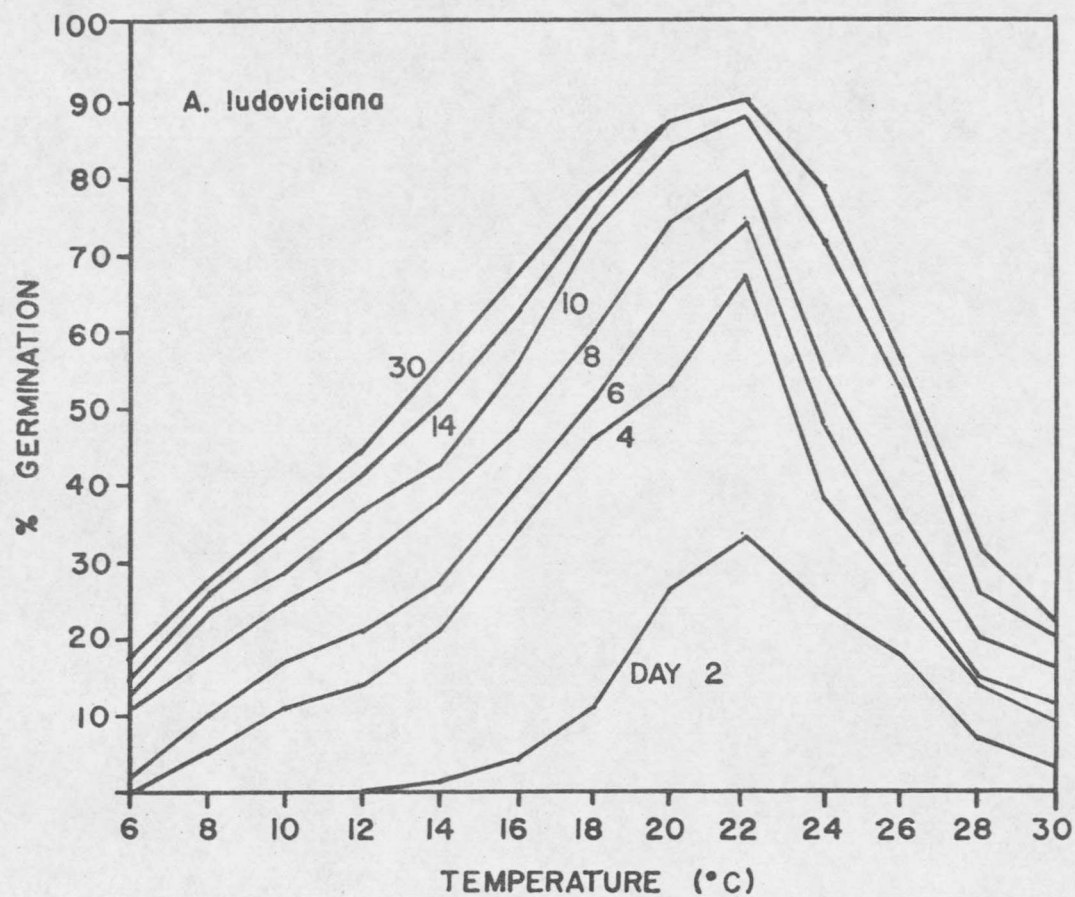


Figure 4.6 *A. ludoviciana* germination (%) after 30 days on a temperature gradient bar at temperatures from 6° C to 30° C

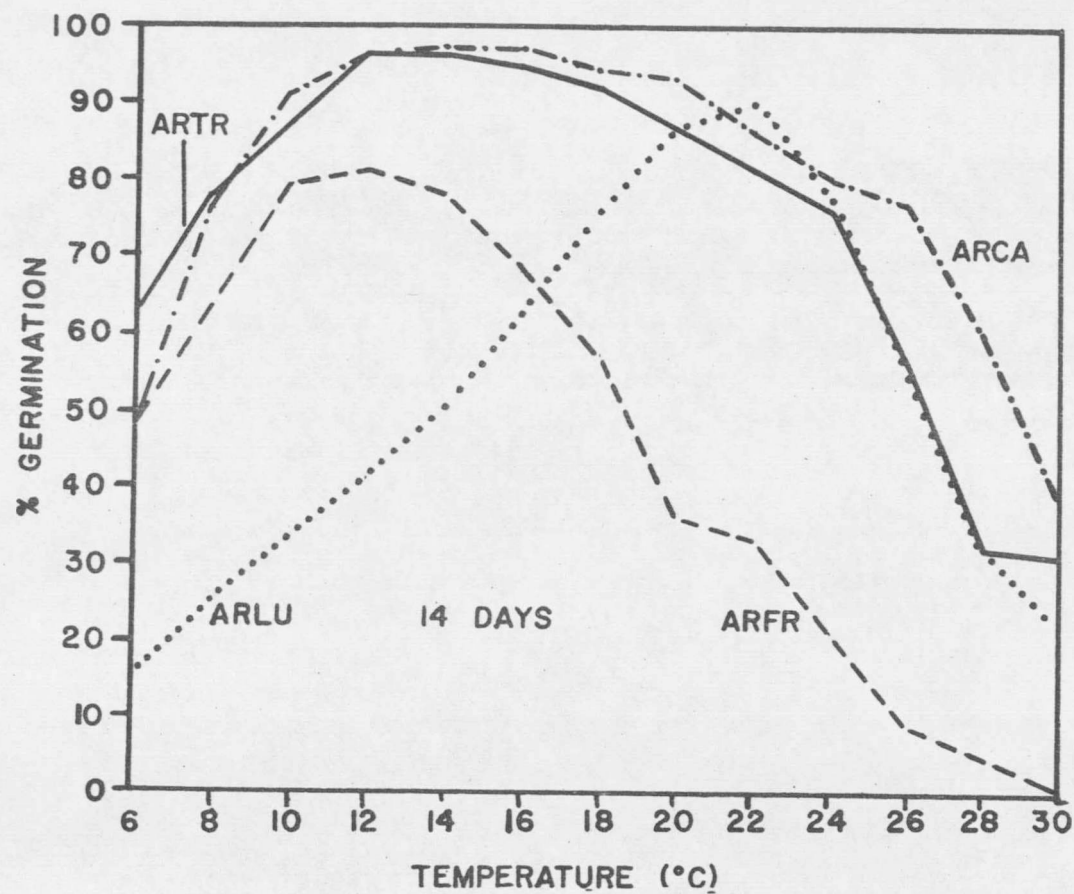


Figure 4.7 *Artemisia* germination (%) after 14 days on a temperature gradient bar at temperatures from 6° C to 30° C

Table 4.3 Percent germination of Artemisia after 14 days on a temperature gradient bar

Temp. (°C)	A. t. vaseyana	A. t. wyomingensis	A. c. cana	A. frigida	A. ludoviciana
6	60 ± 11.5 ^a	62 ± 12.4	46 ± 15.5	47 ± 11.7	15 ± 12.3
8	77 ± 9.3	78 ± 8.7	76 ± 12.2	63 ± 17.1	25 ± 8.7
10	88 ± 11.7	87 ± 12.4	91 ± 8.1	79 ± 12.0	33 ± 6.9
12	96 ± 5.8	96 ± 5.7	96 ± 6.6	81 ± 10.0	41 ± 10.2
14	96 ± 6.1	96 ± 6.3	97 ± 4.7	77 ± 6.1	50 ± 12.6
16	93 ± 9.5	94 ± 8.1	97 ± 5.5	68 ± 6.3	62 ± 18.9
18	90 ± 9.9	92 ± 8.8	94 ± 7.8	57 ± 5.8	76 ± 14.8
20	85 ± 14.4	86 ± 13.5	93 ± 11.7	36 ± 9.8	87 ± 10.3
22	79 ± 15.5	81 ± 15.8	86 ± 15.1	33 ± 8.7	90 ± 13.1
24	74 ± 16.9	76 ± 15.2	80 ± 12.3	21 ± 8.9	78 ± 12.8
26	56 ± 15.2	56 ± 14.7	77 ± 15.4	9 ± 4.6	56 ± 13.2
28	33 ± 10.5	32 ± 9.5	60 ± 18.6	5 ± 5.5	32 ± 10.9
30	28 ± 11.1	31 ± 10.5	38 ± 21.8	1 ± 3.5	22 ± 9.9

a) % germination ± standard deviation

germination percentages 4.7 and 2.7 times less for *A. t. vaseyana* and *A. t. wyomingensis*, respectively, and half-times generally twice those reported here. As discussed above, the low germination reported may have been due largely to autopathy; had they tested germination at more temperatures between 15° and 25° C, a more accurate optimum (therefore higher germination) might have been found.

The shift in optimum germination temperature over time as observed in all the taxa except *A. ludoviciana* might have resulted from combining seed from many individuals into one seed lot or could have resulted from individual plants producing seeds of differing optima. The great variability in germination of *A. tridentata* reported by others (Goodwin, 1956; Weldon et al., 1959; McDonough and Harniss, 1974a, 1974b) could have been influenced by either or both of these explanations. My results show that optimum germination for *A. tridentata* initially occurred at 18° - 20° C, but in four days the optimum had shifted to 16° C and by 14 days was 12° - 14° C. Tests conducted at 20° C with seeds from only one plant could miss the final optimum if the seeds from that plant were most reactive at some other temperature (McDonough and Harniss reported germination differences between individual plants). Collections from only a few plants, each with a difference optimum, would result in large germination variances. McDonough and Harniss used 10 plants while Goodwin and Weldon, et al. do not report how many plants were sampled, but both report large

variances. Approximately 30 plants were used in this study, and the standard deviations are much lower (Table 4.3). If the variation is due to plants producing seeds of different optima on the same plant, large variances would also occur, but should be essentially equal for a group of plants and a single plant. It may also be possible to see more than one optimum if closely spaced temperatures are tested. These possibilities need to be investigated further, possibly including isozyme studies.

Seeds that failed to germinate at lower temperatures germinated when placed at higher temperatures, indicating that the embryo was not damaged during the 14 days at the lower temperature. It is not surprising that low temperatures do not seriously affect viability since seeds are dispersed in the fall and must remain exposed to winter temperatures until spring.

Higher temperatures, particularly 28° and 30° C, inhibited germination markedly. *A. cana* was least affected, although germination was still less than half that recorded at the optimum temperature (Fig. 4.4). Fungus often developed on seed at 30° C and may be destructive, although seed treated with fungicide did little better ($4 \pm 3.5\%$ better). *A. cana* and *A. tridentata* were more susceptible to high temperature than *A. frigida* or *A. ludoviciana*. Seed placed at the optimum temperature following 14 days at 30° C did not readily germinate, indicating a loss of viability due to the exposure of

higher temperatures. Goodwin (1956) reported that *A. tridentata* seed removed from a 27° C treatment and placed at 20° C resumed germination and in some samples more than doubled the percentage. If 28° - 30° C is the upper threshold of viability for *A. tridentata*, residual seed in the soil could be seriously damaged by mid-summer soil temperatures, although with the rapid and rather complete germination at the optimum temperature (Figs. 4.2, 4.3), it is doubtful that many viable seeds would remain by the time the higher temperatures are reached. This should be true for all of the species tested in my study. Mueggler (1956) has shown, however, that some *A. tridentata* seeds remain viable in the soil for at least a year.

The results of the temperature experiments demonstrates the need to conduct germination tests at a series of temperatures. Standard 20° C tests were not indicative of *Artemisia* seed viability except *A. ludoviciana*. *A. frigida*, in particular, was misrepresented by the petri test since its optimum was well below 20° C. The gradient bar can be constructed to test germination in soils (Barbour and Racine, 1967), or modified to test the effects of vapors and other substances over a wide range of temperatures simultaneously.

Planting Depth

The depth from which *Artemisia* seed will emerge apparently is a function of seed size (Tables 4.4, 4.5). Emergence of the large

Table 4.4 Weight, length, and width of Artemisia seed

	Weight (μ g)	Length (mm)	Width (mm)
Artrva ^a	595.6 $\pm$ 61.2 ^b	1.78 $\pm$.20	0.84 $\pm$.12
Artrwy	579.1 $\pm$ 64.4	1.77 $\pm$.24	0.81 $\pm$.11
Arcaca	680.8 $\pm$ 13.9	2.14 $\pm$.24	0.90 $\pm$.10
Arfr	97.5 $\pm$ 4.1	1.21 $\pm$.04	0.40 $\pm$.02
Arlu	136.6 $\pm$ 2.9	1.25 $\pm$.07	0.43 $\pm$.02

a) see Table 4.5 for species identification

b) mean $\pm$ standard deviationTable 4.5 Comparison of emergence of Artemisia seedlings from 3 planting depths; seeds on soil surface and temperature gradient bar were not covered

Depth	Artrwy ^a	Arcaca	Arfr	Arlu
Bar 15°C	96%	96%	81%	56%
Surface	79	51	74	75
2.5 mm	75	75	69	69
5.0 mm	31	62	12	6
7.5 mm	0	0	0	0

a) Artrva = *A. tridentata vaseyana*Artrwy = *A. tridentata wyomingensis*Arcaca = *A. cana cana*Arfr = *A. frigida*Arlu = *A. ludoviciana*

seeded species (*A. tridentata* and *A. cana*) was more than 2-1/2 times that of the small seeded species (*A. frigida* and *A. ludoviciana*) at the greatest depth from which emergence was observed (5.0 mm). No difference was observed between the subspecies of *A. tridentata* or between soil types. The data indicated that the shrubby *Artemisia* species should be planted no deeper than 5 mm while the suffrutescent and herb should be planted shallower than 2.5 mm for maximum emergence. Surface plantings gave higher germination (Table 4.5), but desiccation severely reduced seedling survival. Germination in the soil test (15° C) was lower than the same temperature on the gradient bar except for *A. ludoviciana*.

