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

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

Abstract:

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

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

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APPROVAL

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Todd Patrick Walton

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

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ABSTRACT

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

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INTRODUCTION

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

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

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

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

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

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

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

LITERATURE REVIEW

Introduction to *Artemisia* Taxonomy

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

Characteristics and Taxonomy of Sagebrush

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

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

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

Silver Sagebrush Taxonomy

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

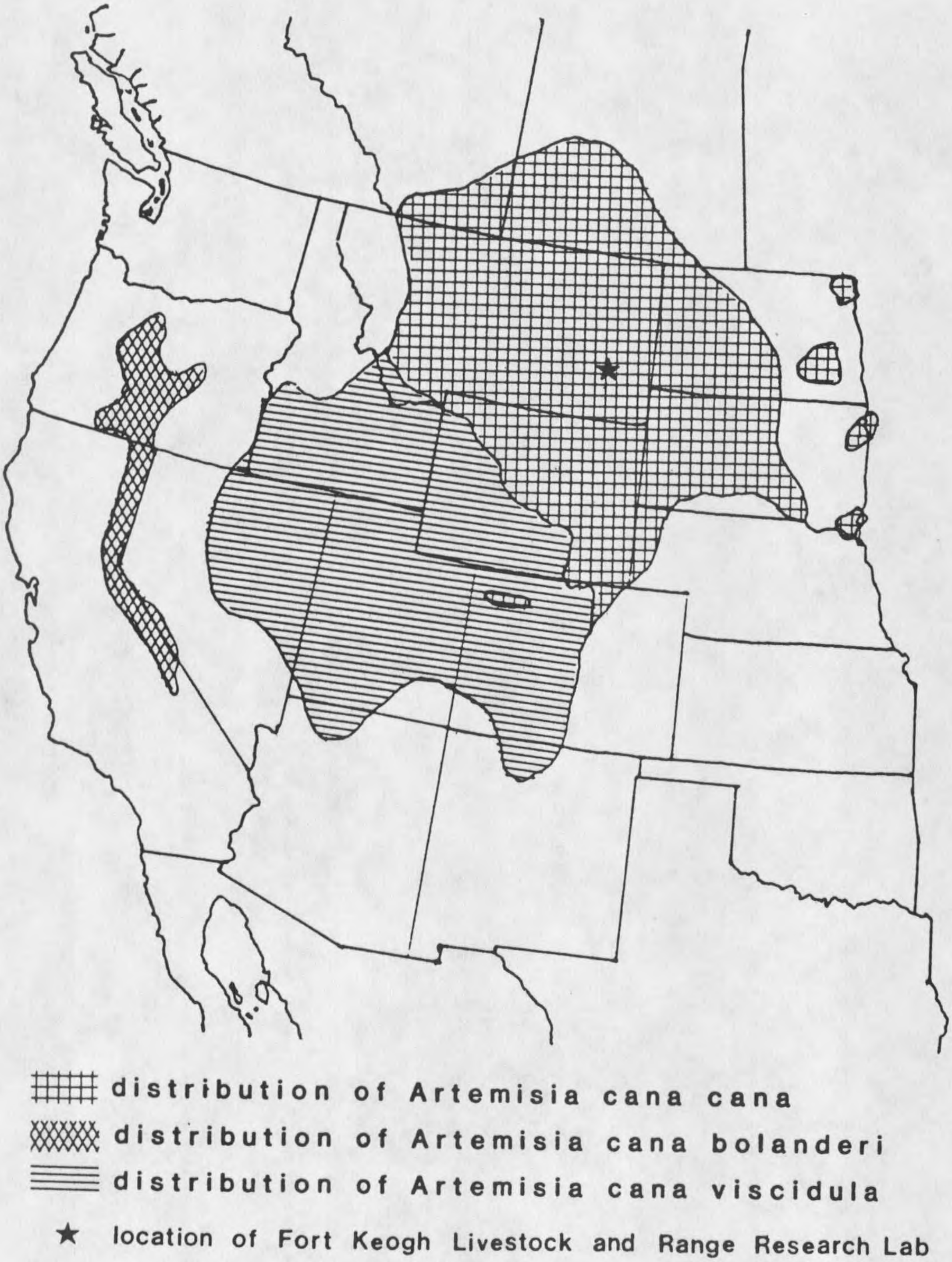

Figure 1. Distribution of the three subspecies of silver sagebrush in western North America (Harvey 1981).

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

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

Distribution of Plains Silver Sagebrush

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

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

Ecology and Characteristics of Sagebrush

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

Control Methods and Results

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

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

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

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

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

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

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

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

Forage Considerations

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

Wildlife Forage Considerations

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

Livestock Forage Considerations

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

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

Sagebrush Chemistry

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

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

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

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

Ecological Aspects of Sagebrush

Grazing Impacts

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

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

Soil Relationships

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

Allelopathy

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

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

Reproductive Characteristics

Seed Dispersal

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

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

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

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

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

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

Germination Factors

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

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

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

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

Stratification

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

Temperature Effects

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

Light and Dark Effects

The light requirement of seeds has also been studied widely. To a large extent, light seems to play an interactive role with other environmental factors. Seed dormancy is terminated in a large number of species when hydrated seed is illuminated. Light is therefore of great ecological importance (Cook 1980). Light can determine whether germination occurs in or on the soil; it controls germination under vegetational canopies; and it interacts with temperature to determine the length of seasonal dormancy. An increase in temperature may decrease the effects of light so much that germination in the dark becomes greater. The opposite can occur whereby some germination occurs at lower temperatures, but light along with increasing temperatures will increase germination (Bewley and Black 1982). Some species that have never been dormant readily germinate in darkness when imbibed with water. Other species, in contrast, seem insensitive to light unless exposed to osmotic stress.

In some species light inhibits seed germination at certain temperatures due to changes in the makeup of the cell membrane. This inhibition seems to occur during the later stages of the germinaton process. There can also be a light requirement at the time of dispersal which is negated after burial and passage of time (Bewley and Black 1982). In contrast, Cook (1980) reports that some species will display no light requirement as fresh seed, but they will have a light requirement after burial. Light-stimulated germination of seedlings involves a complex interaction of the phytochrome system. However, the precise mechanism of maintaining dormancy in seeds that require light is unknown although it seems clear that there are complex interactions with temperature and hormones (Al-Ani et al. 1972, Wooley and Stoller 1978).

Light exerts a variable influence on seed germination of sagebrush depending on the species and associated environmental factors. Fringed sagewort (Artemisia frigida Willc.) showed a light requirement, but this could be circumvented by treating seed with gibberillic acid (Wilson 1982). Sabo et al. (1979) assert that light has no effect on germination of seed in either fringed sagewort or big sagebrush. However, evidence to the contrary has been presented by several researchers that state that light significantly increased germination by as much as three times in big sagebrush (Weldon et al. 1959, Beetle 1960, Caldwell 1978).

The germination response that has been observed in other species clearly demonstrates that light can play a variable role. In Iraq, Al-Ani et al. (1972) reported a variety of reactions among 10 species with respect to germination requirement for light. Two species required light, while six showed no response and two had their best germination in dark. Lettuce, a light sensitive seed, did not require light at temperatures below 20 C (Woolley and Stoller 1978). Most other studies of various species show a requirement for light (Waller et al. 1980, Mayeux and Leotta 1981, Krueger and Shaner 1982).

Osmotic Potential

There are at least three stages of the germination process in which water relationships are important: (1) imbibition, (2) enzymatic transformation and meristematic activities, and (3) start of growth through elongation and emergence of the radicle through the seed coat. All of these are regulated by water uptake from the soil or soil solution. Water stress is an important variable that can influence germination response. Because of the difficulty in measuring matric potential, osmotic potential has usually been used in soil-water studies (Evans and Young 1982). However, matric potential has been found to be an important factor in seed germination (Collis-George and Hector 1966).

Germination rates and totals consistently decrease with a decline in external water potential. Under these conditions, excessive temperatures and moisture stress are usually additive in decreasing germination. Seeds, in a water stress situation, are placed under relatively more stress in extremely warm or cool incubation temperatures (Bewley and Black 1982, Evans and Young 1982).

Increased water stress either delays the completion of germination or reduces germination. This also depends on the vigor of the seed. An ability to germinate under stress may confer certain ecological advantages (Bewley and Black 1982). Parmar and Moore (1966) showed that responses to moisture stress differed between seeds of low and high vigor, and they suggested that increased osmotic potential decreased water absorption, disturbed nutrient uptake, caused abnormal metabolism and ultimately reduced growth.

Big sagebrush responded to more negative osmotic potential with less total germination, but this condition was ameliorated by light (Weldon et al. 1959). In contrast, Sabo et al. (1979) reported little effect of osmotic potential until 10 atm was reached. Fringed sagewort was much more sensitive than big sagebrush and showed initial responses at 2 atm.

Maturity of Seed

Maturity of seed also tends to have an effect on germination with higher values being observed in later seed collections. Clor et al. (1974) reported that _Artemisia herba-alba_ Asso reacted this way, and both prostrate spurge and prostrate kochia (_Kochia prostrata_ (L.) Schrad.) showed higher germination percentages when seed was collected later (Waller et al. 1980, Krueger and Shaner 1982).

Early Seedling Growth

Growth characteristics of sagebrush seedlings seem to be primarily subject to genetic control although environmental influences also contribute to seedling response (McArthur and Welch 1982). Among big sagebrush accessions and subspecies, growth parameters showed significant differences in each measure. Height, crown, length of leaders and annual yield were among parameters differing between accessions and subspecies.

Although seed production is high in sagebrush, very few seedlings emerge and survive. This can be attributed to amount of vegetation present (competition), litter, adverse environmental factors (eg. water stress and depth of burial), and allelopathy (autopathy) (Johnson and Payne 1968, Evernari et al. 1971, Friedman and Orshan 1975, Harniss and McDonough 1975, Eddleman 1979, Cook 1980, Harvey 1981, Evans and Young 1982, Wilson 1982). The maximum depth from which sagebrush seed will emerge has been estimated at 5 mm by Harvey (1981). Burial at 2 mm was considered an optimum depth for plains silver sagebrush. Years that are favorable for natural seedling establishment can occur at irregular intervals with the primary factor being soil moisture (Johnson and Payne 1968, Gordon and Wright 1981). However, establishment can be of little ecological importance unless it occurs on highly disturbed areas according to Harvey (1981).

Vegetative (Asexual) Reproduction

Vegetative reproduction in Artemisia has been examined several times, but few in-depth studies have been completed. Bostock and Benton (1979) studied five perennial composites with varying degrees of lateral extension and growth. They subsequently related seed and vegetative reproductive strategies. Seed was generally more important than vegetative capacity. However, Artemisia vulgaris L. perennates only by vegetatively produced propagules, and it had rhizome growth measured at 30 cm per year.

Went (1979) contends that survival in perennial desert plants depends mainly upon a vegetative strategy, and seeds are only a secondary method of reproduction that becomes important when summer rains allow abundant germination. Contradictory evidence has been presented in a study by Young and Evans (1972). They examined green rabbitbrush which was long thought to invade sites by root sprouting. They discovered that it relied heavily on seedlings to establish new plants. Therefore, either mechanism can be successful.

There are special problems that vegetative reproduction presents for the field and experimental ecologist. Abrahamson (1980) states that vegetative reproduction is more similar to growth than to reproduction with confusion coming from using animals as models. He states further that vegetative reproduction is a distinct and well-defined phenomenon.