These results conflict with those of Goodwin (1956) who observed *A. tridentata* emergence at depths to 15 mm. This difference could be due to the seed year or, more likely, to a difference in the populations between Montana and Washington.

Field Germination

Field germination of all four species was lower than laboratory germination.

A. ludoviciana had the highest overall germination ($17.8 \pm 4.2\%$) followed by *A. frigida* ($8.9 \pm 2.3\%$), *A. c. cana* ($8.7 \pm 3.6\%$) and *A. t. wyomingensis* ($6.2 \pm 3.0\%$); Table 4.6.

A. ludoviciana germinated best at all sites and dates except on

Table 4.6 Field germination (%) of Artemisia species at 3 locations, 1974, 1975, 1976

Year	1974	1975	1975	1975	1976	1976	1976
Site	Bozeman	Bozeman	N-Col ²	S-Col ²	Bozeman	N-Col	S-Col
Atrwy ³	0.2 a/r ¹	8.7 b/r	3.8 c/r	2.9 c/r	7.2 b/r	7.4 b/r	7.0 b/r
Arcaca	1.0 a/r	11.3 b/r	8.0 c/s	6.6 d/r	12.8 e/s	11.9 e/s	11.7 e/s
Arfr	0.3 a/r	24.3 b/s	0.8 c/t	1.3 c/r	11.6 d/t	7.2 d/r	8.3 d/r
Arlu	10.2 a/s	31.6 b/t	3.3 c/r	2.1 d/r	27.8 e/u	21.9 e/t	20.1 e/t

- 1) Values with a letter in common do not differ significantly ($P < .05$)
Use letters 'a' through 'e' to compare within a species, letters 'r' through 'u' to compare between species in a year-location
- 2) N-Col and S-Col are north and south slopes at Colstrip respectfully
- 3) Artrwy = Artemisia tridentata wyomingensis, Arcaca = A. cana cana,
Arfr = A. frigida, and Arlu = A. ludoviciana

the north slope spoils in 1975. *A. cana* ranked second on the Colstrip spoils and tied for the worst at Bozeman. *A. frigida* was second best at Bozeman and tied for the worst at the spoils sites. *A. t. wyomingensis* consistently had the lowest germination of any species except on Colstrip's north slope in 1975.

In 1975, Bozeman had the best germination record overall, both Colstrip sites being equally poor. In 1976, no significant differences between sites were noted. The comparisons in 1974 were not used because of the low germination of the seed planted that year, due perhaps to high soil temperature (planting date = June 20) or viability loss from prolonged storage (seed from 1972 crop).

No trends were apparent from comparisons within species or between species. Similarly, correlations between germination and seed size, seed weight (Table 4.4), species moisture regime or growth habit were not evident.

Summary

Artemisia seeds germinate within a broad range of temperatures (Table 4.3, Fig. 4.7), with the non-shrubs having narrower optimums than the shrubs. In Montana, *Artemisia* seeds are disseminated in October and, in habitats containing and/or adjacent to *Artemisia*, the October mean temperature is 8° - 10° C (Weaver, 1980). Contrary to Beetle (1960), the test results reported here indicate that some

germination would occur in the fall if the soil remains wet for a sufficient length of time.

No differences between *A. t. vaseyana* and *A. t. wyomingensis* germination were noted.

A. ludoviciana growth has been noted to be best in lowland sites which also are, by their nature, cold air drainages. The germination of this species at higher temperatures may be an ecological response for the protection from freezing of newly formed seedlings. *A. frigida* (with a low germination range) grows more often in upland sites that dry more quickly and germinate earlier in the spring (lower temperatures) may provide the seedlings with more favorable moisture conditions.

Tests conducted in petri dishes and/or at few temperatures poorly represent the viability of a seed crop. Tests of *Artemisia* should be conducted in containers with large air volumes to prevent autopathic effects.

While sowing *Artemisia* seeds on the soil surface may maximize emergence, seeds should be sown 2 to 3 mm deep to prevent seedling desiccation and, therefore, improve survival.

Chapter 5.

SEEDLING SURVIVAL

Introduction

Although the appearance and survival of seedlings is the first evidence that establishment is occurring, few papers on *Artemisia* seedling survival and the factors influencing survival have been published, and these refer only to *A. tridentata*. Goodwin (1956) described the development of the seedling and tested the effects of water, shade, low temperatures and soils on seedling growth. Ferguson and Monsen (1974) reported 66 percent survival of transplanted, container grown seedlings. Wallace, et al (1970) reported optimal shoot and root growth at 21° C and Harniss and McDonough (1975) found that below average temperatures reduced shoot and root growth. Fernandez and Caldwell (1975) determined that root growth occurred mainly in April and May and that rates of individual root growth were 10 to 14 mm per day. Several investigators have reported seedling densities in field experiments and some conditions which reduce that density (Shantz and Piemeisel, 1940; Pechanec, 1945; Blaisdell, 1949; Bleak and Miller, 1955; Young and Evans, 1974; Hazlett and Hoffman, 1975).

This chapter reports on the survival of *Artemisia* seedlings in both field and greenhouse plantings, and on observations of natural field survival.

Methods

Field plantings were made at two sites near Colstrip and one site at Bozeman as described in the previous chapter (Germination Tests: Field Planting). A sprinkler system was used in 1974 at Bozeman to ensure adequate water for the late planting (June). The soils were watered to field capacity every third day through August, 1974. Table 4.1 lists weather data for the sites. Results were recorded through November, 1976.

At the Colstrip sites, a grasshopper infestation caused considerable loss of seedlings, especially in 1975. In order to have some seedlings survive for second year survival observations, cones made of window-screen were placed over some seedlings to eliminate grasshopper predation.

In September of 1975 and 1976, several seedlings of each species were excavated at the Bozeman and Colstrip sites to measure root elongation. Roots of *Salsola kali* L. at Colstrip were also excavated and measured.

In the greenhouse, seedlings were grown from seed in root boxes to observe the rate of root elongation. The wooden boxes were 9 cm x 35 cm and 70 cm deep. One side of the box was made of glass and covered with aluminum foil to exclude light except during observation periods. The boxes were stored tilted toward the glass side to encourage roots to grow against the glass. Sterilized sandy loam soil

was used for the six replications of four plants of each species. A day/night temperature regime of $20^{\circ}/13^{\circ} \text{ C} \pm 2^{\circ} \text{ C}$ and a minimum 12 hour photoperiod was maintained.

Results and Discussion

All four *Artemisia* taxa exhibited high mortality early in life (Figure 5.1). This pattern of survival has been described graphically by Pearl (1928) as a type III survivorship curve, which represents rapid initial mortality followed by a rather constant low mortality for the remainder of the populations life. In the absence of insects and annual plant species competition, the initial rapid mortality in *Artemisia* occurred within 120 days (by September 15th) of the time of maximum emergence (mid April to mid June). For the next two years, mortality either did not occur or was extremely low. Predation from insects and competition from annual plants markedly reduced or eliminated seedlings. Seedling survival was different between years and locations in some cases (Figure 5.1).

The parabolic survivorship curve of *Artemisia* can be described by two intersecting lines, one representing the initial rapid mortality and one representing the slow mortality that follows (Figure 5.1). This method of presenting the data lends itself to linear regression analysis. Table 5.1 presents the correlation coefficients and Table 5.2 presents the equations for the initial rapid seedling mortality.

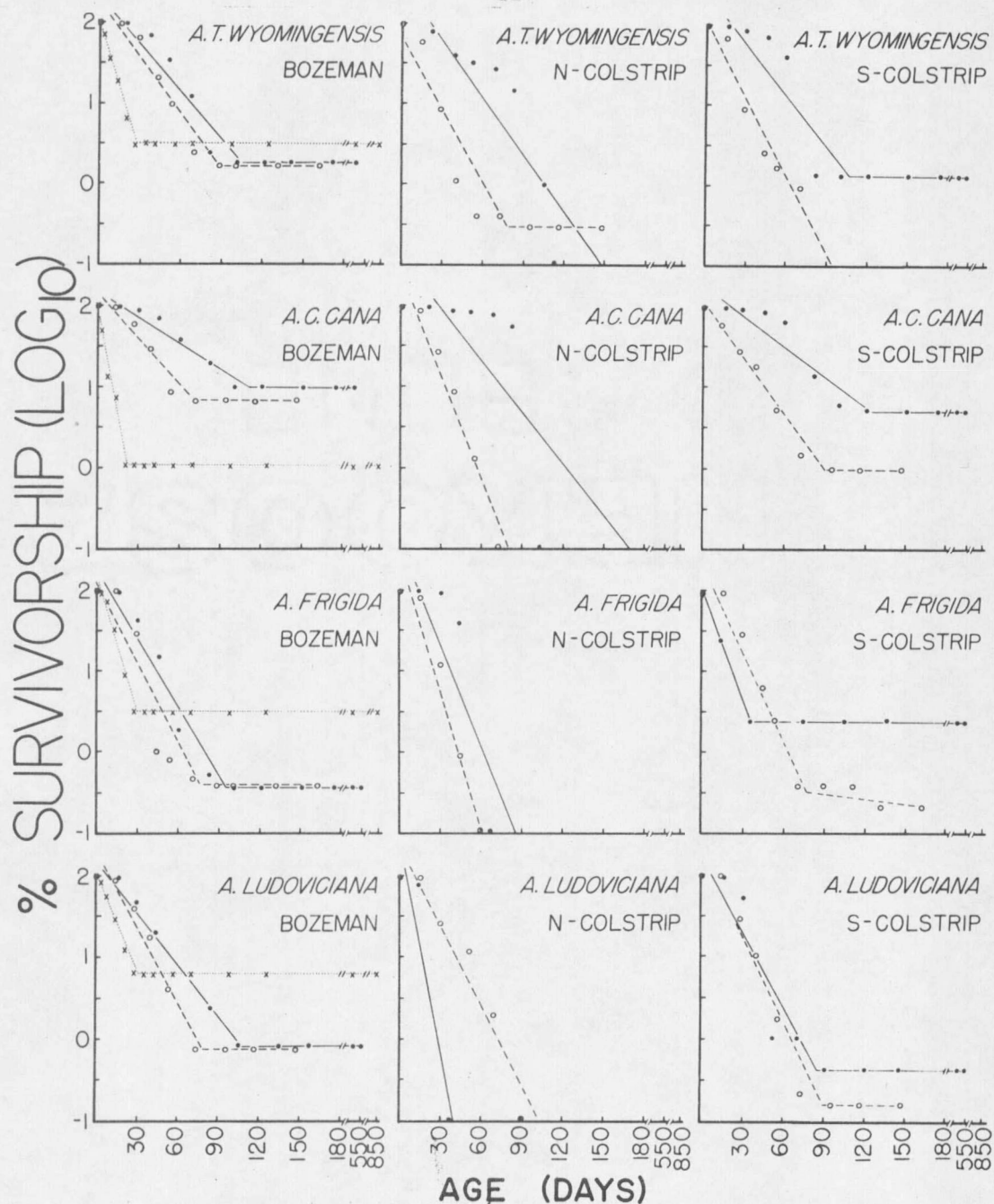


Figure 5.1 *Artemisia* survivorship for 1 to 3 years on disturbed sites. Lines are linear regressions.

x.....x = 1974, o———o = 1975, o-----o = 1976
 2 = 100 %, 1 = 10 %, 0 = 1 %, -1 = 0.1 %

Table 5.1 Relationship (R = correlation coefficient) of seedling survival to time in the initial seedling mortality phase shown in Figure 5.1. All are significant at $P < 0.001$

Year-Location	Artrwy ^a	Arcaca	Arfr	Arlu
1974 Bozeman	- 1.00	- 0.99	- 0.98	- 0.98
1975 Bozeman	- 0.95	- 0.96	- 0.97	- 0.99
1976 Bozeman	- 0.97	- 0.97	- 0.92	- 0.97
1975 N-Colstrip ^b	- 0.82 ^c	- 0.69 ^c	- 0.83 ^c	- 0.94 ^c
1976 N-Colstrip	- 0.92	- 0.97	- 0.96	- 0.96
1975 S-Colstrip	- 0.91	- 0.93	- 1.00	- 0.94
1976 S-Colstrip	- 0.98	- 0.99	- 0.94	- 0.98

a) Artrwy = *A. tridentata wyomingensis*, Arfr = *A. frigida*,
Arcaca = *A. cana cana*, Arlu = *A. ludoviciana*

b) N-Colstrip = north slope site at Colstrip
S-Colstrip = south slope site at Colstrip

c) $P < .01$

Table 5.2 Linear equations describing initial mortality of *Artemisia* seedlings grown in Bozeman and Colstrip gardens, 1974, 1975, 1976

Equation form: $\log(\% \text{ Survival}) = b + m(\text{Time in Days})$						
Year-Location	m	b	Time ^a Limit	m	b	Time Limit
<i>A. t. wyomingensis</i>			<i>A. c. cana</i>			
1974 Bozeman	-.055	2.02	28	-.092	2.00	22
1975 Bozeman	-.019	2.31	105	-.010	2.16	112
1976 Bozeman	-.023	2.24	87	-.019	2.13	71
1975 N-Colstrip	-.023	2.45	120	-.021	2.60	120
1976 N-Colstrip	-.029	1.78	78	-.042	2.39	80
1975 S-Colstrip	-.020	2.37	113	-.012	2.26	124
1976 S-Colstrip	-.034	2.09	92	-.023	2.06	90
<i>A. frigida</i>			<i>A. ludoviciana</i>			
1974 Bozeman	-.057	2.17	30	-.039	2.02	31
1975 Bozeman	-.028	2.27	96	-.021	2.19	107
1976 Bozeman	-.033	2.08	76	-.031	2.28	80
1975 N-Colstrip	-.042	2.60	86	-.088	2.42	39
1976 N-Colstrip	-.057	2.43	60	-.032	2.36	103
1975 S-Colstrip	-.045	2.01	36	-.031	2.23	84
1976 S-Colstrip	-.036	2.33	76	-.035	2.26	88

a) The regression should not be applied past the number of days specified by the time limit

phase. Correlation coefficients for the later slow mortality phase were perfect negative correlations ($R = -1.00$) except for *A. frigida* on the south slope at Colstrip in 1976 ($R = -.87$).

The initial mortality shown at Bozeman in 1974 was more rapid than in the following two years. This may be the result of planting the seed in mid-June, which subjected the emerging seedlings to higher temperatures than normally experienced during spring emergence. Still, the final survival was higher in 1974 (except for *A. c. cana*) than in the following two years, probably due to watering the Bozeman site throughout the summer in 1974. Final survivals in 1975 and 1976 at Bozeman were the same; in 1975, however, the initial rapid mortality was slower by 14 to 31 days; this probably reflects the cooler spring temperatures (February through June) in 1975 than in 1976 (Table 4.1).

Survival at Colstrip was drastically different for the sites on north south slopes (Figure 5.1). Both slopes generally showed slower initial mortality in 1975, as in Bozeman, but on the north slope the mortality was more rapid than in Bozeman and resulted in extinction for all species except *A. t. wyomingensis* in 1976. On the south slope, survivorship was similar to the Bozeman site in the same year. Only *A. t. wyomingensis* in 1976 became extinct. The final survival probably was over-estimated because some plants were protected from grasshopper predation by window-screen cones.

The disparity between the north and south slopes at Colstrip apparently resulted from competition for water with *Salsola kali*. On the south slope, *Salsola* seedlings were thin (1,000 seedlings/meter²), but on the north slope were 100 times as dense (100,000 seedlings/meter²). In those dense stands, soil water stress to a depth of 25 cm reached -5 bars by mid-July and -20 bars by the first week of August. The thin *Salsola* areas never exceeded -5 bars even at a depth of 10 cm at any time of the year (Harvey and Weaver, 1979). *Artemisia* roots in September did not exceed 12 cm, while those of *Salsola* often exceeded 20 cm, with some longer than 30 cm. The dense stands of *Salsola* on the north slope were able to deplete the soil water in the zone of *Artemisia* roots enough to cause its demise, but in the thin stand areas of the north slope and the whole of the south slope, *Salsola* was not dense enough to deplete the water in the soil profile to any great extent even though its roots were significantly deeper than *Artemisia*. The only *Artemisia* seedlings that survived on the north slope (two *A. t. wyomingensis* in 1976) were in small areas with thin stands of *Salsola*.

The field excavation of *Artemisia* seedlings on the planted sites occurred only in September after approximately 120 days of growth. Figure 5.2 and Table 5.3 present the results of the greenhouse tests of root elongation in 1976. Elongation of 1 mm/day was achieved by all four taxa within two weeks of planting and by 45 days had reached

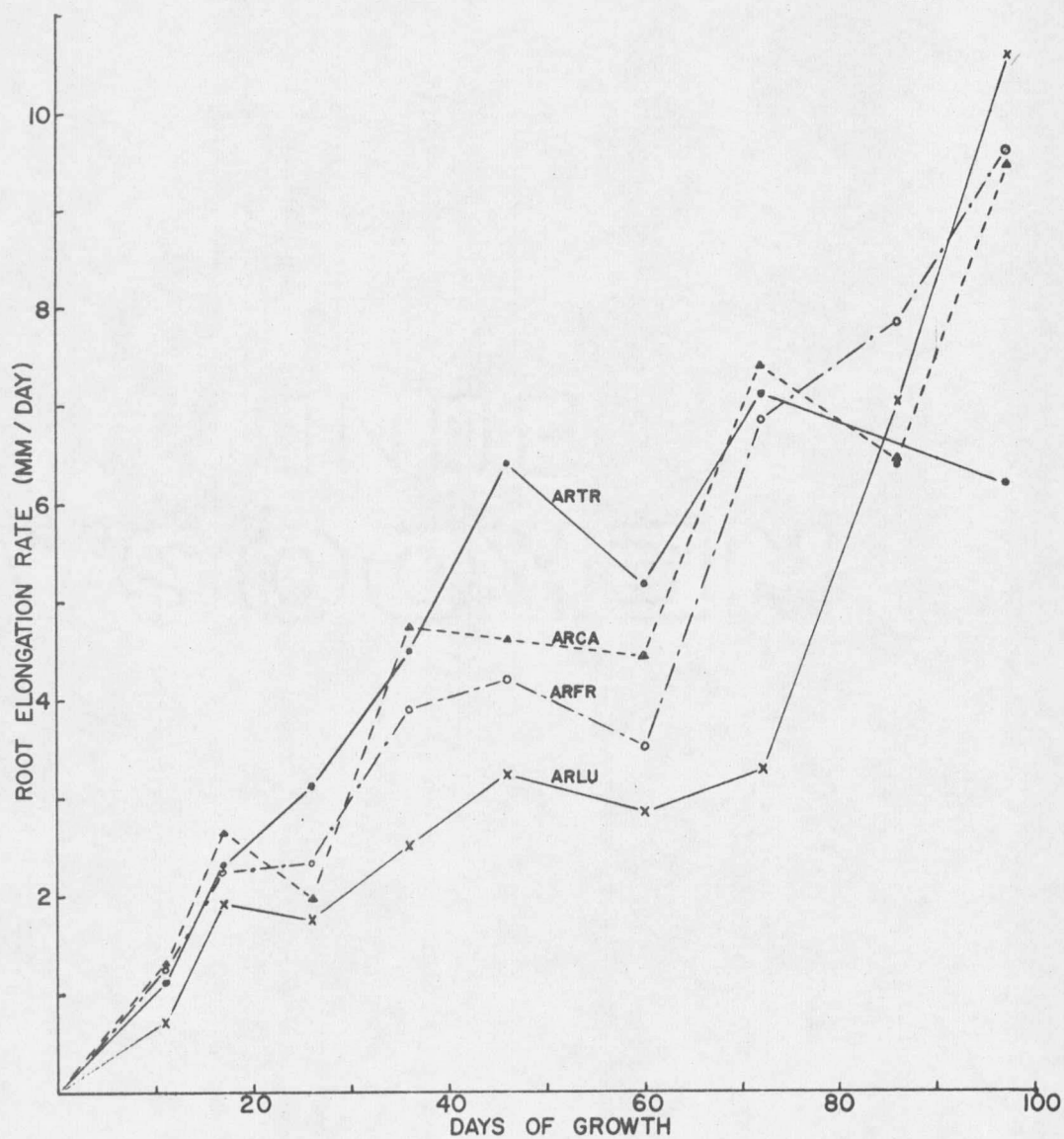


Figure 5.2 *Artemisia* greenhouse root elongation rate versus time; *A. t. wyomingensis* (ARTR), *A. c. cana* (ARCA), *A. frigida* (ARFR), and *A. ludoviciana* (ARLU)

Table 5.3 Root elongation rates (mm per day) of Artemisia seedlings grown in glass walled root boxes in a greenhouse, 1976

Data expressed as Mean $\pm$ Standard Deviation					
Days of Growth	Rate ^a Period (Days)	Artrwy ^c	Arcaca	Arfr	Arlu
12	12	1.1 $\pm$ 0.3	1.3 $\pm$ 0.1	1.3 $\pm$ 0.2	0.7 $\pm$ 0.2
17	5	2.3 $\pm$ 0.6	2.6 $\pm$ 0.3	2.2 $\pm$ 1.1	1.9 $\pm$ 0.6
26	9	3.1 $\pm$ 0.7	2.0 $\pm$ 0.7	2.3 $\pm$ 1.0	1.8 $\pm$ 0.2
36	10	4.5 $\pm$ 2.6	4.7 $\pm$ 0.8	3.9 $\pm$ 0.8	2.5 $\pm$ 0.9
46	10	6.4 $\pm$ 2.6	3.6 $\pm$ 0.9	4.2 $\pm$ 1.5	3.2 $\pm$ 0.7
60	14	5.2 $\pm$ 1.7	4.5 $\pm$ 1.2	3.6 $\pm$ 1.0	2.9 $\pm$ 0.4
72	12	7.1 $\pm$ 1.9	7.4 $\pm$ 1.9	6.9 $\pm$ 3.7	3.3 $\pm$ 0.7
86	14	6.4 $\pm$ 3.2	6.5 $\pm$ 0.6	7.8 $\pm$ 0.8	7.0 $\pm$ 0.8
97	11	6.2 $\pm$ 2.5	9.4 $\pm$ 2.0	9.6 $\pm$ 1.5	10.6 $\pm$ 1.7
Cumulative ^b		4.4 $\pm$ 0.3	5.0 $\pm$ 0.5	4.9 $\pm$ 0.8	4.4 $\pm$ 0.8

a) rate period = the number of days used to determine the the root elongation rate

b) cumulative = rate averaged over the full 97 days growth

c) Artrwy = *A. tridentata wyomingensis*, Arfr = *A. frigida*,
Arcaca = *A. cana cana*, Arlu = *A. ludoviciana*

2-3 mm/day. This compares well with the field rates observed by Goodwin (1956) for *A. t. tridentata*. My tests showed the elongation rate to increase through the first 35 to 45 days, then slacken for 2 to 3 weeks, then increase again. The slack period corresponds to the period just prior to and during the time of primary leaf emergence. At the rates observed in the greenhouse, a depth of 21 cm was reached in 42 to 47 days, except *A. ludoviciana* that required 56 days; 25 cm, the length of roots at Bozeman in September, was reached in 64 to 70 days (84 days in *A. ludoviciana*). The root elongation rate in the field (averaged over 120 days) was 1 mm per day at Colstrip and 2 mm per day at Bozeman for the longest roots, whereas the averaged rate for the greenhouse experiment (97 days) was 4.5 mm per day. These data suggested that root elongation in the field ceased long before the seedlings were excavated in September.

Foliage development at Bozeman appeared normal, but at Colstrip, the leaves that emerged never enlarged as did leaves in natural stands or at Bozeman. Even in the second year of growth, the seedlings at Colstrip remained stunted with primary leaves little larger than when they emerged. Seedlings in natural *Artemisia* stands in the Colstrip area, but not on coal spoils, showed good leaf expansion and height growth. Since water was not limiting for those seedlings that survived the first 120 days on the spoils, some other factor apparently was limiting, possibly nutrients or the ability to secure those

nutrients. Williams and Aldon (1976) observed endomycorrhizal associations with *A. tridentata* in New Mexico which may increase water and phosphate uptake. Farnsworth and Hammond (1968) and Farnsworth (1975) found that *A. ludoviciana* and *A. michauxiana* form nitrogen fixing bacterial root nodules in Utah and Idaho. Critical micro-organisms may be missing from the spoils because of the soil manipulation incurred in the strip mining process.

Survival beyond the three years observed on the planted plots was estimated from native vegetation as the data source. Densities of one year old seedlings of *A. t. wyomingensis*, *A. c. cana* and *A. frigida* (25, 11, and 10 per m² respectively) was obtained in June, 1976, from a strip cleared of most vegetation. The strip 1) transected stands of both shrub species and grassland containing *A. frigida*, 2) was near Colstrip on a 3% south slope, and 3) had been invaded by few plants other than *Artemisia*. Because of these three factors and because the seedlings used for the density data emerged in 1975, the survivorship from the south slope at Colstrip was used to calculate an estimated initial population. The following equation was used:

$$P_s = D_s \cdot \frac{100}{10^Y}$$

where Y is the log of the final percent survival of that species on the south slope at Colstrip in 1975 (see below), D_s is the seedling density of the species as measured on the disturbed strip, and P_s

is the initial seedling density to be calculated. Y was 0.13, 0.72 and 0.38 for *A. t. wyomingensis*, *A. c. cana* and *A. frigida*, respectively; D_s was 25, 11, and 10 respectively; and P_s was 1853, 210 and 417, respectively. *A. ludoviciana* was not measured because seedlings were not found anywhere in the state and because the ages of mature plants could not be determined.

The age structure of mature stands was measured by counting growth rings of randomly selected plants, and the density of the stand measured in a 100 m² plot. The density (D_x) from even aged stands was then employed to calculate the percent survival (Y') at age X , the stand age in years, using P_s as the initial seedling density. The log of Y' was then regressed against X (Table 5.4).

The regression was then used as a trend line to predict when the last individuals of a given starting population would perish if the stand was not disturbed. Using the estimated emergent seedling densities (P_s), a hectare plot of new seedlings on a heavily disturbed site would have one of those plants remaining after 60, 56 and 22 years for *A. t. wyomingensis*, *A. c. cana* and *A. frigida*, respectively; in the field no plants over age 37, 31 and 8 years, respectively, were found.