Vegetative reproduction is common in forest herbs, aquatic plants, and at higher latitudes and altitudes where ecosystems are more influenced by fire, climatic and other disturbances (Abrahamson 1980, Legere and Payette 1981). A clone is defined as the aggregate of individual organisms descended by asexual reproduction from a single sexually produced individual (Barnes 1966). Many plants in such diverse genera as _Ophioglossum_, _Pteridium_, _Populus_, _Equisetum_, _Carex_, _Rhus_, _Cornus_, _Prunus_ and _Artemisia_ form clones by initiating shoots from underground parts. It is common for clonal growth to be much more prevalent than sexual reproduction in spite of the fact that there may be a large and viable seedbank in the soil (Evernari et al. 1971, Hazlett and Hoffman 1975, Cook 1980, Harvey 1981, Lovett-Doust 1981). The degree to which cloning plays a role in some ecosystems can be quite large. In Finland, 80 percent of the angiosperm vegetation in a local flora had the capacity to clone (Abrahamson 1980), while in Great Britain, two-thirds of the common perennial species are clonal (Cook 1983). Moreover, the most pernicious weeds usually become more serious economic pests precisely because they grow from underground roots, rhizomes and buds.

Importance of Vegetative Reproduction

Several reasons can reasonably explain why vegetative reproduction is of such importance. Vegetative reproduction allows survival of perennial polyploids in spite of their typically inferior seed being less able to successfully establish or maintain vigor. In addition, reproduction by seed: (1) generally requires higher temperatures than those for vegetative growth, (2) seems at a disadvantage with respect to effectiveness of gene transmission, and (3) is usually in competition with vegetative reproduction for the same limited resources (Abrahamson 1980). When both methods occur simultaneously, vegetative offspring will commonly develop immediately and quickly become adult. This is apparently accomplished with larger carbohydrate reserves than those individuals developing from seed. Cloning seems to be a low risk mechanism for increasing longevity and perennation of the genet. The genet is defined as all genetically identical members of a clone derived from a single zygote (Cook 1983). Abrahamson (1980) also predicts that when population density is low and clonal expression is possible, vegetative reproduction would be more advantageous because it facilitates local spread and occupation by the genet. However, when plant density is high, seeds would be better. Seeds facilitate dispersal to new sites that may be less densely populated and therefore more favorable for seedling growth. Life expectancy of plants regenerating from seed is frequently less than that of vegetatively produced plants (Abrahamson 1980, Cook 1979). This has been attributed to more intense competitive stress for light and other resources.

Cook (1983) reiterates the belief that nothing in biology makes sense except in light of evolution. He further states that benefits of clonal reproduction include: (1) an enhanced ability to utilize scarce resources, (2) greater competitive ability both to invade other clones and to resist invasion of seedlings, and (3) reduced probability of genet extinction by spreading risk among a number of individuals.

Characteristics of Vegetative Reproduction

Populations of individual genets can extend over a large area and can attain substantial ages. Shrubs pose special demographic problems in that age structure of aboveground shoots may diverge sharply from that of belowground parts (Fernandez and Caldwell 1975, Harper 1977, Noble et al. 1979). Demography of clonal shrubs is ultimately determined by the morphology of the growth system and will have a complex age structure. Thus, rhizome ages will usually be quite different than that of aerial shoots, and the ages of buds will be different from that of either rhizomes or shoots. Harberd (1967) reported on one large population of Holcus mollis L. that consisted of only four genotypes. One of the genotypes was 1/2 mile (0.8 km) wide. Comparable analysis of sheep's fescue (Festuca ovina L.) revealed one genotype that was considered to be over 1000 years old (Harberd 1962). Aspens (Populus tremuloides Michx.) have been recognized for their clonal nature and can cover 43 hectares with 47,000 ramets (individuals) (Kemperman and Barnes 1976). They frequently attain very great age (>10000 years). Creosote bush (Larrea tridentata (Ses. & Moc. Exdc.) Cov.) in the Mojave Desert clone by irregular radial growth on outer edges of stem segments (Vasek 1980). They have been estimated to reach ages of almost 12000 years. Longevity of the rhizome system can be as long as the life of the genet, as in sand sedge (Carex arenaria L.) (Noble et al. 1979), or rhizomes can disintegrate after establishment of daughter plants with independent root systems (Lovett-Doust 1981). The mere presence of physical connections between vegetative offspring is insufficient for demonstrating physiological interdependence (Ashmun et al. 1982).

The occupation of horizontal space, characteristic of clonal growth (Ito et al. 1976, Noble et al. 1979, Cook 1983), may be greatly affected by physical features of the habitat. The success of of the clone is greatly increased by: (1) capacity to detect nutrient gradations, (2) initiation of adventitious roots, and (3) establishment of new shoots. This clonal capacity seems to overcome limiting aspects of the soil and competitive influences (Noble et al. 1979, Cook 1983). Storage of carbohydrates in a perennial rhizome has been noted as adventageous to rapid development and survival of clones (Ashmun et al. 1982). Rhizome formation of mugwort was observed from April to May in Japan with lateral extension being 5.4 meters (Ito et al. 1976). Endogenous hormones have been related to stolon development with gibberillic acid stimulating stolon elongation and cytokinin initiating leafy shoot development from stolons (Kumar and Wareing 1972). Silver sagebrush cuttings root easily within eight weeks when collected at the leaf growth phenological stage (Everett, Meeuwig and Robertson 1978).

Factors that stimulate vegetative reproduction are general in nature (Abrahamson 1980). Soil moisture can promote either means of reproduction. Increased soil moisture was shown to favor seed reproduction in wild garlic (Allium carinatum L.) (Salisbury 1942). Little seed was set in a wet summer by two other species, yellow deadnettle (Galeobdolon luteum Hudson) and blue gromwell (Lithospermum purpureo-coeruleum L.), each of which was reproducing vigorously by vegetative means. Soil texture influences what strategy is favored, with clay content usually favoring vegetative reproduction (Abrahamson 1980). Increasing litter decreased the success of cloning, while increased environmental severity accentuated vegetative reproduction.

Methods were designed to examine certain reproductive strategies in plains silver sagebrush with results from this literature examination in mind. Specifically, experiments dealing with dispersal, germination factors, early seedling growth and vegetative reproduction were implemented.

METHODS AND SITE DESCRIPTIONS

Introduction

This project was conducted at the Fort Keogh Livestock and Range Research Laboratory near Miles City in southeast Montana. Fieldwork was initiated in June of 1982 and completed in October 1983. The station has a variety of range sites and topography representative of much of the Northern Great Plains (Johnson 1978). Topography ranges from rough breaks to alluvial floodplains and terraces. Land forms are intersected by numerous intermittent stream channels where substantial populations of plains silver sagebrush exist.

The climate is fairly typical of the Northern Great Plains with drought playing a substantial role (Johnson 1978). Average annual precipitation at Miles City for the period 1878-1981 has been 34.29 cm (13.5 in). Deviations from this average can be extreme as evidenced by historic maximums and minimums: 57.9 cm (22.8 in) in 1879 and 14.0 cm (5.5 in) in 1934, respectively. Precipitation was below normal preceding this study with 1979, 1980 and 1981 receiving 22.1 cm (8.7 in), 26.7 cm (10.5 in) and 26.9 cm (10.6 in), respectively. The precipitation and temperature data for 1981, 1982 and 1983 are summarized by month in Appendix A. Data for 1981 was included because Olson (1982) found that precipitation from the previous year was important in determining subsequent vegetation response.

Four distinct aspects of sagebrush reproduction were examined during the course of my research. They included: seed dispersal, germination, seedling development and asexual reproduction. Dispersal characteristics were measured in field populations. Germination factors were observed in growth chambers. Emergence, growth and survival parameters were differentiated in field, growth chamber and greenhouse studies. Finally, field excavations were conducted to evaluate the relative importance of vegetative reproduction.

Seed Dispersal

Three study sites were selected in the fall of 1982 to evaluate seed dispersal in plains silver sagebrush. These sites were typical of plains silver sagebrush communities throughout the Northern Great Plains. They were located so as to allow easy access during the late fall and early winter. These three pastures are referred to locally as Paddy Faye, Lower Flood and Lower Black Springs.

Site Descriptions

Paddy Faye is an alluvial bottomland that is located approximately 11 km southeast of station headquarters and adjacent to the Tongue River. The pasture is intersected by an intermittent drainage, Paddy Faye Creek. Plains silver sagebrush is a prominent vegetative characteristic of Paddy Faye, but plant density ranges from sparse to dense. Understory vegetation consists of green needlegrass (Stipa viridula Trin.), buffalograss (Buchloe dactyloides (Nutt.) Engelm.), blue grama (Bouteloua gracilis (H.B.K.) Lag.) and considerable western wheatgrass (Agropyron smithii Rydb). Introduced species include Japanese brome (*Bromus japonicus* Thunb.) and cheatgrass (*Bromus tectorum* L.).

Soils in Paddy Faye are predominantly Kobar silty clay loams. Kobar silty clay loams are classified as fine, montmorillonitic Borollic Camborthids. They are deep, well-drained, nearly level soils that are formed in alluvium. The soils have moderately slow permeability and high available water capacity. Available water capacity is the amount of water capable of being stored in the soil profile. The range site is classified as clayey and is located in the 25 to 36 cm (10-14 in) precipitation zone. Paddy Faye has a high water table underlying much of the pasture.

Paddy Faye has had a long history of heavy grazing use. During early settlement it was situated along the Tongue River Trail. As such, it received continuous, season-long grazing by large livestock herds. More recently this pasture has been used during the summer as a breeding pasture. Because of drought conditions and a change in grazing management, the study site had not been grazed for the past five years prior to this study.

Lower Flood Pasture is an alluvial floodplain adjacent to the Tongue River and located 7-9 km southeast of station headquarters. Vegetation is similar to that of Paddy Faye. Plains silver sagebrush is the dominant shrub species present. It is found in sparse to dense stands with western wheatgrass, green needlegrass, blue grama, buffalograss, Japanese brome and cheatgrass constituting most of the understory. The principle soils found in Lower Flood are Harlem Variant silty clays. They are classified as fine, montmorillonitic

Borollic Camborthids. Permeability is slow while available water capacity is high. These deep, well-drained, alluvial soils are best described as clayey range sites.

Grazing in Lower Flood has traditionally been imposed during the spring and early summer. Grazing begins every year at calving (early April) and continues through the early season with intermittent grazing during the summer.

The Lower Black Springs study site is represented by a small area on a terrace of the Yellowstone River approximately 6.5 km west of station headquarters. Although herbaceous vegetation for this site would normally be western wheatgrass and associated species, it is currently occupied by crested wheatgrass (Agropyron cristatum (L.) P. Gaertn.) that was seeded several years ago. A moderately dense stand of plains silver sagebrush dominates this area with greasewood (Sarcobatus vermiculatus (Hook.) J. Torr.) being occasionally interspersed. Crested wheatgrass is the major understory constituent. Havre-Variant loams are the common soil found in Lower Black Springs. It is a deep, well-drained soil formed in alluvium. Moderate permeablity and high available water capacity are characteristic of this fine-loam, mixed (calcareous) frigid Ustic Torrifluvent. The range site is considered as silty. Use by grazing cattle traditionally has been as a breeding pasture in the summer.

Experimental Methods

Five plants were selected in each of the three study sites and marked for seed dispersal measurements. The shrubs were selected to typify the average adult (seed bearing) size structure of the community. In addition, care was taken to select plants with sufficient area around them to accomodate six unobstructed line transects for monitoring dispersal. All seedheads were removed from adjacent sagebrush plants within a 10 m radius of the marked shrubs to eliminate their influence on the dispersal measurements. Six permanent line transects were then established in a radial fashion from the center of each marked shrub. Transects were oriented so that one line lay along the prevailing wind direction. The other five transects were equally spaced at 60 degree angles from one another around the central shrub. Aluminum sheet-metal plates (36x36 cm) were anchored to the ground at one meter intervals (0,1,2,3 and 4 m) along each transect (Figure 2).