Three basic assumptions are necessary in order to apply the survivorship regressions beyond the 3 years of data collected at the planted plots. 1) The survivorship at Colstrip fairly represents the

Table 5.4 Artemisia survivorship after the initial high mortality phase (Described in Figure 5.1). Regression equations predict the time to reach a population size of one, for starting populations of 1,000 to 1,000,000 plants

Equation form: $\log(\% \text{ survival}) = b + m(\text{time in years})$

	Slope b	Intercept m	R	Years to % Survival ^c			
				10 ⁻³	10 ⁻⁴	10 ⁻⁵	10 ⁻⁶
Artrwy ^a (-.00024) ^b	-0.086	-0.067	-0.90 *	34	45	57	69
Arcaca (-.00029)	-.106	+ .624	-.93 *	34	44	53	63
Arfr (-.00075)	-.275	+ .605	-.99 **	13	17	20	24

a) Artrwy = *A. tridentata wyomingensis* *) P .10
 Arcaca = *A. cana cana* **) P .01
 Arfr = *A. frigida*

b) Slope expressed in days for comparison to Table 5.2

c) For starting populations from 100 to 100,000

actual occurrence on non-spoil sites, 2) survivorship on the south slope at Colstrip represents an average year, and 3) the seedling densities sampled in the disturbed natural vegetation represent densities of an average year.

Seedlings were quite rare (less than 0.02 per m²) in mature, lightly disturbed stands of native vegetation. This was also observed by Hazlett and Hoffman (1975) for *A. t. wyomingensis* and *A. c. cana* in North Dakota. Shantz and Piemeisel (1940) found 0.6 seedlings per m² for *A. tridentata* in Utah, while Pechanec (1945) considered less than 0.1 seedlings per m² normal for most types of sagebrush-perennial grass range. Neither paper reports the ages of the plants considered seedlings. Bleak and Miller (1955) found densities of *A. tridentata* to vary from 0.02 to 0.56 seedlings per m² one year after eradication treatment of mature stands. Young and Evans (1974) found a mean of 0.06 seedlings per m² (maximum of 0.09 per m²) in partially killed stands, but in stands that had 100% kill of mature shrubs, annual plants invaded and eliminated the *Artemisia* seedlings.

The regression for survival beyond one year is probably an overestimation, since 1) seedling densities in the majority of *Artemisia* habitats were considerably less than the densities observed in heavily disturbed habitats, and 2) competition from non-*Artemisia* species (lacking in the seedling stands) reduced the survival of emergent seedlings dramatically, and therefore may cause an under-

estimation of the density of the initial population (P_s).

Summary

Artemisia had high mortality early in life. This initial rapid mortality (based on the number of emergent seedlings) takes place in the first 120 days following emergence, and is followed by a slow, rather constant, mortality for the remainder of the population's existence. Seedling survival in the first year varied from 0% to 10%. The mean survival of seedlings was 5.3, 3.4, 0.0 and 1.2 percent for *A. t. wyomingensis*, *A. c. cana*, *A. frigida* and *A. ludoviciana*, respectively; survival per 1000 seeds, however, was 14 to 100 times lower (0.05, 0.23, 0.03 and 0.07, respectively).

Survival varied with the year, the geographical location and the slope. Competition from annual plants and insect predation can cause severe mortality. Lower temperatures and/or more moisture caused delay in mortality as well as an increase in survival. The root elongation rate in the greenhouse increased with time.

Survival beyond the three years observed on the planted plots was estimated from age-density measurements of native vegetation, but are probably overestimates.

Seedling development on coal spoils was poor even though soil water was available and the roots were deep enough to tap that water

supply. Absence of nutrients, or absence of nodule-forming bacteria and/or myccorhizal fungi may be responsible.

Chapter 6

BIOMASS AND PRODUCTION

Introduction

It is often desirable to know the biomass and production of organisms to study dominance and competition in a community. It is useful in the study of population dynamics, nutrient cycling and productivity (Daubenmire, 1968) and is used by wildlife biologists in estimating browse production and by range managers and foresters in determination of fuel availability.

In *Artemisia tridentata*, biomass and production have been used in the study of nutrient cycling and ecosystem productivity by West (1972) and West and Fareed (1973), and methods for estimating biomass and annual production have been reported in several articles (Harniss and Murray, 1975; Brown, 1976; Rittenhouse and Sneva, 1977; Uresk, et al., 1977).

This chapter reports on the relationship of age, linear, area and volume measurements to aboveground biomass and production of four *Artemisia* species.

Methods

In 1974, 1975 and 1976 whole plants of each taxon were cut at ground level and placed in separate plastic bags following in situ

measurement of the number of inflorescences, basal area (BA), and, to the nearest cm, the vegetative crown height (H), maximum diameter (D_M), minimum diameter (D_m) at right angles to D_M , and the circumference (C). Measurements in the non-shrubby taxa included the inflorescences in the crown measurements. *A. frigida* vegetative measurements were also recorded. Elliptical basal area and crown area were calculated as

$$\pi \cdot D_M/2 \cdot D_m/2$$

and crown volume (V) calculated as area x height. Age of all species except *A. ludoviciana* was determined by counting the growth rings at ground level.

The cut materials were air dried to constant weight (one end of the bag open), and then separated into biomass classes. Classes for the shrubs were as follows: inflorescences, leaves (L), wood 0 to 0.3 cm (.3), wood 0.3 to 1 cm, wood 1 to 2 cm, wood 2 to 3 cm, wood 3 to 4 cm, wood greater than 4 cm, total wood (W), and total mass (T). Total mass was the sum of total wood and leaves; inflorescences were not included because the shrubs were not collected at the maximum inflorescence production. Classes for the non-shrubs were: inflorescences, leaves, wood, vegetative total (leaves plus wood) and total mass (vegetative total plus inflorescences). Plants of all sizes were selected to represent the entire spread of variation.

A variety of regressions were then conducted using height, area,

etc., as the independent variable and biomass classes as the dependent variable. $\log_{10}$ transformations of both independent and dependent variables were performed and semi-log and log-log regressions performed.

The annual radial spread of *A. ludoviciana* clones was measured by marking the perimeter of the clones in the fall of 1974 and 1975, then measuring the radial increase of the perimeter the following fall (measured to the nearest cm). Clone age was then estimated from the radial annual increase and the clone size.

Artemisia seed and inflorescence characteristics were recorded as the length of the inflorescence, number of heads per cm of inflorescence, number of flowers per head, number of filled seed per head, length and width of seed (to nearest 0.1 mm), and the weight of 1000 seeds (to nearest 0.0001 gm). From these data and from shrub measurements, seed production of single shrubs was estimated.

Results and Discussion

The range of plant parameters and above ground biomass components is presented in Table 6.1 *A. c. cana* was tallest and had the largest basal area, but *A. t. vaseyana* had the largest diameters, circumference, area and volume. *A. c. cana* was higher in all biomass classes except wood 0.3 to 1 cm, wood 1 to 2 cm and wood 3 to 4 cm. *A. t. vaseyana* was higher than *A. t. wyomingensis* in all categories

Table 6.1 The range of biomass and crown measurements observed in Artemisia in Montana, 1974 - 1976.

	Artrwy ^a low high x 10 ³	Artrva low high x 10 ³	Arcaca low high x 10 ³	Arfr low high x 10 ³	Arlu low high x 10 ³
Height cm	3 0.080	4 0.120	2 0.150	1 0.045	6 0.117
Dia _M ^b cm	4 .120	4 .140	2 .120	1 .036	3 .013
Dia _m cm	3 .120	3 .130	2 .120	1 .030	3 .013
Circ cm ²	10 .360	9 .400	6 .350	3 .047	9 .044
Basal Area cm ²	.1 .014	.1 .017	.1 .032	- -	- -
Area cm ²	11 10	9 14	3 11	1 .775	7 .133
Volume cm ³	40 622	38 1715	8 1696	1 29	42 13.6
Biomass (Grams) ^d					
Leaves	.2 .166	.3 .293	.3 .537	.2 .002	.1 .001
W 0 - .3 ^c	.5 .402	.6 .564	.3 .820	.2 .004	.1 .001
W .3 - 1	.1 .405	.1 .475	.1 .445	- -	- -
W 1 - 2	.5 .444	.3 .361	.2 .377	- -	- -
W 2 - 3	3.0 .288	2.3 .388	4.3 .353	- -	- -
W 3 - 4	27.0 .201	17.8 .370	16.8 .346	- -	- -
W 4	28.8 .081	94.8 .123	61.3 .396	- -	- -
Total W.	.5 1.80	.6 1.96	.3 2.29	.2 .004	.1 .001
Total Mass	.7 1.97	.9 2.26	.6 2.83	.4 .015	.2 .009

a) Artrwy = *A. t. wyomingensis* (n=22), Artrva = *A. t. vaseyana* (n=18), Arcaca = *A. c. cana* (n=38), Arfr = *A. frigida* (n=20), Arlu = *A. ludoviciana* (n = 22)

b) Dia_M = maximum diameter, Dia_m = minimum diameter, Circ = circumference

c) Wood size classes in cm

d) Aboveground

except wood 1 to 2 cm; this resulted from the trunk of the latter splitting into wedge shaped sections, each with its own attending branches and leaves that forms an almost independent shrub unit.

A. frigida had higher maximum values in all categories except height and leaf weight than did *A. ludoviciana*.

Correlation of biomass with plant parameters in the non-shrubs were poor ($R^2 = 0.01 - 0.50$) in all classes of biomass except inflorescences and total mass. Only one wood class was necessary because all stem material of both species was less than 0.3 cm in diameter. Regression of the log of the height (including inflorescence) with the log of the inflorescence mass and log of the total mass were the only reasonable results. Log-log of the inflorescence regression produced correlation coefficients of 0.98 and 0.70 for *A. frigida* and *A. ludoviciana* respectively. For log-log of the total mass, the correlation coefficients were 0.79 and 0.99 respectively; equations for total mass are presented in Table 6.5 and represented graphically in Figure 6.1. Correlation coefficients of all other regressions were less than 0.60 (most below 0.30) and are therefore not presented.

Regressions in the shrubby species produced much better results. Table 6.2, 6.3 and 6.4 present the correlation coefficient matrices of the three taxa. In general, log-log transformations were best and semi-log the poorest, however, the semi-log form was best for wood greater than 4 cm. Volume, area, minimum diameter and circumference

Table 6.2 *A. t. wyomingensis* relationship (R = correlation coefficient) of various above ground biomass components to various easily measured predictive parameters

	cm Height lg H	cm Dia M lg D _M	cm Dia m lg D _m	cm Circ lg C	cm ² Area lg A	cm ³ Volume lg V	cm ² Basal lg BA	yrs Age lg
<i>gms</i>								
Leaves	.84	.92	.94	.94	.89	.84	.93	.81
lg L	.89	.86	.86	.87	.70	.64	.83	.87
lg L	.97	.97	.98	.98	.98	.99	.97	.87
Wood 0-.3 ^b	.80	.93	.95	.94	.95	.91	.92	.74
lg 0-.3	.92	.90	.91	.91	.76	.71	.87	.87
lg 0-.3	.97	.98	.98	.99	.99	.99	.97	.87
Wood .3-1	.84	.92	.94	.93	.93	.90	.93	.76
lg .3-1	.76	.71	.71	.72	.56	.52	.67	.71
lg .3-1	.90	.85	.90	.89	.88	.89	.89	.72
Wood 1-2	.71	.85	.88	.87	.88	.82	.85	.68
lg 1-2	.74	.68	.67	.69	.53	.48	.64	.70
lg 1-2	.92	.87	.84	.87	.86	.89	.87	.71
Wood 2-3	.75	.84	.87	.87	.87	.83	.87	.67
lg 2-3	.86	.82	.81	.83	.65	.59	.78	.81
lg 2-3	.88	.92	.91	.92	.92	.91	.88	.82
Wood 3-4	.61	.85	.86	.84	.93	.88	.83	.58
lg 3-4	.73	.81	.83	.83	.81	.78	.85	.70
lg 3-4	.61	.67	.69	.69	.68	.67	.71	.66
Wood > 4	.66	.74	.77	.77	.80	.77	.81	.57
lg > 4	.76	.76	.79	.80	.80	.81	.82	.63
lg > 4	.60	.61	.63	.64	.62	.62	.65	.59
Total Wood	.77	.89	.92	.91	.93	.88	.90	.71
lg W	.92	.89	.89	.90	.75	.70	.86	.88
lg W	.97	.97	.98	.99	.99	.99	.97	.87
Total Mass ^c	.78	.90	.92	.91	.92	.88	.91	.72
lg T	.92	.89	.89	.90	.75	.69	.86	.88
lg T	.97	.98	.98	.99	.99	.99	.97	.87
Age	.84	.80	.80	.86	.68	.64	.85	-
lg Age	.82	.79	.78	.84	.65	.61	.82	-
lg Age	.82	.85	.84	.89	.85	.85	.87	-

a) Dia M = maximum diameter, Dia m = minimum diameter, Circ = circumference, Basal = Basal area, lg = log₁₀

b) Wood diameter classes (cm)

c) Total aboveground biomass

Table 6.3 A. t. vaseyana relationship (R = correlation coefficient) of various above ground biomass components to various easily measured predictive parameters

gms	cm	cm	cm	cm	cm ²	cm ³	cm ²	yrs
	^a Height Height lg H	Dia M Dia M lg D _M	Dia m Dia m lg D _m	Circ Circ lg C	Area Area lg A	Volume Volume lg V	Basal Basal lg BA	Age Age lg
Leaves	.93	.92	.94	.92	.95	.94	.86	.69
lg L	.95	.95	.91	.94	.81	.73	.92	.87
lg L	.98	.99	.99	.98	.99	.99	.97	.77
Wood 0-.3 ^b	.91	.91	.95	.92	.98	.97	.85	.68
lg 0-.3	.94	.94	.91	.94	.81	.73	.91	.85
lg 0-.3	.99	.99	.99	.99	.99	.99	.98	.75
Wood .3-1	.93	.92	.93	.92	.90	.85	.93	.74
lg .3-1	.78	.77	.74	.77	.63	.55	.76	.80
lg .3-1	.91	.89	.87	.88	.89	.90	.91	.77
Wood 1-2	.91	.91	.94	.91	.99	.99	.86	.61
lg 1-2	.75	.73	.70	.72	.60	.53	.71	.64
lg 1-2	.92	.88	.86	.87	.89	.89	.93	.56
Wood 2-3	.81	.84	.88	.85	.93	.93	.80	.60
lg 2-3	.88	.90	.86	.90	.74	.65	.89	.86
lg 2-3	.89	.93	.93	.94	.93	.92	.90	.75
Wood 3-4	.81	.75	.79	.76	.77	.76	.74	.61
lg 3-4	.91	.90	.90	.88	.85	.79	.91	.70
lg 3-4	.79	.80	.83	.78	.82	.81	.76	.58
Wood > 4	.74	.69	.73	.71	.77	.79	.61	.51
lg > 4	.76	.72	.77	.75	.82	.85	.63	.50
lg > 4	.57	.56	.60	.56	.58	.58	.50	.39
Total Wood	.94	.92	.96	.93	.97	.95	.89	.70
lg W	.95	.94	.91	.94	.81	.72	.93	.85
lg W	.99	.99	.99	.99	.99	.99	.98	.74
Total Mass ^c	.94	.92	.96	.93	.97	.95	.89	.70
lg T	.95	.94	.91	.94	.81	.73	.93	.85
lg T	.99	.99	.99	.99	.99	.99	.98	.75
Age	.80	.80	.79	.81	.68	.60	.79	-
lg Age	.68	.69	.66	.69	.56	.49	.67	-
lg Age	.72	.78	.76	.77	.77	.76	.71	-

a) Dia M = maximum diameter, Dia m = minimum diameter, Circ = circumference, Basal = basal area, lg = log₁₀

b) Wood diameter classes (cm)

c) Total aboveground biomass

Table 6.4 A. c. cana relationship (R = correlation coefficient) of various above ground biomass components to various easily measured predictive parameters

gms	^a cm Height lg H	cm Dia M lg D _M	cm Dia m lg D _m	cm Circ lg C	cm ² Area lg A	cm ³ Volume lg V	cm ² Basal lg BA	yrs Age lg
Leaves	.90	.88	.91	.89	.95	.97	.94	.73
lg L	.92	.93	.93	.93	.82	.75	.87	.96
lg L	.98	.97	.98	.98	.98	.98	.93	.91
Wood 0-.3 ^b	.89	.87	.89	.87	.94	.96	.92	.74
lg 0-.3	.92	.93	.93	.93	.82	.74	.86	.97
lg 0-.3	.98	.98	.98	.98	.98	.98	.93	.92
Wood .3-1	.90	.91	.90	.91	.92	.88	.88	.73
lg .3-1	.70	.71	.70	.71	.57	.50	.64	.82
lg .3-1	.89	.90	.90	.90	.90	.90	.93	.90
Wood 1-2	.85	.84	.86	.86	.88	.87	.85	.73
lg 1-2	.72	.74	.74	.75	.59	.51	.68	.88
lg 1-2	.89	.90	.92	.91	.92	.91	.94	.91
Wood 2-3	.82	.83	.84	.85	.86	.83	.81	.67
lg 2-3	.73	.75	.74	.74	.63	.56	.69	.77
lg 2-3	.79	.79	.78	.77	.78	.79	.72	.72
Wood 3-4	.89	.88	.89	.87	.94	.94	.90	.69
lg 3-4	.92	.90	.90	.91	.90	.86	.88	.75
lg 3-4	.74	.71	.71	.72	.71	.72	.62	.59
Wood > 4	.67	.66	.67	.64	.76	.82	.80	.54
lg > 4	.79	.78	.80	.78	.88	.91	.88	.62
lg > 4	.57	.55	.55	.55	.55	.56	.49	.45
Total Wood	.93	.92	.94	.92	.98	.98	.95	.76
lg W	.91	.92	.92	.93	.80	.72	.85	.97
lg W	.99	.99	.99	.99	.99	.99	.94	.93
Total Mass ^c	.93	.92	.93	.92	.98	.98	.95	.76
lg T	.92	.92	.92	.93	.81	.73	.86	.97
lg T	.99	.98	.99	.99	.99	.99	.94	.92
Age	.91	.92	.92	.92	.81	.74	.86	-
lg Age	.77	.78	.78	.78	.64	.56	.71	-
lg Age	.94	.95	.95	.95	.95	.95	.94	-

a) Dia M = maximum diameter, Dia m = minimum diameter, Circ = circumference, Basal = basal area, lg = log₁₀

b) Wood diameter classes (cm) c) Total aboveground biomass

Table 6.5 Best equations predicting above ground biomass components of *Artemisia* species from easily measured predictive parameters

Equation $Y = mX + b$, where m = slope and b = Y intercept					
Y variable	X variable	m	b	R	R ²
<u>A. tridentata wyomingensis</u> n = 22					
log leaves	/ log volume	.65	- 1.65	.99	.98
log wood 0-.3	/ log volume	.66	- 1.47	.99	.98
wood .3-1	/ min. diameter	3.14	-45.12	.94	.88
log wood 1-2	/ log height	5.42	- 7.35	.92	.85
log wood 2-3	/ log circumference	6.53	-13.67	.92	.84
wood 3-4	/ area	.014	- 7.85	.93	.86
log wood >4	/ basal area	.49	- 5.69	.82	.68
log total wood	/ log volume	.81	- 1.68	.99	.98
log total mass	/ log volume	.78	- 1.45	.99	.98
log age	/ log circumference	.33	0.47	.89	.79
<u>A. tridentata vaseyana</u> n = 181					
log leaves	/ log volume	.66	- 1.68	.99	.98
log wood 0-.3	/ log volume	.65	- 1.36	.99	.99
wood .3-1	/ min. diameter	3.91	-59.87	.95	.90
wood 1-2	/ volume	.00023	4.43	.99	.98
log wood 2-3	/ log circumference	5.58	-11.78	.94	.87
log wood 3-4	/ height	.079	- 6.18	.91	.83
log wood >4	/ volume	.000005	- 5.12	.85	.72
log total wood	/ log volume	.79	- 1.59	.99	.99
log total mass	/ log volume	.76	- 1.38	.99	.99
age	/ circumference	.033	7.85	.81	.65
<u>A. cana cana</u> n = 38					
log leaves	/ log volume	.61	- 1.40	.98	.96
log wood 0-.3	/ log volume	.61	- 1.25	.98	.97
log wood .3-1	/ log basal area	2.25	- 0.43	.93	.86
log wood 1-2	/ log basal area	2.98	- 1.54	.94	.89
wood 2-3	/ area	.022	- 1.60	.86	.74
wood 3-4	/ volume	.0002	- 0.50	.94	.89
log wood >4	/ volume	.000005	- 5.25	.91	.82
log total wood	/ log volume	.73	- 1.36	.99	.98
log total mass	/ log volume	.70	- 1.11	.99	.98
log age	/ log area	.30	0.13	.95	.91
<u>A. frigida</u> n = 20					
log total mass	/ log height	.61	- 0.20	.79	.53
<u>A. ludoviciana</u> n = 22					
log total mass	/ log height	1.63	- 2.38	.99	.98

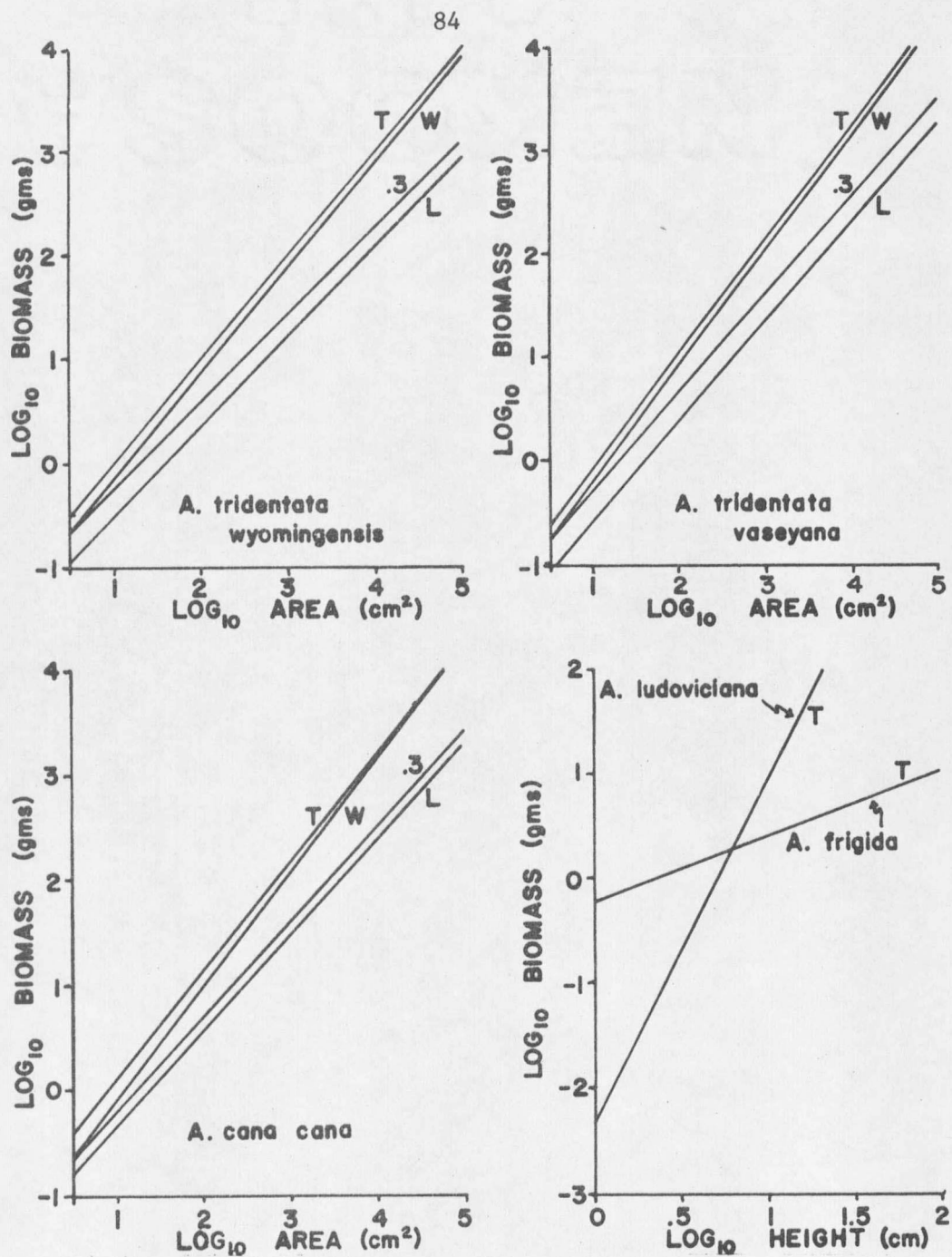


Figure 6.1 Regression of above ground biomass components to plant area or height in 4 species of *Artemisia*. Components are leaves (L), small wood (.3), total wood (W), and total mass (T)

or their transformations were first, second, third and fourth respectively in correlations with biomass or its log transformation. The best equation for each biomass class is presented in Table 6.5. Ages correlated poorly with all categories in the *A. tridentata* subspecies, but was reasonable in *A. c. cana* except for the largest wood classes.

Brown (1976) correlated log transformed basal diameter with log transformed leaves and total aboveground mass of *A. t. vaseyana* in Montana forests. His results compare favorably to my use of basal area, although my correlations are a few points higher. Rittenhouse and Sneva (1977) compared log-log regressions of leaves and total wood with minimum diameter, maximum diameter, height and area of *A. t. wyomingensis* in Oregon and had correlation coefficients from 0.85 to 0.94 for leaves and 0.92 and 0.97 for total wood. This compares well with my results (0.97 to 0.99). Uresk, et al., 1977, working with *A. t. tridentata* in Washington, had correlations of leaves (0.82), wood (0.88) and total mass (0.92) with volume; similar to my results with *A. t. wyomingensis* (0.88 to 0.89) but much lower than *A. t. vaseyana* (0.94 to 0.95). Harniss and Murray (1976) used height and circumference combined in relation to leaf weight of *A. t. vaseyana* in Idaho and obtained a highly correlated ($R = 0.96$) relationship. My results with log transformed height and circumference used separately are comparable, but higher ($R = 0.98$).

Lonner (1972) compared age and log transformed maximum diameter,

area and volume of *A. tridentata* and *A. cana* in Montana and obtained better correlations (0.72 to 0.73) than my results (0.49 to 0.79). He also reported that browsed *A. tridentata* correlated better than unbrowsed plants.