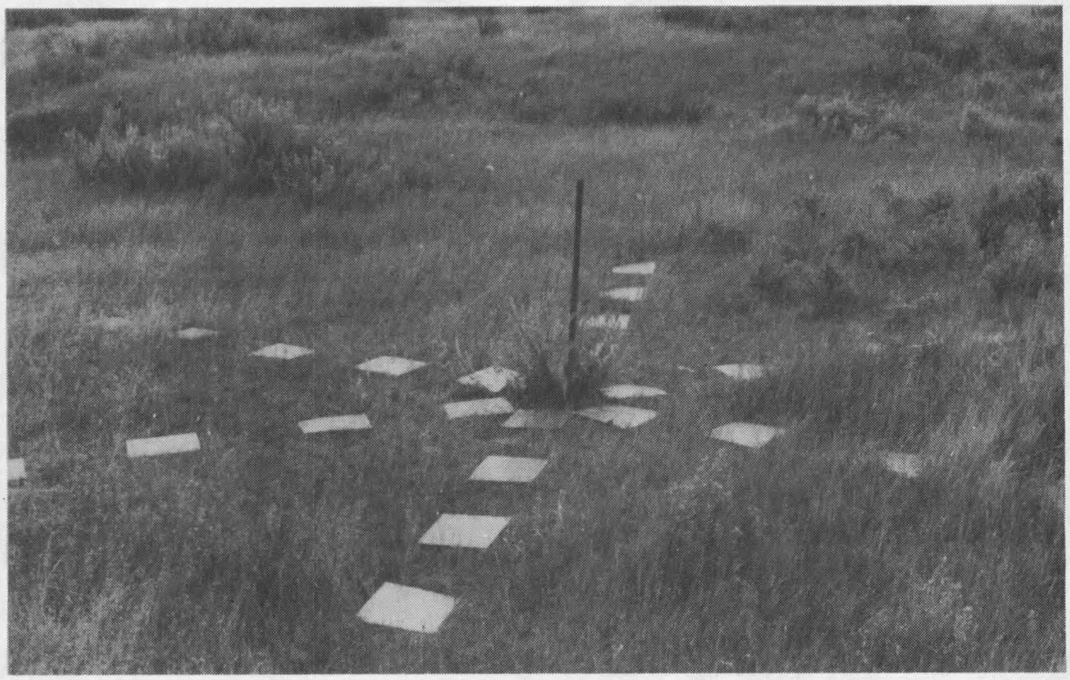

Figure 2. Dispersal study layout with six transects at equal angles (60 degrees) surrounding the central shrub. Five spaced (at 0,1,2,3 m) plates were for collection of dispersed seed in each transect.

Each plate (Figure 2) was coated with an adhesive (petroleum jelly) in order to catch individual seeds as they fell. This spatial arrangement allowed for an investigation of wind effect. Seeds that dropped on the plates were collected and counted through the November dispersal period. Sample collections were repeated every 3 or 4 days. An ongoing record was maintained on numbers and timing of seed dispersal in relation to distance and direction from the parent plant.

New adhesive was reapplied as needed after each collection. Application was accomplished by heating the petroleum jelly until it melted in a 0.47 liter metal paint can. A portable, white-gas camp stove was used for this purpose in the field. Liquid petroleum jelly was then either rolled or brushed onto the aluminum plates depending on air temperature. Use of the roller was most effective if air temperatures were below 10 C, and the brush was most effective above this temperature. This method was used successively at temperatures ranging from -18 to 25 C. Precipitation occuring during the study period had no adverse effect.

Counting was handled in two ways. If the number of seeds was low and could be counted quickly, they were tallied in the field and discarded. However, if seeds were too numerous to be readily counted, they were collected for later enumeration. A paint scraper was employed to collect the mixture of petroleum jelly, seeds and any additional material such as leaves. This mixture was then placed in a shallow-sided, disposable aluminum pan (22x15x3 cm) for later separation in the laboratory.

Seeds were separated from the petroleum jelly by first placing the solidified mixture on four layers of cheesecloth that were stretched and stapled over the aluminum pans. Pans were then placed in a 100 degree oven until the petroleum jelly melted. This resulted in lateral spreading of the mixture, leaving seeds spread out on the cheesecloth and the petroleum jelly in the pan below. Seeds could then be easily counted and recorded.

Statistical Analysis

Seed dispersal was analyzed with a split-split plot design with date being a covariant (see Appendix B). Because seed counts on plots at the 4 m distance contained many zero values, this distance was disregarded in the analysis. Mean separation tests for all factors and combinations were evaluated with Student t-statistics.

Germination

Germination success of plains silver sagebrush was examined in relation to five different factors that have been widely reported to affect seed germination. The five factors were studied concurrently so that the effects of an individual factor could be examined along with associated interactions. Although one or two factors are commonly evaluated in germination research, studies of this magnitude (ie. five factors) are seldom reported in the literature. None have involved plains silver sagebrush.

Methods

The five factors (treatments) considered in this study were: (1) date of seed collection, (2) stratification (prechilling), (3) temperature, (4) light/dark, and (5) osmotic potential. Seed was gathered from the Lower Black Springs study site on three occasions during the dispersal period. The first seed collection was made in late October just after dispersal started. The second collection was made in late November, and the final one took place in early January. The method that was used to collect seeds involved striking the inflorescence branches so that seeds would fall into a paper sack that was held alongside. This technique resulted in a large proportion of mature seeds. A total of 15 to 25 plants were collected from in this fashion at each collection date. Seeds were pooled to ensure adequate numbers of filled seeds, to provide a representative sample of seeds from the plant population, and to reduce the effects of semi-sterile individuals. After each collection, filled seeds were hand-separated from leaves, floral bracts and unfilled seed.

Seeds from each collection were subdivided into groups of 50 so that individual treatment combinations could be imposed and evaluated. Each group of seeds was then exposed to different combinations of stratification, light, temperature or osmotic potential for each collection date. All treatments were replicated three times. Seed was considered germinated when radicles had emerged and achieved a length of at least 3 mm.

After half the groups of seeds had undergone a stratification treatment, all groups were placed in petri dishes having two pieces of

No. 3 Whatman filter paper. The paper was moistened with one of four osmotic solutions (0,2.5,5.0,7.5 bars). Each petri dish was either open to light or wrapped in aluminum foil for a dark treatment and then placed in one of three growth chambers set at individual constant temperatures (10,20,30 C).

Germination counts were made for 21 days on seeds in every petri dish for each seed collection. After 21 days, counts were discontinued on those petri dishes in which no new germination had occured during the previous seven days. When dishes contained seeds that had germinated within the previous seven days, counts were continued until a period of seven consecutive days of no germination occured. A few individual seeds germinated up to 45 days after inception of the germination trials.

Stratification was achieved by placing half of the groups of seeds in cold storage of -23 C for 30 days. The non-stratified seeds were kept at room temperature of 18 to 21 C (65 to 75 F). The 50 seeds in each group were then placed in the petri dishes having moistened filter paper with the four osmotic solutions.

The four concentrations (0,2.5,5.0,7.5 bars) of osmotic solutions were achieved by using polyethylene glycol (PEG-6000) as a solute in distilled water. PEG-6000 solutions have been widely used to provide accurate osmotic concentrations; and because of chemical inertness, it may be superior to other commonly used solutes such as d-mannitol (Weldon et al. 1957, Parmar and Moore 1966, Sabo et al. 1979, Berkat and Briske 1981, Wilson 1982). The amount of PEG-6000 needed to simulate different osmotic potentials were adjusted for the three different temperatures using the standard formula presented by Helmrick and Pfeifer (1954).

Three growth chambers were used to control the factors of temperature and light. Each growth chamber was set at one of three constant temperatures: 10, 20, and 30 C. The petri dishes were placed in the chambers with half of them exposed to both incandescent and fluorescent light. The other half were wrapped in aluminum foil for a complete dark regime. The seeds in the dark regime were counted under ultraviolet (UV) light.

Statistical Analysis

Two germination responses (total and rate) were analyzed to determine the relative importance of individual factors. A five factor (3x2x2x3x4) factorial design with three replications was employed to analyze total germination percentages. Analysis of variance was run to determine the significance of main effects and interactions (see Appendix C). When significant F values were obtained, Duncan's multiple range test was used to separate means and determine where differences in means occured. Rates of germination were evaluated by graphic methods. Germination percentages from individual days during the germination trials were plotted against single factors, such as temperature, and combinations of factors found to be significant in the factorial analysis. Student t-statistics were run to evaluate significance on individual days.

Early Seedling Growth

Seedling emergence, growth and survival were investigated in three different studies. One study utilized transplanted seedlings in growth chambers to deliniate the effects of different diurnal temperatures on growth. A second study involved fall seeding in the field with subsequent measurements on emergence, growth and survival during the following growing season. The third study consisted of greenhouse work in which emergence, growth and survival were observed under more controlled circumstances than the field study would be.

The first study was initiated to evaluate the effect of different temperature regimes on early growth of seedlings under controlled conditions. The second study was to ascertain emergence, growth and survival of seedlings in the field planted at four depths (0,0.5,1.5,2.5 cm) and under different moisture regimes. The final study was to determine seedling emergence from the same four depths (0,0.5,1.5,2.5 cm) and subsequent growth and survival under more contolled circumstances.

Methods

Transplanted Seedlings

In June of 1982, 100 plains silver sagebrush seedlings of approximately the same height (28 mm) and growth stage were transplanted individually from the field into 10x10x12 cm plastic pots. The pots were filled with 2 cm of sand in the bottom and native topsoil to within 2 cm of the top. Seedlings were initially placed in the greenhouse for one month to recover from any transplant shock. Eighty plants were then selected based on similarity to one another and placed in growth chambers set at one of two diurnally fluctuating temperature regimes. These regimes were choosen to roughly simulate cool and warm conditions found in different seasons. Regimes consisted of a 12 hour photoperiod with day/night temperatures being set at either 90/70 F (32/21 C) or 70/50 F (21/10 C). Forty seedlings were placed into each chamber. Preliminary measurements of plant height and number of leaves were obtained at the time seedlings were put into the growth chambers.

Growth measurements were made on seedlings every five weeks. These included height, number of leaves, and two horizontal axes (length, width). In addition, eight seedlings were randomly selected at each recording period for destructive sampling. Measurements on these plants included leaf area, root and shoot weights. Leaf area was determined by the light attenuation method and employed a Licor model LI-3000 area meter. Leaf area of each sample was measured three times and the results averaged. Shoot weights included total weights of both stem and leaf tissue cut at ground level. Root weight was determined after all soil was throughly washed away. Both shoot and root material was oven dried and weighed. This study was completed in December 1982.

Greenhouse Seeding

The effects of seeding depth on seedling emergence, growth and survival was examined in the greenhouse. Ten pots were filled with with sifted native soil from Paddy Faye and seeded at one of four depths (0,0.5,1.5,2.5 cm). Ten seeds were planted in each plot in a definite, mapped pattern. As each seed emerged it was recorded and mapped as to location so that later growth measurements could be made in relation to emergence date.

Once seedlings passed the cotyledon stage and entered the two-leaf stage of phenology, measurements on height, number of leaves and the two horizontal axes were recorded weekly for eight weeks. The pots were watered so as to keep soil near field capacity, and temperatures were maintained at about 21 C (70 F) throughout the trial.

Field Seeding

Seeds were collected during the fall of 1982 and planted into native soil in the Paddy Faye pasture (see Seed Dispersal site description) on November 3, 1982. Three replications were established so that associated water treatments and planting depths could be evaluated for effects on seedling emergence, growth and survival.