Age determination in *A. ludoviciana* proved unreliable. The annual increase in the perimeter of the clones was consistently 3 cm, and when this is divided into the clone radius, age estimates of more than 200 years for the larger clones resulted.

Annual production (= browse production) per plant was estimated in the shrubs by summing the leaves and the wood 0 to 0.3 cm in diameter. Annual production for *A. t. wyomingensis* ranged from 0.71 gms in small plants to 570 gms in large plants. That of *A. t. vaseyana* ranged from 0.85 to 875 gms and that of *A. c. cana* ranged from 0.56 to 1,357 gms. Wood 0 to 0.3 cm in diameter was equal to or slightly greater in mass than leaves, but approximately one half was estimated to be second year wood. Inflorescence mass was generally one half the leaves, therefore the absence of inflorescence mass in the annual production estimate is largely compensated for by the presence of second year wood. No estimate of annual wood production on stems larger than 0.3 cm was attempted. Leaf mass in the subspecies of *A. tridentata* was slightly underestimated because of the ephemeral and persistent leaves. Collections made before mid June missed the full development of the persistent leaves and collections made after

mid June occurred after ephemeral leaf drop had begun. West (1972) and West and Fareed (1973) report litter fall highest in June and July. Ephemeral leaf loss also occurred when the shrubs were being cut down in the field.

A. ludoviciana annual production is simply the total aboveground biomass since it is herbaceous and dies back to the ground each winter (range 0.2 to 15 gms per plant per year). *A. frigida* annual production ranged from 0.1 to 10.6 gms per plant per year, and is best estimated from the log-log regression equation for height with inflorescence mass:

$$Y = 4.55 X - 6.27 \quad (R^2 = 0.96),$$

where Y is the log of the inflorescence mass and X is the log of the height (cm). No reliable correlations between crown diameters, area, volume or height and vegetative leaf production occurred. For plants without inflorescences, this resulted in considerable underestimation, but for plants with inflorescences, the annual production was not greatly underestimated.

Seed and inflorescence characteristics are presented in Table 6.6. The shrub species have fewer flowers and seeds per head and had larger and heavier seeds than the non-shrubs. Less than half the flowers in the shrub species produced filled seed while more than half the flowers in the non-shrubs produced filled seed. *A. frigida* produced 1.5 times and *A. ludoviciana* produced 1.8 times as many seeds

per inflorescence as the shrubs did. From the data in Table 6.6, the number of inflorescences per plant and leaf mass per plant of actual sample plants, seed production per plant and per gram of leaves was calculated (Table 6.7). Only leaves on vegetative shoots are considered in the leaf mass.

The non-shrubs produced, on the average, more seed, both in number and mass, per gram of leaves than the shrubs; 4.6 to 8.3 and 12.1 to 21.7 times greater in *A. ludoviciana* and *A. frigida* respectively. The large difference in mass of seed per mass of leaves between the shrub life form and the non-shrub life form suggests that 1) leaves and bracts of the inflorescences in *A. ludoviciana* and especially *A. frigida* contributed more photosynthate to seed production than they did in the shrubs, or 2) shrub photosynthate was diverted for annual wood production. Combined with the lower individual seed mass of the non-shrubs (4 or more times lower), the result was a much greater number of seeds per leaf mass (by a factor of ten or more) in *A. ludoviciana* and *A. frigida*. In the shrubs, *A. c. cana* had higher seed production than *A. t. vaseyana*, which was higher than *A. t. wyomingensis*. No apparent correlation of seed production per unit of leaves and plant age, height or number of inflorescences existed. The number of seeds per plant was correlated with the number of inflorescences on the plant ($R = 0.84$ or 0.86 , 0.77 , 0.94 and 0.74 respectively, for *A. t. wyomingensis*, *A. t. vaseyana*, *A. c. cana*, *A.*

Table 6.6 Artemisia inflorescence and seed characteristics

	Flowers per Head	Seeds per Head	Heads per cm escence	Mean escence Length cm
A. tridentata wyomingensis	3.0 ± .5 ^a	1.15 ± .6	25.2 ± 6	10.1 ± 2
A. tridentata vaseyana	2.9 ± .4	1.10 ± .6	22.9 ± 8	12.2 ± 6
A. cana cana	4.7 ± .6	0.95 ± .4	20.3 ± 9	11.9 ± 6
A. frigida	22.2 ± 4.1	14.60 ± 6.4	25.7 ± 6	15.1 ± 6
A. ludoviciana	21.3 ± 6.2	12.30 ± 7.2	15.8 ± 9	29.6 ± 15

	Grams per 1000 Seeds	Seed Length mm	Seed Width mm
A. tridentata wyomingensis	.53 ± .140	1.77 ± .24	.87 ± .11
A. tridentata vaseyana	.60 ± .060	1.78 ± .20	.84 ± .12
A. cana cana	.68 ± .010	2.14 ± .24	.90 ± .10
A. frigida	.10 ± .004	1.21 ± .04	.40 ± .02
A. ludoviciana	.14 ± .003	1.25 ± .07	.43 ± .02

a) expressed as mean ± standard deviation

Table 6.7 Artemisia seed production calculated from
Table 6.6 data and actual samples, 1974 - 1976

	^a age	height cm	number flower stems	1000's seeds /shrub	weight seeds (gm)	weight leaves /shrub	number seeds / gram leaves	gms seeds /gram leaves
A. tridentata wyomingensis								
low	15	30	6	1.7	0.9	16.9	102	.05
	19	40	82	23.6	12.5	54.7	431	.23
high	9	20	21	6.0	3.2	4.1	1466	.78
	19	80	312	89.7	47.5	92.2	973	.52
mean gms seed / gm leaves = .29 ± .20 n = 22								
A. tridentata vaseyana								
low	15	30	10	3.0	1.7	13.6	223	.12
	16	60	176	53.4	29.9	80.0	668	.37
high	12	25	22	6.7	3.7	5.4	1244	.70
	20	100	380	115.4	64.6	246.4	468	.26
mean gms seed / gm leaves = .34 ± .19 n = 18								
A. cana cana								
low	14	50	86	19.6	13.3	260.4	75	.05
high	15	80	237	54.0	36.7	62.4	860	.59
	12	35	111	25.3	17.2	11.3	2240	1.52
mean gms seed / gm leaves = .52 ± .45 n = 38								
A. frigida								
low	4	30	1	5.7	0.6	0.3	19640	1.96
	6	38	10	56.9	5.7	1.2	47450	4.74
high	6	23	4	22.8	2.3	0.2	108450	10.85
mean gms seed / gm leaves = 6.3 ± 4.2 n = 40								
A. ludoviciana								
low	-	15 (10) ^b	1	2.0	0.3	1.1	1757	.25
	-	65 (45)	1	8.9	1.2	0.6	15540	2.18
	-	49 (34)	1	6.7	0.9	0.3	22300	3.12
high	-	117(100)	1	19.7	2.8	0.6	32800	4.59
mean gms seed / gm leaves = 2.4 ± 1.6 n = 36								

a) Age, height, number flower stems and weight of leaves are actual sample values.

b) Height in () is length of inflorescence in cm

frigida and *A. ludoviciana*).

Summary

A. c. cana was tallest and had the largest basal area, but *A. t. vaseyana* had the largest crown diameters, circumference, area and volume. *A. c. cana* was heavier in all biomass classes except wood 0.3 to 1 cm, wood 1 to 2 cm and wood 3 to 4 cm in diameter. *A. t. vaseyana* was heavier than *A. t. wyomingensis* in all categories except wood 1 to 2 cm. *A. frigida* had heavier values than *A. ludoviciana* in all categories except height and leaf mass.

Regressions of plant height (including the inflorescence) with total aboveground mass and inflorescence mass were the only good correlations in the non-shrubs. In the shrubs, volume, area and minimum diameter of the crown correlated better with the biomass classes. Log transformations of both variables generally produced better correlations than non- or semilog transformed data. Age was poorly correlated with biomass except in *A. c. cana*.

Aboveground annual production per plant in the shrubs was highest in *A. t. vaseyana*, followed by *A. c. cana* and *A. t. wyomingensis*. Annual production was estimated as the sum of leaves and wood 0 to 0.3 cm in diameter. Sampling of the shrub species for biomass or annual production should be made in early to mid June to maximize the presence of both ephemeral and persistent leaves.

Aboveground annual production per plant in the non-shrubs was much lower than in the shrubs due to the smaller size of the former. In *A. ludoviciana*, annual production is equivalent to total above-ground mass. In *A. frigida*, it was best estimated as the inflorescence mass. Height was correlated with biomass and production better than any other crown measurement in either species. Sampling for biomass or production in the non-shrubs should be done during the seed maturation phenological stage.

The shrub species had fewer flowers and seeds per head, but larger, heavier seeds than the non-shrubs. Non-shrubs produced more mass and number of seed per gram of vegetative leaves than did the shrubs. Seed production per unit of leaves in any species was not correlated to any parameter measured in this study. Seed per plant was correlated to the number of inflorescences of the plant.

Chapter 7

SEED DISPERSAL

Introduction

Seed dispersal is of interest to the autecologist, the synecologist, the plant geographer and the range manager. The environmental factors involved in seed dispersal, such as wind and water, are concerns of autecology; the interspecific and intraspecific competition for space that of the synecologist (Daubenmire, 1968). Long distance dispersal is more important to the plant geographer in determining methods of migration and causes of distribution (Gleason and Cronquist, 1964). The range manager is interested in seed dispersal as related to reinvasion of an undesirable plant into an area free of it, or to the reestablishment of desirable plants to a depleted or disturbed area.

In *Artemisia*, studies of seed dispersal of only the shrub species have been published. This chapter reports on the dissemination pattern within close proximity to individual plants of both shrub species (*A. tridentata* and *A. cana*), and a non-shrub (*A. frigida*).

Mueggler (1956) concluded that windborne seeds are dispersed only a few hundred feet at the maximum, and Goodwin (1956) found windborne dispersal of 33 meters (no testing beyond 37 meters) in *A. t. tridentata* in Washington. Frischnecht and Plummer (1955)

observed *A. tridentata* seed dispersal was mostly windborne, but some was attributed to animals (zoochory). Animals are probably the most important means of long distance dispersal. Eaton (1936) reported a stand of *A. tridentata* 3,000 km east of its normal range that probably resulted from the use of wool combings as mulch. Short distance dispersal of *A. herba-alba* Asso in the Negev Desert of Israel has been described by Friedman and Orshan (1973).

Methods

Ten isolated plants each of *A. t. wyomingensis*, *A. t. vaseyana*, *A. c. cana* and *A. frigida* (nearest neighbor > 10 meters) were selected for study during the first week of dissemination in October, 1975.

Eight 3.5 cm wide by 3.7 m long boards were placed at progressive 45° compass points around a plant. The boards were covered with double-sided carpet tape in contact with the trunk of the shrub, or in the case of *A. frigida*, the tape was placed to the center of the plant. The traps were left in place for 24 hours, then removed and seed counted.

Data were recorded as the percent of total counted seed in a distance equal to one quarter of the canopy radius for the first two radii, then half radius intervals out to a distance of 3.5 m. The canopy was considered to be equivalent to the elipsoidal projection on the ground of all the foliage and branches of the plant.

Inflorescences projecting beyond the margins of vegetative growth were not considered as part of the canopy. The canopy radius was determined using one half the average of the shortest and longest diameters.

A. ludoviciana was not studied because isolated individuals with seed production could not be located.

Results and Discussion

Most *Artemisia* seeds fell within close proximity to the parent plant. This pattern of dispersal has been termed achory by Pijl (1969). In the shrubs, the majority of the seeds fell under the canopy (Figures 7.1 and 7.2). *A. t. wyomingensis* had a higher proportion of seed (59.5%) fall within the canopy projection than did the other shrubs. This pattern is very similar to that reported for *A. herba-alba* by Friedman and Orshan (1973). *A. t. vaseyana* and *A. c. cana* had 52.1% and 50.3% of the seeds fall under the canopy, respectively.