The three replications were located on level, open ground within a plains silver sagebrush community. Plots were mowed to ground level to facilitate planting. Eight seven meter lines were staked out for seeding and randomly selected to receive one of four depth treatments (see Figure 3). A weighed sample of mature seeds, unfilled seeds and floral bracts was placed in a hand-operated, single row cone seeder and planted at the desired depth (0,0.5,1.5,2.5 cm). Depth was controlled by adjusting penetration of double disk openers. Seeds in ten samples of this weighed amount of seed material were counted to determine how many filled seeds were actually planted. It was

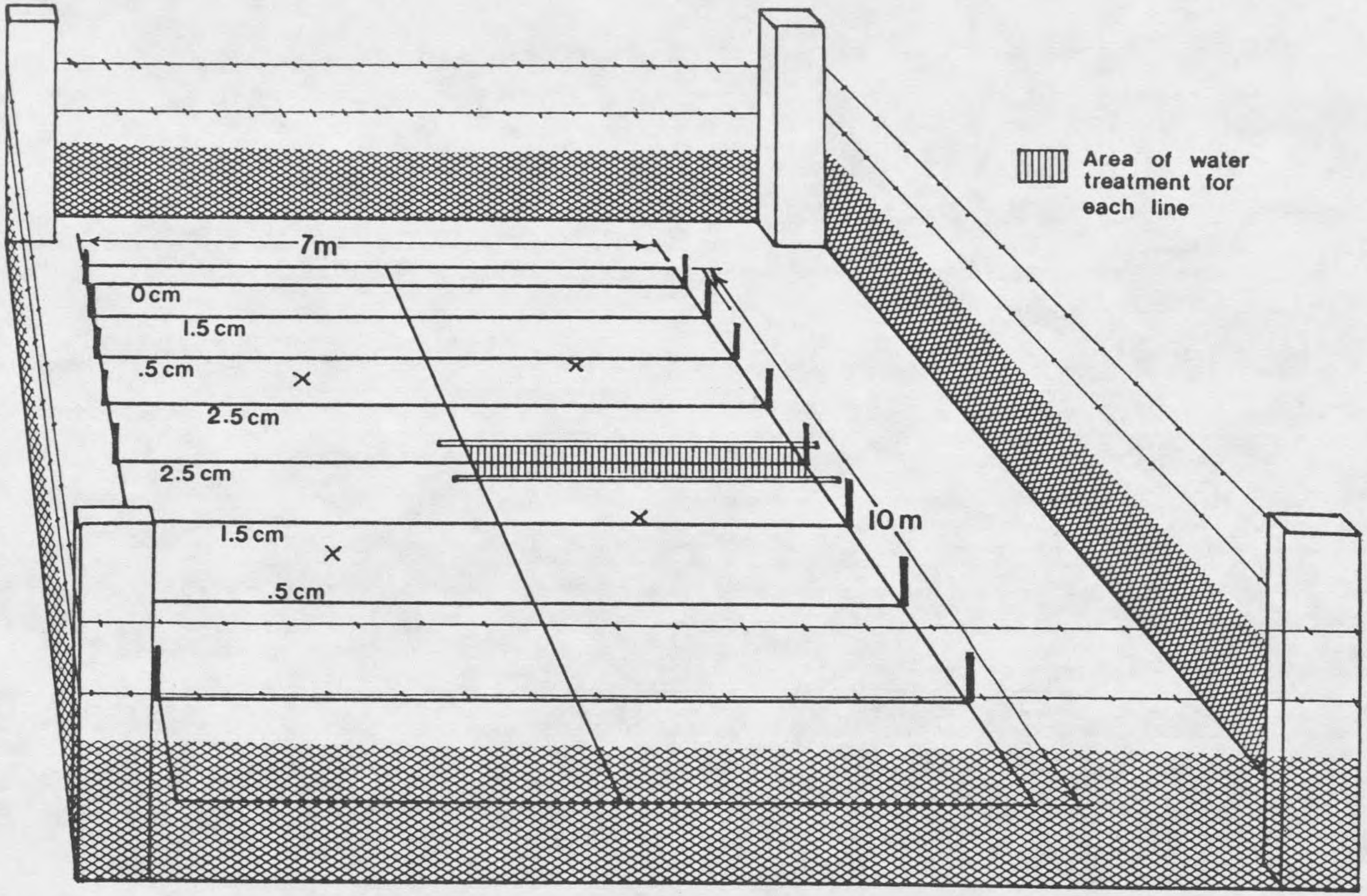

Figure 3. Perspective view of field planting replication giving dimensions and a sample of randomized array of planting depths. One-half of each row was given a water treatment. Rabbit-proof fence and barbed wire surrounded entire plot.

determined that each sample contained an average of 706±43 seeds. Therefore, each of the lines that were planted contained 101±6 seeds/m.

Each replication was enclosed in a rabbit-proof fence constructed with railroad ties as corner posts, two thicknesses of .61 m high chicken wire, and two strands of barbed wire above the chicken wire (Figure 3). Seeded plots passed through the winter in a dormant state and seedlings began to emerge the following spring.

Watering treatments started May 15, 1983, and measurements of seedling emergence and survival began on June 15. This schedule was based upon previous work which reported that sagebrush seedlings will emerge from April through July (Beetle 1960, Harvey 1981). Consequently, there was an initial period during which natural germination and emergence could occur without being subjected to stressful conditions that might cause mortality. Each emerged seedling was marked with a large washer on June 15. Subsequent seedlings were marked with flags. Supplementary water was applied as needed once each week to provide seeded areas with a minimum of 2.5 cm (1 inch/per week). Adjustments were made for any precipitation that occured during the preceding week. Distilled water was transported into the field and applied in 30.5 cm strips adjacent to seeded lines. This application was imposed upon half of each row by using 1 gallon hand garden sprinklers. Precipitation was monitored by four wedge type rain gauges located within 50 m of the study plots.

Seedling height, number of leaves and two horizontal axes (length, width) measurements were recorded each week in June and July. During August, these same measurements were taken every other week.

Soil moisture levels and temperatures were recorded by burying calibrated fiberglass wafers at depths of 7.5 and 15 cm within each replication. Four wafers were placed in each replication so that two depths were measured in both watered and unwatered sections of the plot. Thermistors measured resistance for soil temperatures while soil moisture was gauged by capacitance. Core samples were taken periodically to check gravimetric determinations with the soil moisture wafers.

Statistical Analysis

Data evaluation was accomplished by chi-square analysis for emergence and survival responses. Growth curves were constructed from data means and tested with Student t-statistics. Graphs were also constructed to help interpret results.

Sprouting and Seedling Establishment

The sprouting nature of plains silver sagebrush was evaluated by two separate studies. These were initiated to quantify to what degree the shrub relies on either vegetative reproduction or seedling establishment to recruit new members into a community. The first phase of this work involved examination of individual plants from several representative communities. Individual plants of a uniform height class (16 to 40 cm) were selected along line transects and excavated to determine whether that plant originated independently from seed or was a sprout from an already established shrub. The second phase was comprised of excavating areas around two, large, fairly isolated plants that were surrounded by numerous small plants. The entire area, including the main shrub, was excavated in order to determine: (1) whether plants were of clonal or seed origin, (2) what potential plants had for vegetative spread based on number of sprouts surrounding a plant, and (3) the degree to which adventitious buds were present on established rhizomes.

Transect Excavations

Six separate sites were selected as representative of plains silver sagebrush communities in the Northern Great Plains. Three sites had been subject to some form of recent disturbance such as fire or ice scraping. These sites are referred to as the Yellowstone River, Lower Black Springs and Lower Flood pastures. The other three sites were not subjected to recent disturbance except for periodic grazing by cattle. These areas were Lignite Creek, Paddy Faye and Moon Creek pastures. For site descriptions on Paddy Faye, Lower Flood and Lower Black Springs see Seed Dispersal site descriptions.

Site Descriptions

The Yellowstone River pasture is located on terraces on the northern side of the Yellowstone River near a railroad bridge approximately 5 km northwest of station headquarters. Plains silver sagebrush is the dominant shrub and is found in sparse to dense stands. The understory is dominated by western wheatgrass, needleandthread and annual bromes. Two basic soil types are present depending on proximity to the river. Soils are dominated by deep, well drained fine sandy loams and loams near the river. Such soils have moderate to moderately rapid permeability and moderately available water capacity from 15 to 25 cm. These soils are classified as sandy range sites. As distance from the river increases, the soils grade into deep, well-drained loams of moderate and slow permeability and high available water capacity. The soils throughout the study site are dominately frigid, Ustic Torrifluvents.

Lignite Creek is an intermittent stream dissecting much of the southern portion of the station for several kilometers in a north-south direction. The study area was 10 km directly west of headquarters close to where this drainage joins the Yellowstone River. It was located on alluvial deposits that were close to the stream channel. The site had moderately dense stands of plains silver sagebrush with western wheatgrass and annual bromes dominating the understory vegetation. Soils were in the Camborthid-Torrifluvent complex and were characterized by not having a typic profile. Permeability can be slow to moderately rapid with low to moderate available water capacity from 8 to 28 cm. The soils range from fine sandy loams to silty clay loams with strata of sand and gravel common in some areas. Range sites are silty and overflow.

Moon Creek is an intermittent stream on the western border of the station. Minor drainages dissect the Moon Creek flood plain regularly. Plains silver sagebrush is the dominant species throughout this drainage with small groves of plains cottonwood (_Populus deltoides_

Bartr.) scattered along the creek. The dominant understory vegetation is western wheatgrass, often in dense stands. Green needlegrass is also common. Some of the drier areas of the terraces have large proportions of Japanese brome, cheatgrass and blue grama. Dominant soils in Moon Creek are in the Gerdrum-Creed complex with some scattered Torrifluvents. This study area is classified as a clay pan range site and the soils belong to the fine, montmorillonitic Borollic Natriargids. Soils are about evenly divided between Gerdrum silty clay loams and Creed loams with small areas of slick spots. A prevailing influence in these soils is their salt and sodium content. Permeability is slow and their high available water capacity is decreased to 15 to 20 cm due to salt content.

Methods

After study areas were selected, four 25 m transects were established and used to sample individuals from plains silver sagebrush populations. Sampling proceeded so that the nearest plant within a particular height category (16 to 40 cm) was flagged at intervals of five meters. This size category was chosen after preliminary excavations and aging had established that such plants represented stem material between one and four years old. The preliminary study also established that underground material varied considerably according to whether the plant originated from parent rhizomes, plants or seedlings.

Roots of flagged plants were excavated with great care so that fragile rhizome connections remained intact. The plant was sufficiently excavated to determine if it was connected to another plant or was an independent individual. After this determination, measurements were recorded on plant height, length of rhizomes (roots), and stem and rhizome (root) diameters. Root distribution from each individual excavation was mapped, and line sketches of each plant were drawn for a pictorial record. Samples were taken from major sections of each excavated plant. These included stem, root, rhizome and connecting rhizome sections. They were placed in sealed plastic bags in the field and transported to the laboratory for age determination. Aging of sagebrush was feasible in spite of common stem splitting and layering (Ferguson 1964).

Isolated Plant Excavations

Two large plants were selected in Lower Flood to be individually excavated for a study on asexual (vegetative) reproductive potential. Only two plants were selected due to high labor requirements involved. The plants were subjectively selected by two criteria. The first criteria was that the plant should be relatively isolated from other large plains silver sagebrush plants so that competitive influences from other individuals were minimized. In this way, vegetative potential could be freely expressed. The second criteria was a predominance of smaller "individuals" surrounding this larger plant which was 1 m or greater in height. Areas around the large plants (approximately 4 to 5 m radius) were excavated so that roots and rhizomes of all the smaller plants were exposed and relationships to the larger plants determined. Root distribution from the excavations were mapped so that seedlings and sprouts could be differentiated and size category recorded.

Statistical Analysis

Chi-square analysis was performed on transect data to determine whether major disturbances had an effect on the ratio of seedlings to sprouts and if there were differences among individual sites. Student t-statistics were run to determine overall significance of the ratio of seedlings and sprouts. The isolated plant excavations were not designed to be analyzed, rather this experiment was designed to provide additional insight into asexual reproductive potential.

RESULTS AND DISCUSSION

Seed Dispersal

One of the primary features to investigate in regards to reproductive strategies is the number of propagules that are produced and dispersed. Seed dispersal in plains silver sagebrush was investigated in regards to site comparisons, direction of seed fall, distance that seed fell from parent plants, and date of seed dispersal. Statistically significant differences were not found among the three study sites in terms of numbers of seeds dispersed, direction of seed fall and distance relationships of seed fall. However, highly significant interactions ($p < 0.01$) existed between study sites and time of seed dispersal. Numbers of seeds that dispersed also changed significantly from the first recording date to following dates. The seed dispersal distance from the parent plant followed a definite pattern. Direction of dissemination displayed a three-lobed stellate type distribution. Wind played the major role in determining seed dispersal in plains silver sagebrush at the study sites.

The majority of seed dispersed throughout the study period was in the same three principle directions. However, date played a significant role because it determined the total number of seeds that fell, and this indirectly affected the number of seeds that were dispersed at varying distances on the different transects.

Although dispersal of sagebrush seeds has been attributed to wind, water and animals, wind (anemochory) seems to be of major importance (Beetle 1960, Harper 1977, Bostock and Benton 1979, Tisdale and Hironaka 1981, Evans and Young 1982). My study confirmed that wind dispersal was an important factor in the dispersal of plains silver sagebrush seed. However, the study design did not allow for catergorizing water or animal influences as lesser factors. The sites on which this study was conducted and the morphological characteristics of the seed seemed to point to a lesser contribution by these factors.

Although the three study areas were separated by several kilometers, no notable differences in dispersal characteristics could be detected. The same environmental influences, especially prevailing and storm winds, seemed to exert similar influences on dispersal throughout the study area vicinity. Prevailing winds as well as cyclonic winds from atmospheric disturbances would not ordinarily be expected to change within the geographical range of the project. Therefore, this resulted in wind directions that were relatively consistent for all three study sites. The patterns of seed dispersal that were observed were characteristic of each individual plant, and for this reason they should not vary regardless of where a population was located.

Timing of dispersal varied between sites (Figure 4). Paddy Faye showed a significantly larger number of seeds falling on the first measurement date (7.1 seeds per plate) with a second peak on the fourth measurement date (3.5 seeds per plate). A gradual decrease in

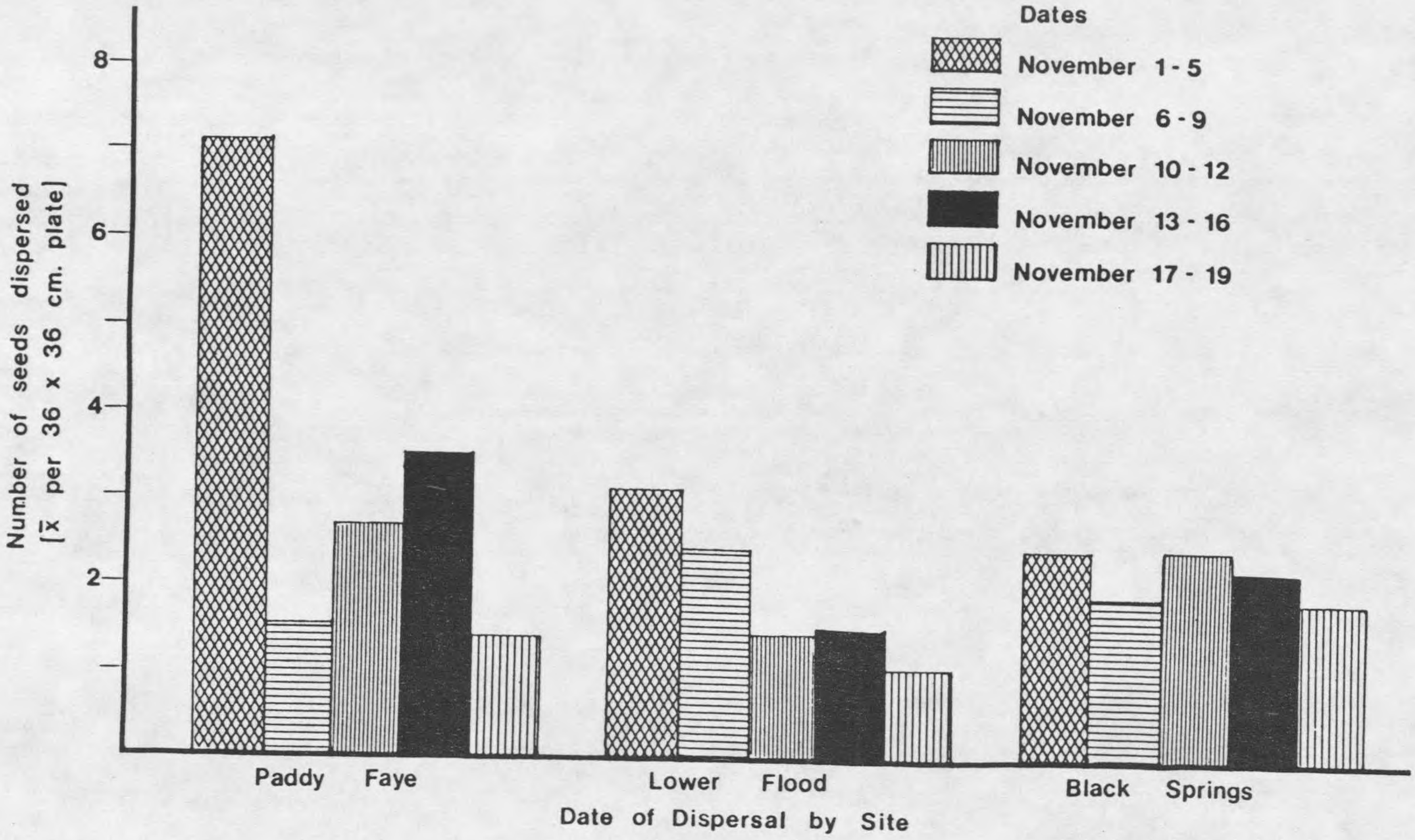

Figure 4. Mean numbers of plains silver sagebrush seed dispersed per plate in all directions from a parent plant. Dispersal from five plants in each study area is summarized. Differences in each study site are summarized by date at which dispersal was acheived.

seed numbers was observed on Lower Flood after the initial high value (from 3.1 to 1.1 seeds per plate). The decline in seed numbers and differences among dates were less pronounced. Lower Black Springs showed a fairly uniform distribution of dispersed seeds among all dates, and thus no statistically significant differences in numbers of seeds dispersed were detected. Differences among sites can best be explained by dissimilar phenological maturation of plants at each site. Individual plants were selected for measurement before seed dispersal was initiated. Consequently, plants that were sampled represented a heterogeneous mixture with respect to how rapidly phenological development occured. As the season progressed, there were more individuals reaching seed maturity early on the first two sites. The third site had about equal numbers of plants attaining seed maturity throughout the study period. These differences are possibly due to two influences, namely microenvironment and soils. Paddy Faye and Lower Flood are characterized by similar vegetation and soil components. Both study sites have a relatively short vegetation cover and soils with a dominant clay fraction. Lower Black Springs, in contrast, has a dominant cover of crested wheatgrass and more silty to sandy soils. The microenvironment and soil moisture relationships would most likely be different between Lower Black Springs and the first two sites. Therefore, this would influence the differing phenoloical development for plains silver sagebrush between the first two sites and Lower Black Springs.

Phenological development in most sagebrush species is such that the majority of seeds are shed in late fall and winter. Most of the viable seed is dropped during the first seven days after dispersal is initiated (Goodwin 1956, Beetle 1960, Harvey 1981, Tisdale and Hironaka 1981). Over the following two to four weeks of these studies dispersal was observed to consist primarily of aborted flowers and half-filled seeds. In my study, however, variability in maturity of individual plants resulted in an extended dispersal period when considered on a population basis. Dispersal was proportionately greatest in the first week (4.2 seeds per plate) (Figure 5). This would be consistent with previously reported results. However, phenological differences in the plant population influenced the number of viable seeds that fall in subsequent dispersal periods. No statistical differences existed among the second, third or fourth sampling periods (1.97, 2.2, 2.4 seeds per plate, respectively), although significantly less seed fell in the last period (1.4 seeds per plate).

Results indicated there was a sharp decrease in the number of plains silver sagebrush seeds (from 5.4 to 1.4 seeds per plate) that were dispersed between the zero and one meter area adjacent to the parent plant (Figure 6). No statistical difference could be found among measurements for the next three meters. Therefore, these results are consistent with previous research which reported that most seeds were dispersed near the parent plant with seed density declining sharply as distance increases (Harper 1977, Cook 1980). This dispersal pattern has been shown to exist in Artemisia species (Beetle 1960, Friedman and Orshan 1975, Harvey 1981, Tisdale and Hironaka 1981).

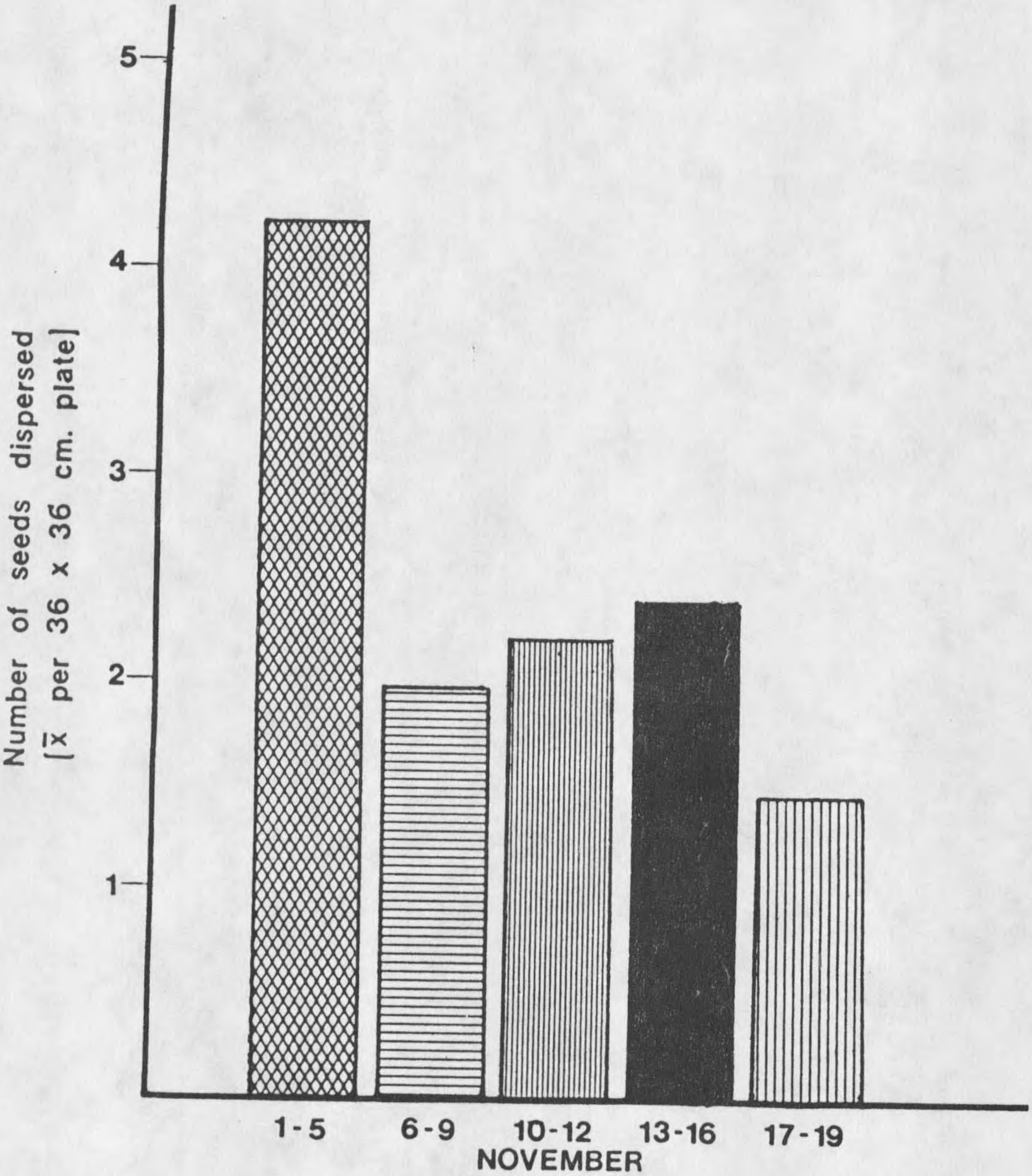

Figure 5. Mean numbers of plains silver sagebrush seed per plate dispersed in all directions from a parent plant. Dispersal from a total of 15 plants is summarized. Differences are summarized for each date at which dispersal was achieved.