The proportion of seed falling within the canopy appears to be a function of the shrub morphology. *A. t. wyomingensis* typically splits along the trunk axis, with each resulting section spreading away from the center of the shrub. This spreading produces the rounded appearance described by Winward (1970), partly causing *A. t. wyomingensis* to be shorter (35.8 ± 7 cm) than the other shrub taxa, which, in turn, provides less vertical distance for the wind

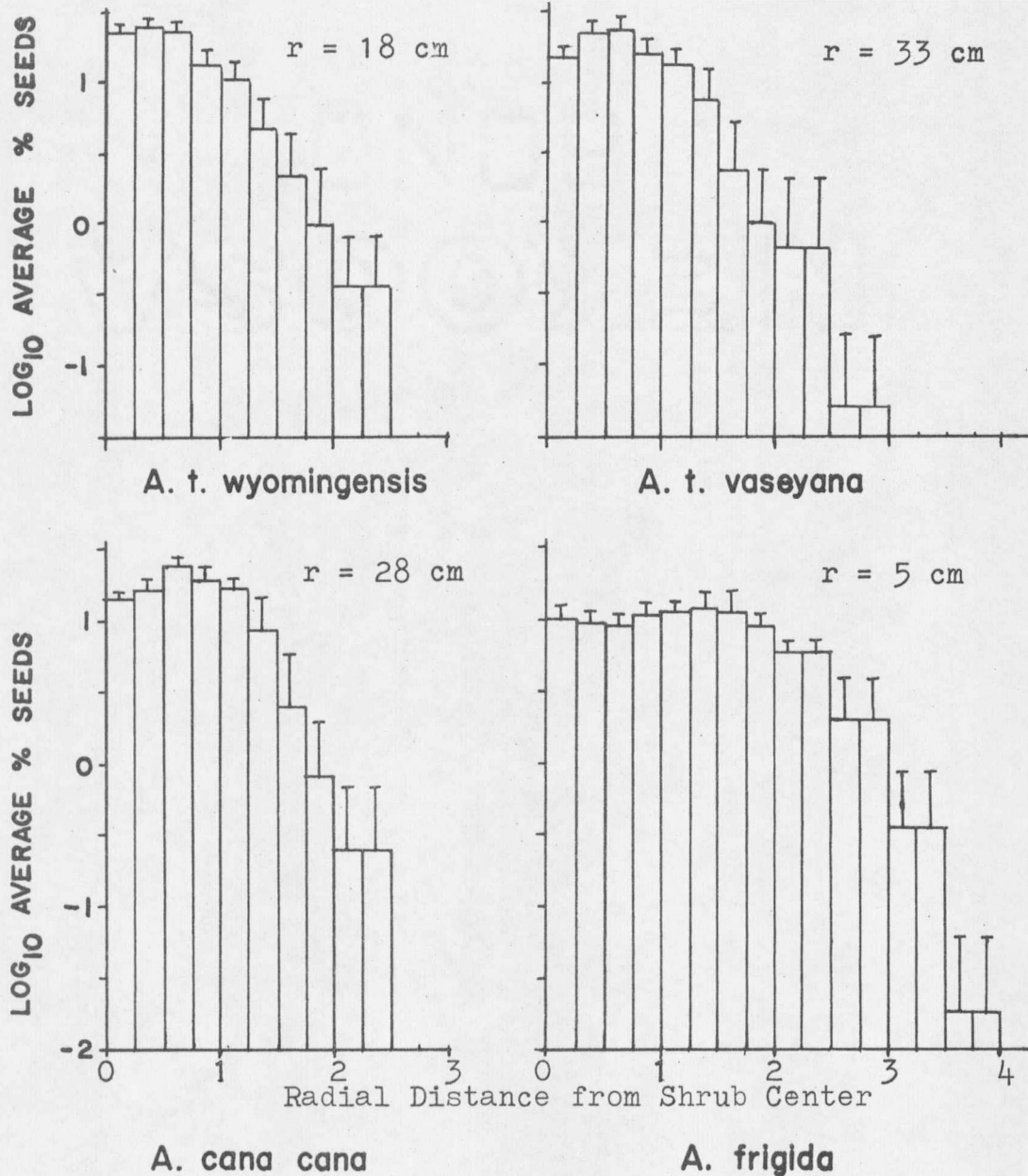
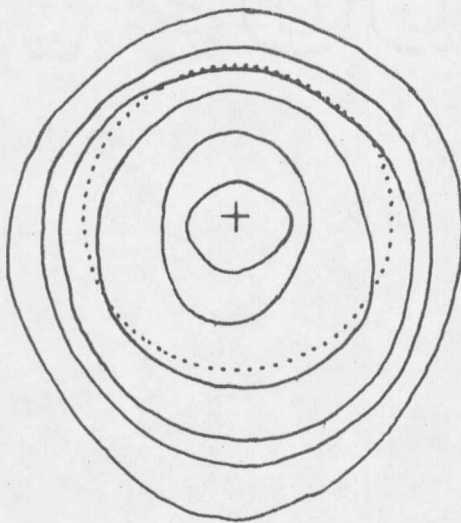
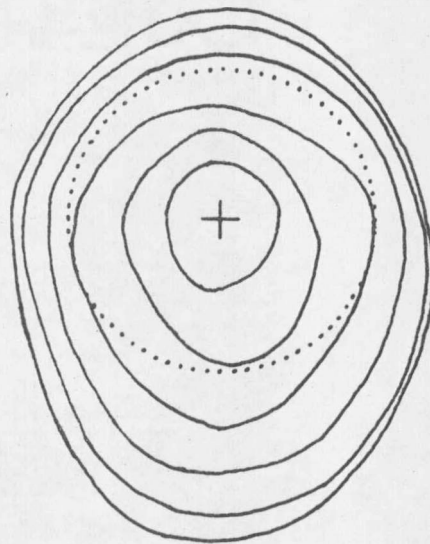


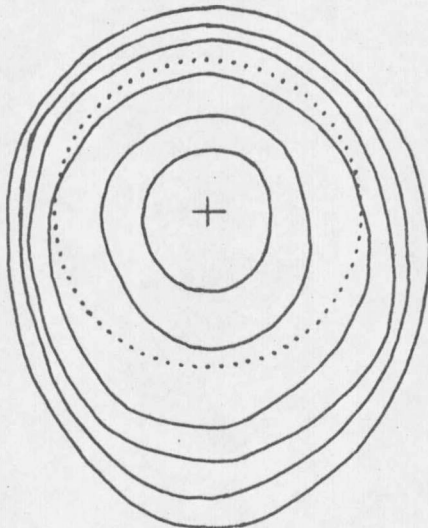
Figure 7.1 Probability of *Artemisia* seed dispersal to a given distance on an average radius. Bars indicate proportion of seeds a distance expressed in plant radii away from the plant center. Bar height shows the log of % seeds in each region and vertical lines indicate SD



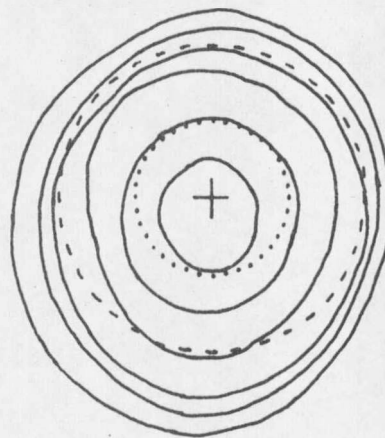
canopy radius = 18cm
A. t. wyomingensis



canopy radius = 33cm
A. t. vaseyana



canopy radius = 28cm
A. c. cana



canopy radius = 5cm
A. frigida

Figure 7.2 Isolines show the effect of wind on seed dispersal patterns of Artemisia. Each line shows the probability of seeds dispersing along a radius falling within lines containing 25%, 50%, 75%, 90%, 95% and 98% of the seeds

prevailing wind is from top of page
+ = plant center ... = vegetative canopy limit n = 10
--- = inflorescence limit in A. frigida

to catch and transport the seed. *A. t. vaseyana* is taller (58.7 ± 15 cm) and presents an even-topped or flat appearance because of the inflorescences projecting above the vegetative canopy (Winward, 1970). The height and the better exposure of the seed to wind provides a greater possibility of the seed being carried outside of the canopy influence. *A. c. cana* is as tall (61.4 ± 4 cm) as *A. t. vaseyana*, and has similar seed dispersal within the canopy.

A. frigida (Figures 7.1 and 7.2) presented a much different dispersal; less than one fourth of the seed (16.0%) fell within the vegetative canopy (68.2% if the canopy includes the floral growth), due primarily to the life form of the species. The vegetative canopy remains small because much of the annual growth dies back to the base of the plant during the winter. The floral stalks (ephemeral) typically extend beyond the canopy, and in some cases may be entirely outside of it.

Dispersal away from the canopy quickly diminishes with distance (Figure 7.1). Less than 13% of the seeds of the shrub taxa are dispersed beyond 1.5 radii from the shrub center (*A. t. wyomingensis*, *A. t. vaseyana* and *A. c. cana* radii are 17.9 ± 6.6 , 32.8 ± 9.7 and 28.1 ± 9.4 cm, respectively). Less than 5% are further than two radii from the shrub center; and only *A. frigida* dispersed seed beyond 3 radii (3%). In the 24 hours of the test, no seed exceeded 3 meters from the plant center. Dispersal downwind from the prevailing wind

direction was slightly further than either upwind or across the wind (Figure 7.2).

During a walk through a stand of *A. t. vaseyana* that had snow covering the ground, I noticed that more seeds were thrown back toward the direction of my approach than in the direction I was headed. This might suggest that the backlash of the branches could be an important propulsion mechanism in seed dispersal in areas with large game animals or livestock. Some seeds stuck to the front of my moist pants and at least some remained there during a walk of one kilometer. The seed of *A. tridentata* (all three subspecies) and *A. c. cana* is ribbed with mucilage that sticks to almost any moist surface. Goodwin (1956) also noted the mucilage in *A. t. tridentata* and Friedman and Orshan (1973) noted a similar occurrence in *A. herba-alba*. The mucilage may provide a means of adherence to passing animals (the probable presence of *Artemisia* seed in the wool combings in Massachusetts (Eaton, 1936) adds support).

Achory, dispersal within close proximity to the parent plant, may cost the loss of many of the seeds produced. I found *Artemisia* vapors to self inhibit germination and Hoffman and Hazlett (1977) found vapors and aqueous extracts to be authopathic; *Artemisia* is also allelopathic (Klarich and Weaver, 1973). This may preclude germination of the seeds that fall under the canopy, and indeed, no seedlings were observed in the field except in the open spaces between shrub canopies

or in disturbed areas without mature shrubs.

SUMMARY

Artemisia seed dispersal is achoric. This is probably fatal for most of the seeds produced by the plant. *A. frigida* has more seed dispersed beyond the vegetative canopy than any of the shrub taxa; *A. c. cana* > *A. t. vaseyana* > *A. t. wyomingensis* in the dispersal of seed beyond the canopy. This is the result of differences in life form (between shrubs and suffrutescent) and between shrub morphology (within the shrubs).

Dispersal beyond the canopy diminishes rapidly with distance. More seed is dispersed outside the canopy downwind than either upwind or crosswind. Dispersal is facilitated by large animal movement through the canopy. Mucilage on the pericarp may improve adherence to animals for long distance dispersal.

Chapter 8

VEGETATIVE REPRODUCTION

Introduction

Knowledge of factors involved in reproduction are of value whenever propagation or control of a species is involved. Much work in the past has been directed at control or eradication of *Artemisia* in the western United States (Holmgren, 1974; Harniss et al., 1981). Knowledge of vegetative reproduction may influence the method of control or eradication and give insight to the possible results (Blaisdell, 1953, 1958; Mueggler and Blaisdell, 1958). Plants with vegetative reproduction have been used to advantage in land rehabilitation since the start of this century (Griffiths, 1910; Gladding, 1945) and have also been used successfully for reproducing material for fire control (Davis, 1970), landscaping (Charles, 1962), revegetation (Carlson, 1974), forage production (Ellern, 1973; Nord, 1959) and various other endeavors (Case and Strain, 1966; Lunt, et al., 1973; Weisner and Johnson, 1977).

This chapter summarizes 1) reports in the literature of field observations of vegetative reproduction, 2) my own field observations, and 3) the results of attempts to root cuttings of *Artemisia* in the greenhouse.

Methods

Measurement of rooting potential. Hardwood cuttings of the woody *Artemisia* species were tested for rooting potential on a greenhouse misting bench. One hundred 15 cm cuttings of each taxon were collected in late October, 1975. The lower 4 cm of each cutting was stripped of leaves, trimmed to a node and dipped in a rooting compound ('Rootone', Amchem Products Inc.) containing three growth regulators (naphthaleneacetimide, methylnaphthaleneacetimide, and indole-3-butyric acid) and the fungicide tetramethylthiuramdisulfide. The shoots were inserted at 3 cm intervals into the propagation bench filled with a mixture of sand (50%), vermiculite (25%), perlite (10%), and peat (15%). Moisture conditions were maintained and controlled by an evaporation controlled misting system (Emery, 1968). Twenty cuttings were removed for examination after ten weeks on the mist bench and the remaining eighty cuttings were removed after seventeen weeks on the bench. *A. frigida*, *A. ludoviciana* and *A. t. tridentata* were not tested in the rooting experiment.

Field evidence of vegetative reproduction. The taxa listed in Table 8.1 were excavated in the field to look for signs of vegetative reproduction such as stolons, rhizomes, shoots with adventitious roots (layering), and roots with adventitious shoots (root sprouts) that may become separated from the parent plant and form self-sufficient

Table 8.1 Vegetative reproduction of *Artemisia* species in the field and the greenhouse, 1974 - 1976

	Greenhouse ^a % Rooting		Field Evidence	
	10 Weeks	17 Weeks	My ^b Observ.	Literature ^c
<i>A. frigida</i>	--	--	No	12
<i>A. ludoviciana</i>	--	--	Yes	3, 6, 8, 9
<i>A. tridentata</i> ssp. <i>tridentata</i>	--	--	No	No
<i>A. tridentata</i> ssp. <i>wyomingensis</i>	0	6	Rare	No
<i>A. tridentata</i> ssp. <i>vaseyana</i>	25	16	Yes	4, 11
<i>A. c. cana</i> X <i>A. t. vaseyana</i>	--	67	Yes	No
<i>A. cana</i> ssp. <i>cana</i>	100	87	Yes	1, 2, 5, 7 9, 10

a) Number of twigs per hundred that rooted in a greenhouse mist bench following treatment with 'Rootone'

b) Results of field excavations and manipulations. See text for type of vegetative reproduction

c) Literature citations are keyed to numbers of the reference below. All citations are positive evidence

- | | |
|-------------------------------|----------------------------|
| 1. Beetle, 1960 | 7. Loepe and Gruell, 1973 |
| 2. Cornelius and Graham, 1958 | 8. Moss, 1959 |
| 3. Davis, 1952 | 9. Munz and Keck, 1959 |
| 4. Hall and Clements, 1932 | 10. Pechanec, et al., 1965 |
| 5. Harrington, 1954 | 11. Winward, 1970 |
| 6. Hitchcock, et al., 1955 | 12. Microshnichenko, 1964 |

individuals (Kains and McQuesten, 1938). Observations were made throughout southern Montana, from Madison County to Rosebud County.