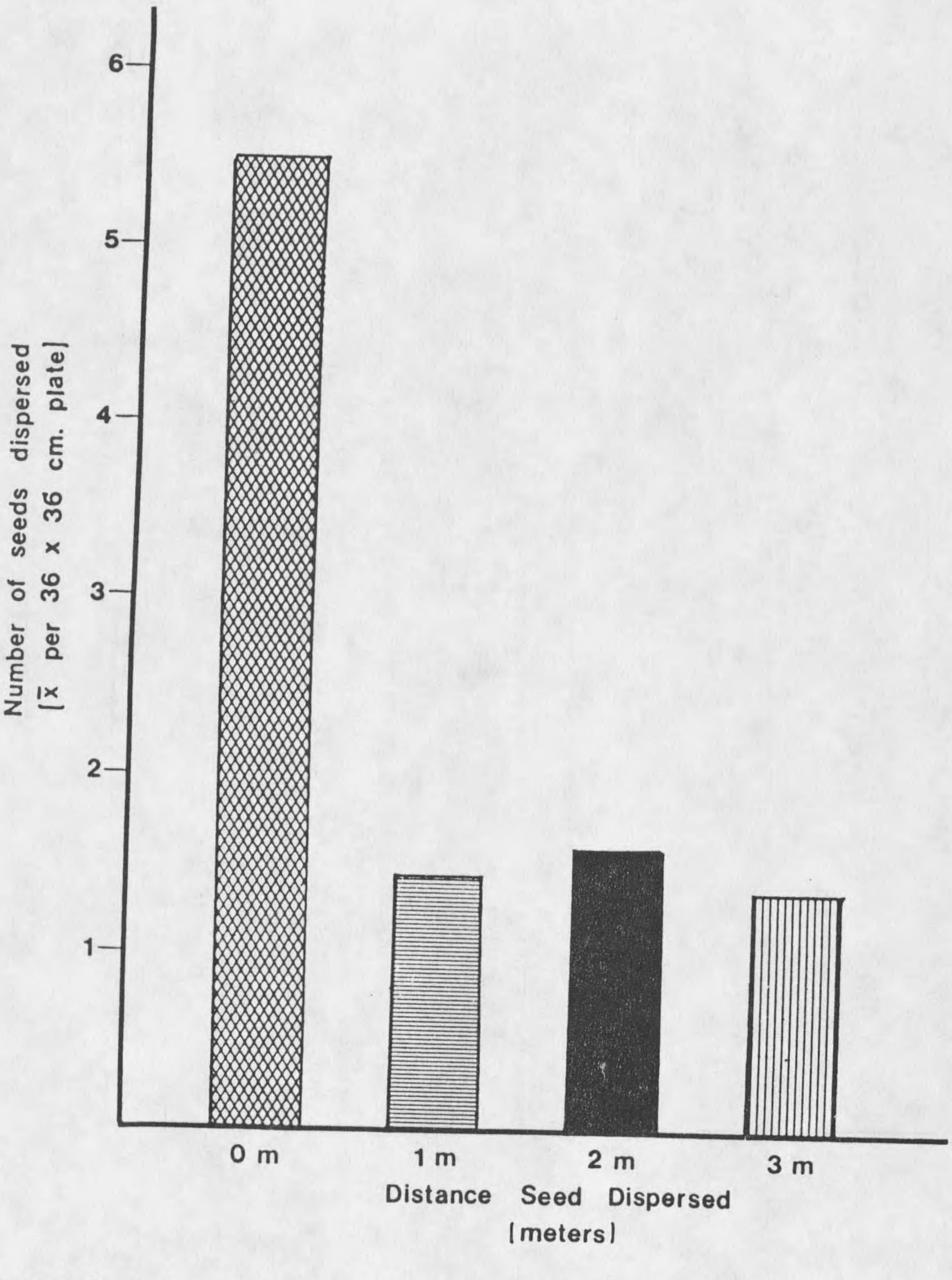

Figure 6. Mean numbers of plains silver sagebrush seed per plate dispersed in all directions from a parent plant over entire study period. Dispersal from a total of 15 plants is summarized. Differences are summarized for each distance at which dispersal was achieved.

Measurement date had a considerable effect on the number of seeds that were dispersed at increasing distances from the parent plant (Figure 7). In three of the five dispersal periods investigated, the majority of seeds fell under the parent plant with substantially less being found at distances of one or more meters. However, in two cases, the second and fifth sampling periods, dispersal was evenly distributed across all four distances. On at least one sampling interval (November 17-19), dispersal was significantly higher at two meters (2.3 seeds per plate) than at the one meter distance (0.6 seeds per plate) from the parent plant. On another sampling interval (November 13-16), dispersal at three meters (1.8 seeds per plate) was higher than at either one (1.1 seeds) or two (0.9 seeds) meters distance from the parent plant. Strong cyclonic winds on these two sampling intervals best explain the apparent deviation from what would be expected in dispersal patterns. The gusty winds inherent in these winds would disperse seeds to a greater distance than normal conditions might.

Dispersal patterns showed three principle regions where seeds were usually concentrated. The majority of seeds fell directly downwind from the prevailing northwest winds. In addition, two secondary regions of seed concentration were located at 120 degree angles on either side of the primary dispersal region. Significantly higher quantities (2 to 9 times) of seed were found in these three areas than the remaining areas. This resulted in a three-lobed stellate figure when seed numbers were plotted as a function of dispersal direction (Figure 8). Variation between the three prominent

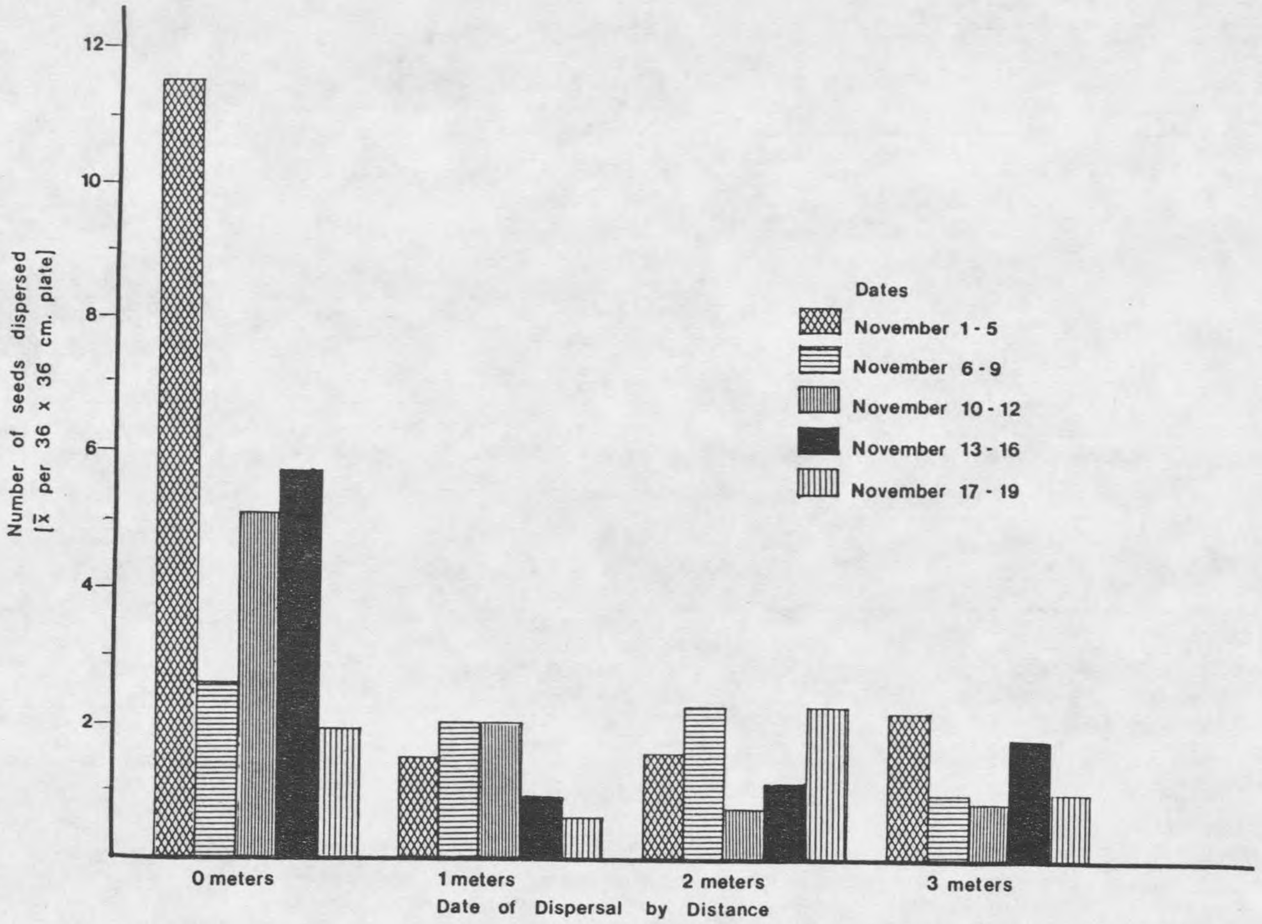

Figure 7. Mean numbers of plains silver sagebrush seed dispersed per plate in all directions from a parent plant. Differences are summarized for each distance by date dispersal was acheived.

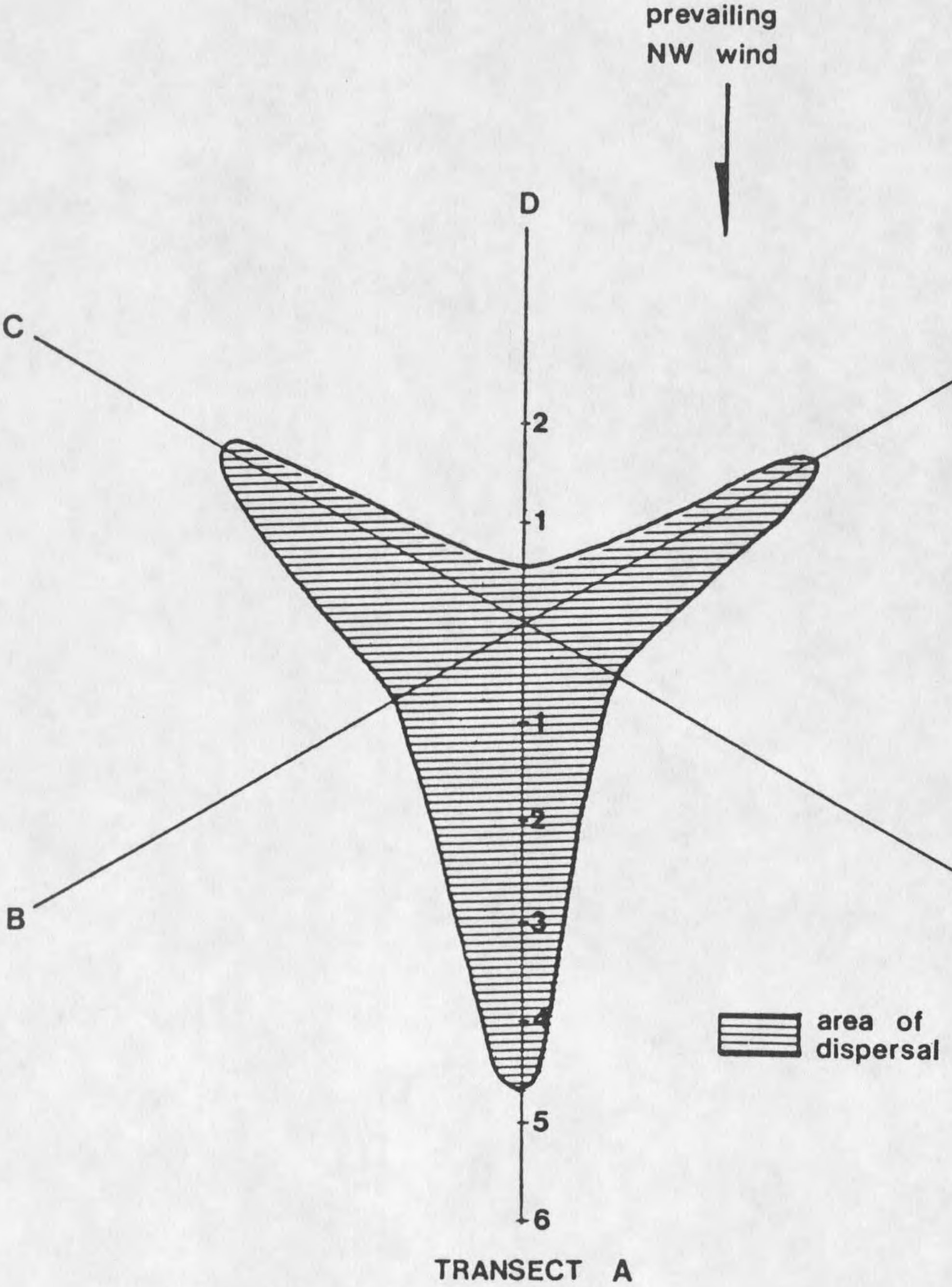

Figure 8. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions. Numbers on axes represent mean numbers of seeds dispersed. Shaded area represents a generalized seed dispersal pattern. See Appendix D for example of how this graph was constructed.

lobes of the figure occurred as distance was considered. The primary dispersal region (transect A) received the greatest amount of seed with the majority falling directly under the parent plant (0 meters) (Figure 9). A second peak of seeds fell at two meters. Although fewer seeds fell in the northerly lobe along transect E, the seed distribution pattern was the same as in transect A. With respect to dispersal distance, the southwest lobe (transect C) demonstrated a statistically different dispersal pattern with seeds falling mainly at the one and three meters distances from the parent plant. In the first transect, a mean of 13.8, 1.1, 3.5, and 0.3 seeds fell at the respective distances of 0, 1, 2, and 3 meters. In contrast, transect C exhibited a mean of 1.3, 5.7, 0.3 and 6.7 seeds falling at the respective distances of 0, 1, 2 and 3 meters. This general pattern of seed dispersal was observed on plains silver sagebrush throughout the study period although some variations were encountered among sampling intervals (Figures 10 to 14). Essentially the same type of three lobed geometric shape was found for all five sampling periods. However, the principle regions of seed dispersal did change according to collection date. For example, on the second (Figure 11) and third (Figure 12) sampling period, the largest proportion of seeds fell in transects C and E, respectively. Observations on wind direction and speed during these two periods showed a differing pattern from the dominant prevailing winds and speeds that would explain these diparities. The other three periods exhibited a similar pattern to that described for Figure 9, that is, transect A received the largest proportion of dispersed seeds.

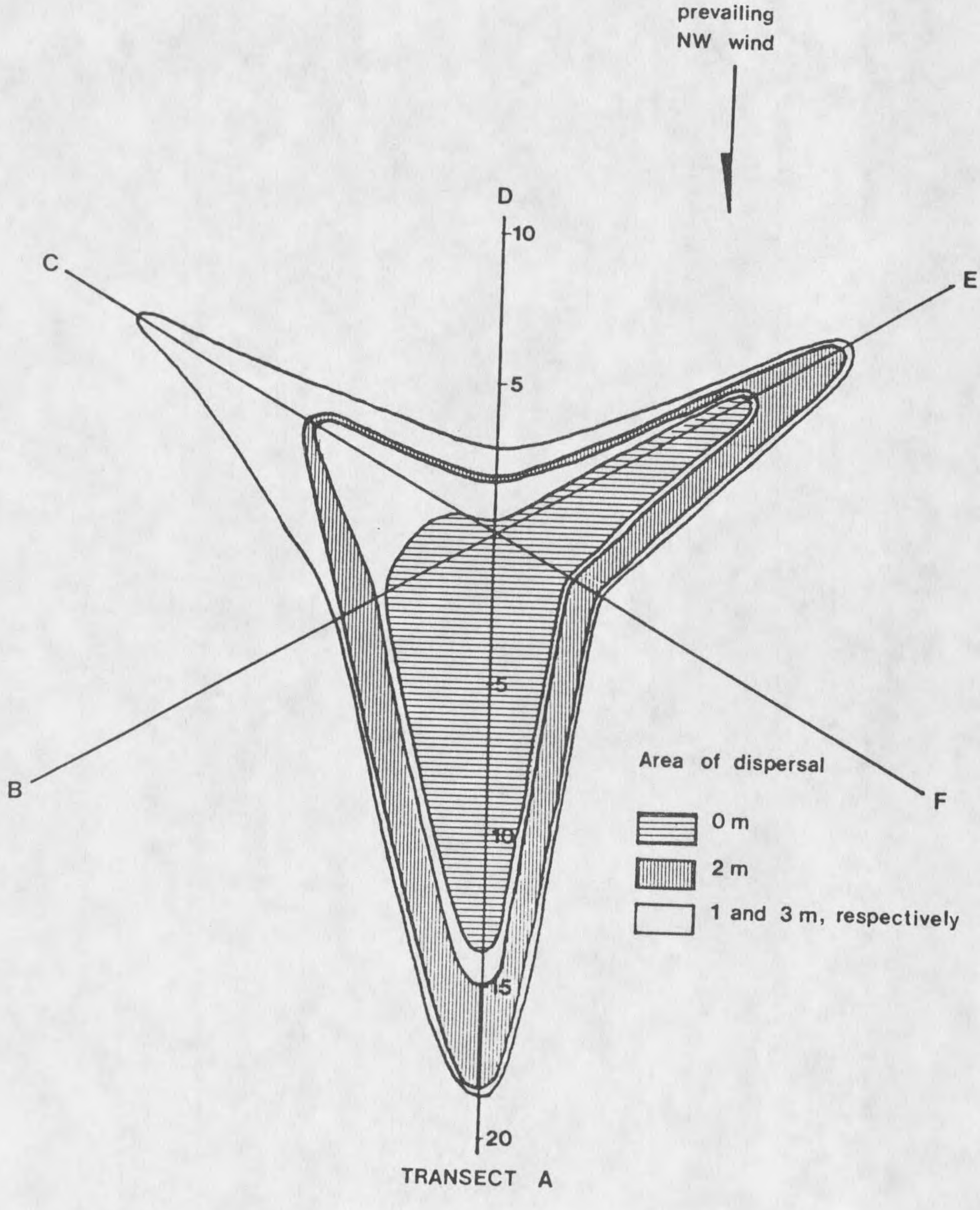

Figure 9. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Numbers on axes represent mean numbers of seeds dispersed. Shaded area represents a generalized seed dispersal pattern. See Appendix D for example of how this graph was constructed.

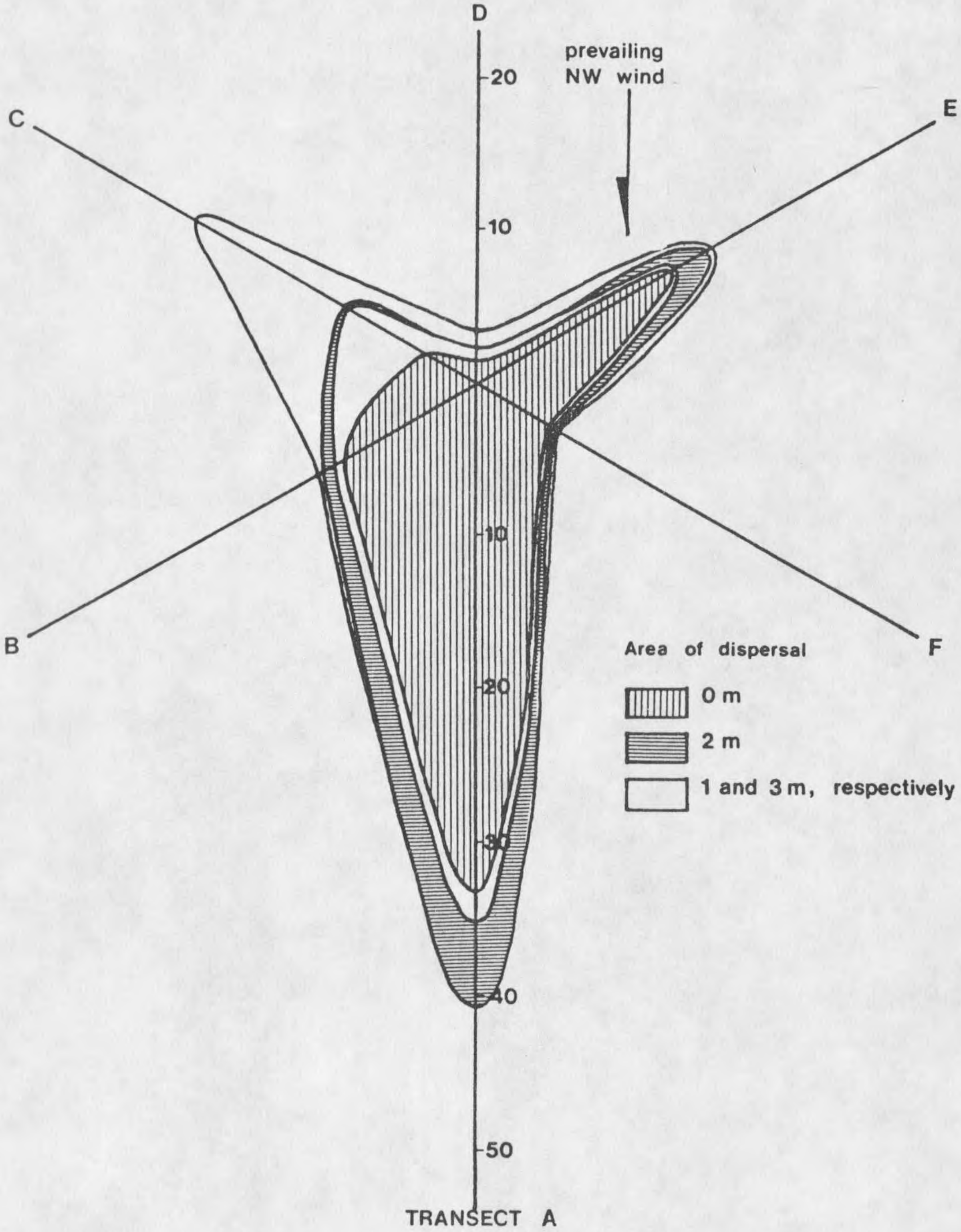

Figure 10. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Date of dispersal was from November 1-5. Numbers on axes represent mean seeds dispersed. Areas are a generalized seed dispersal pattern at each successive distance. See Appendix D for example of how this graph was constructed.