The shrubby taxa were also tested for their capability to root adventitiously in the field. In September, 1974, twenty branches each of *A. c. cana*, *A. t. vaseyana*, and *A. t. wyomingensis* were secured to the soil with U-shaped, heavy gauge, wire pegs and covered with 4 cm of soil at all points of contact with the ground. Ten branches of each were excavated in July, 1975 and the remaining ten in July, 1976. Site locations and soil textures were as follows: *A. c. cana*, Gallatin and Rosebud Counties (silty clay loam); *A. t. vaseyana*, Gallatin County (silt loam); and *A. t. wyomingensis*, Rosebud County (silty clay loam).

In Gallatin, Stillwater and Rosebud Counties, the rate of radial spread of *A. lucovicianae* colonies was determined by tagging the outermost stems in the fall of 1974 and 1975 and measuring the increase in colony diameter during the summers of 1975 and 1976.

Results and Discussion

I saw no evidence of vegetative reproduction of *A. frigida* in Montana as Microshnichenko (1964) reported in Mongolia. Underground branching was evident, but this may have been from soil deposition. Adventitious rooting of these short sections (1-3 cm long) were evident; however, none of the rooting was considered sufficient to

sustain that segment were it separated from the rest of the plant, and no individuals were ever found in the field that appeared so derived.

A. ludoviciana is highly rhizomatous (Davis, 1952; Munz and Keck, 1959; Moss, 1959; Hitchcock, et al., 1955) and forms colonies as large as 15 meters in diameter. Perimeter tagging showed an average annual radial increase of 3.0 ± 0.35 cm ($N = 36$), with no significant difference ($P < .05$) between years or location (county). On wet sites, the colonies advanced in all directions but dry site colonies increased diameter only in wet microsites, such as along drainage depressions. Wet site colonies showed advances both years but three dry site colonies had no radial increase in either year.

Vegetative reproduction in the shrubby species of *Artemisia* in western North America has been noted by several investigators. Wood (1966) observed layering in *A. spinescens* D. C. Eaton. *A. tripartita* Rydb. has been noted to variously reproduce by root sprouting, stump sprouting and layering, especially following fires (Beetle, 1960; Goodwin, 1956; Pechanec, et al., 1954, 1965).

If found no evidence that *A. tridentata* formed root sprouts as reported by Hall and Clements (1932). This phenomenon also was not observed in studies by Goodwin (1956); Blaisdell (1953) and Winward (1970), and big sagebrush is widely recognized to be readily destroyed by fire (Pickford, 1932; Blaisdell, 1953; Beetle, 1960; Loope and Gruell, 1973). However, layering has been observed. Winward (1970)

found layering to occur often in *A. t. vaseyana* form *spiciformis* (Osterhout) Beetle, a form found above 2100 meters in Idaho. He did not find any layering in subspecies *tridentata*, *wyomingensis* or other forms of *vaseyana*. I found only three individuals of *wyomingensis* natural layering; all were in Rosebud County, Montana. However, 10% of the branches that I secured to the soil in the field showed adventitious root development by 1976 and in the greenhouse experiment, 6% of the cuttings rooted in 17 weeks (Table 8.1). Subspecies *vaseyana* had 25% and 16% rooting in 10 and 17 weeks respectively. Many individuals of subspecies *vaseyana* in the field had natural layering (elevation 1375 to 2100 meters), but none of the branches I secured to the soil developed roots. I found no evidence of vegetative reproduction in subspecies *tridentata*.

I observed root sproutings in *A. c. cana*, as did Beetle (1960), Cornelius and Graham (1958) and Pechanec, et al. (1965). One parent plant's taproot that I excavated proceeded horizontally for nine meters before turning down into the B and C soil horizons. This root remained within 5 cm of the soil surface and had 14 root sprouts arising from it. Each sprout-derived 'plant' developed adventitious roots to help ensure its independence of other shrubs in the complex should separation from the parent plant occur. Only in severely disturbed sites were seed-derived seedlings found, and these were mixed with root sprouts from undamaged roots in the disturbed area.

In erosion gullies where *A. c. cana* was covered with silt from periodic floods, both root sprouts and adventitious rooting of buried branches were abundant. No layering of this species was observed in habitats that did not have evidence of periodic flooding. Cuttings in the greenhouse rooted well: 100% and 87% in the 10 and 17 week periods respectively. A hybrid individual (*A. c. cana* X *A. t. vaseyana*) found in Gallatin County, which showed more morphological characteristics of *A. c. cana*, also rooted well in the greenhouse (67% in 17 weeks) and in the field had root sprouts (Table 8.1).

Layering in the shrubby *Artemisia* species may be an adaptation for drought survival and preservation of the individual rather than reproduction of the species. Ginzburg (1963) found that discontinuities of cambial activity in the secondary xylem of *A. herba-alba* caused sectional splitting of the shrub axis. Each section was then somewhat physiologically independent, being directly connected to a sector of the root system. A layer of cork separates each year's growth of xylem apparently to separate and protect the water column. Moses (1940) and Dale (1968) have described this cork layer in *A. tridentata* and I have observed the discontinuous cambial activity and radial sectioning in *A. t. vaseyana*, *A. t. wyomingensis* and *A. c. cana*. Cook and Stoddart (1960) observed self-supporting units in *A. tridentata* like those described in Ginzburg. The adventitious rooting of these independent sections would enhance the ability to

survive a drought period by providing a greater root surface area for the acquisition of water.

Summary

A. frigida does not reproduce vegetatively. *A. ludoviciana* and *A. c. cana*, both found in habitats that are often flooded, vegetatively produce siblings that are relatively distant from the parent and appear capable of survival if separated from that parent plant. *A. tridentate vaseyana* and *A. t. wyomingensis* exhibit only layering, which may enhance drought survival but does not produce new individuals.

Chapter 9

SUMMARY

Artemisia tridentata is common throughout western North America. Subspecies *tridentata* occurs west of the continental divide, ssp. *vaseyana* west of the divide except in Wyoming and Montana where it is east of the divide as well, and ssp. *wyomingensis* occurs in three distinct areas both east and west of the continental divide. *A. cana* distribution is slightly more northern, with ssp. *cana* east of the divide and to the north, ssp. *viscidula* west of the divide and southern, and ssp. *bolanderi* restricted to the extreme west side of the Great Basin. *A. frigida* is widely distributed in the mountains and valleys of the Rocky Mountains and in the northern Great Plains north to Alaska and in Eurasia. *A. ludoviciana* is widely distributed in western North America from Mexico through the Great Basin, Rocky Mountains and the short grass prairie to northern Alberta, Canada.

Phenological development was very similar in all three life forms, except for cessation of vegetative growth which was later by four weeks in the shrubs than in the non-shrubs. Vegetative growth began in April and ended in June or July. Inflorescence initiation occurred in late May to early June, anther development in August, flowering in September and seed dispersal in late October and early December. Phenological stages started later and ended earlier with

increase in elevation or latitude.

Artemisia germinates over a broad range of temperatures, with the non-shrub forms having a narrower optimal range. *A. frigida* had the coolest optimum, *A. ludoviciana* the warmest optimum and *A. c. cana* the broadest optimum. Germination tests conducted in petri dishes were not representative of the potential germination except for *A. ludoviciana*. All four species were autopathic. To maximize emergence and survival, *Artemisia* seed should be planted a mere 2.5 mm deep.

Artemisia had high mortality in the first four months following emergence, then a slow mortality for the remainder of its life. Initial mortality was greater for the non-shrub life forms, perhaps due to their smaller seed size. Competition from annual plants and predation by insects caused severe loss of seedlings. Seedling development on coal spoils in eastern Montana was retarded even when water was not limiting. Absence of nutrients or symbiotes may be responsible.

The shrubs were larger, but had lower seed production per unit of vegetative leaves than the suffrutescent or herb. Many individual plants of each of the life forms produced an estimated 10,000 seeds and a few plants produced 50,000 or more (115,000 in *A. t. vaseyana*). Seeds of the shrubs are larger and heavier than non-shrub species.

A. frigida had greater crown dimensions and biomass than *A. ludoviciana* except for leaf mass and height. Height proved to be the

only good correlation with biomass in the non-shrub life forms.

In the shrubs, *A. c. cana* was tallest and had the largest basal area, but *A. t. vaseyana* had greater crown diameters, circumference, area and volume. *A. c. cana* was highest in all the biomass classes except wood 0.3 to 1 cm (*A. t. vaseyana*), wood 1 to 2 cm (*A. t. wyomingensis*) and wood 3 to 4 cm in diameter (*A. t. vaseyana*). *A. t. wyomingensis* was lowest in all categories except wood 1 to 2 cm. The best correlations of biomass with shrub crown dimensions occurred with area, volume and minimum diameter. Age was poorly correlated with biomass except in *A. c. cana*. Log transformations of both dependent and independent variables generally improved correlations.

Annual aboveground production per plant in the shrubs was estimated as the sum of leaf and wood 0 to 0.3 cm; *A. t. vaseyana* was greater than *A. t. wyomingensis*. Non-shrub production per plant was lower and was estimated as the mass of the inflorescence. For all the taxa, these estimates are probably low due to the omission of radial trunk growth.

Seed dispersal in *Artemisia* is achoric (the majority of the seeds fall under the plant canopy), and this is probably fatal to the majority of the seed produced by the plant. *A. frigida* dispersed more seed beyond the vegetative canopy limit than any of the shrubs. *A. c. cana* beyond the canopy was greater than *A. t. vaseyana*, which was greater than *A. t. wyomingensis*. Dispersal beyond the canopy limit

diminished rapidly with distance from the plant. Animals may be the most important agent of long distance dispersal.

Vegetative reproduction was associated with habitat rather than life form. *A. c. cana* and *A. ludoviciana* were common in habitats prone to flooding or erosional deposition and both species had vegetative reproduction. Both subspecies of *A. tridentata* exhibited the ability to layer, but this appeared to enhance drought survival rather than produce new individuals. *A. frigida* was not found to have vegetative reproduction.

Of special interest to reclamation engineers are the observations that concern the establishment of *Artemisia* species on disturbed land; *A. c. cana* and *A. ludoviciana* can be reproduced vegetatively and *A. tridentata* and *A. frigida* probably cannot. If reproduction from seed is to be used, the data presented can be applied to the season of seed collection, methods of determining viability, and determining seeding rates. Field observations suggest that seedling establishment is best on natural topsoils.

Chapter 10

RECLAMATION CONSIDERATIONS

In selecting an *Artemisia* species for use in reclamation, its potential role in a management plan must be considered. The following list provides some management considerations and the impressions of the best species suited to each: 1) Erosion Control, *A. ludoviciana*, *A. cana*; 2) Water (snow) Retention, *A. tridentata*, *A. cana*; 3) Wildlife Cover, *A. tridentata*, *A. cana*; 4) Forage Value, *A. ludoviciana*, *A. frigida*, *A. tridentata*, and *A. cana*.

On difficult reclamation sites, establishment of *Artemisia* by vegetative reproduction means may be the best method. This is likely to be difficult with *A. tridentata* and *A. frigida*, but should prove easy with *A. ludoviciana* and *A. cana* (Table 8.1, page 103). Further investigations of vegetative establishment methods are needed. To allow root establishment before shoot growth begins in the spring, rhizomes, root sections or stem cuttings should be planted before April (page 23).

Much of my effort has been directed toward the potential establishment of plants from seeds because of the presumed economical savings. Collection of seeds should be made in mid October (page 26) and one might expect to obtain 190, 270, 1950 and 3750 seeds per decimeter of inflorescence for *A. cana*, *A. tridentata*, *A. ludoviciana*

and *A. frigida*, respectively (Table 6.6, page 89). Seeds stored at room temperature had 80% germination (Table 4.2, page 38); stratification of Montana seed therefore appears unnecessary. The standard method of petri plate germination tests substantially underestimates the germination potential found by tests conducted on a temperature gradient bar (page 39-40). Treatment of seeds with a fungicide (Arasam 75) improved petri plate germination but had little effect in soil germination tests (page 37,39). The possibility of inoculating *Artemisia* seeds with microbes (e.g. micorrhizal fungi or nitrogen-fixing bacteria) needs further study, but might improve seedling survival. To obtain a density of one plant per m^2 , seeds should be shown at rates of approximately 14, 27, 27 and 38 kg of seeds per hectare for *A. cana*, *A. tridentata*, *A. frigida* and *A. ludoviciana*, respectively, and the number of seedlings per m^2 at the end of one year would approximately be 5, 3, 8 and 9 respectively (pages 70-72, 87-90). Where insect predation and weed competition on *Artemisia* seedlings are significant, seeding rates should be increased by unknown amounts (page 60).

Secondary dispersion of *Artemisia* will thicken stands. It will occur early by vegetative reproduction in *A. ludoviciana* and by seeds in both *A. ludoviciana* and *A. frigida*. It will require, however, about 4 years in *A. tridentata* and *A. cana*. It is

speculated that vegetative reproduction of *A. cana* will occur only after several years. Long distance dispersal by seeds or vegetative reproduction will be rare.

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