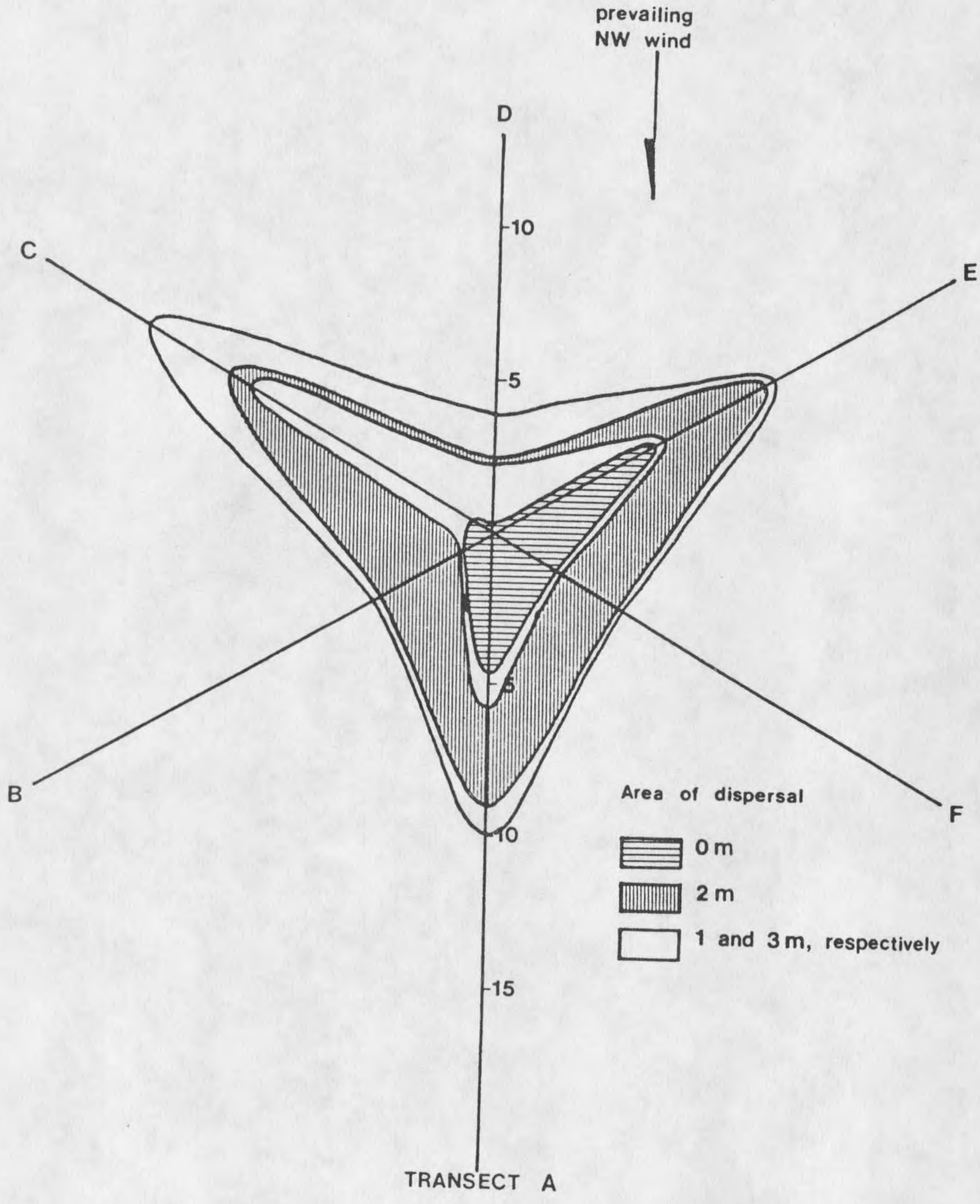

Figure 11. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Date of dispersal was from November 6-9. Numbers on axes represent mean seeds dispersed. Areas are a generalized seed dispersal pattern at each successive distance. See Appendix D for example of how this graph was constructed.

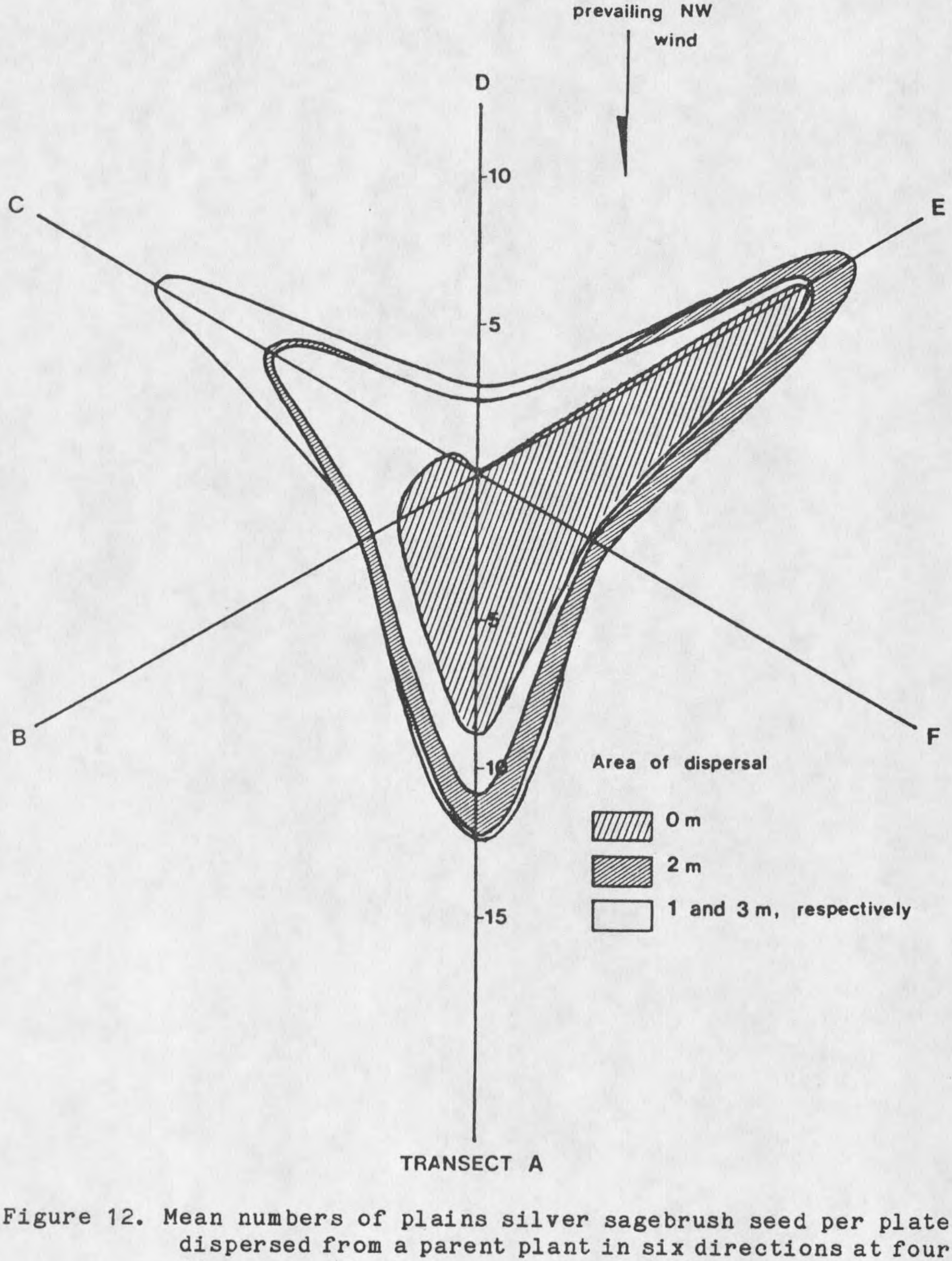

Figure 12. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Date of dispersal was from November 10-12. Numbers on axes represent mean seeds dispersed. Areas are a generalized seed dispersal pattern at each successive distance. See Appendix D for example of how this graph was constructed.

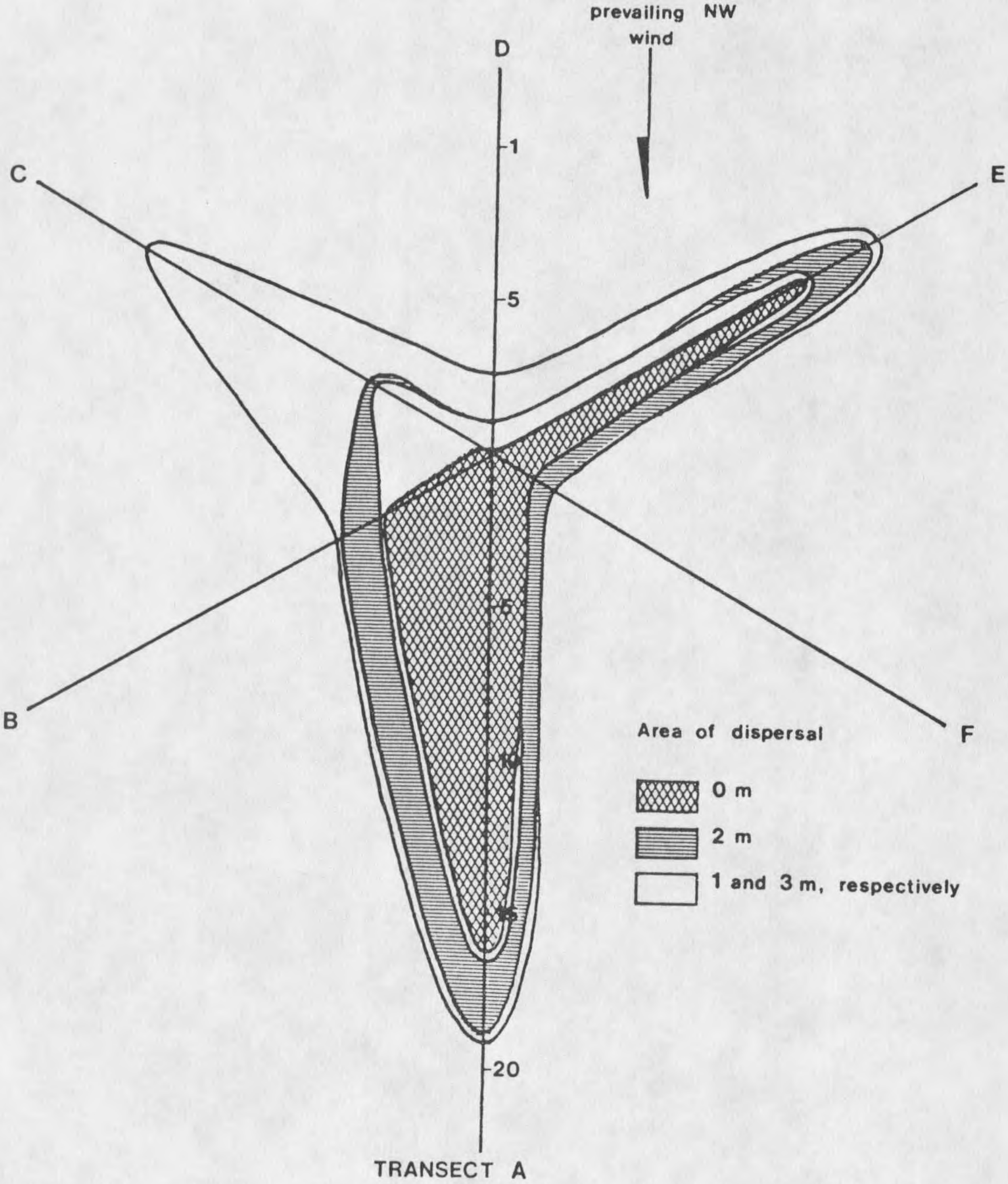

Figure 13. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Date of dispersal was from November 13-16. Numbers on axes represent mean seeds dispersed. Areas are a generalized seed dispersal pattern at each successive distance. See Appendix D for example of how this graph was constructed.

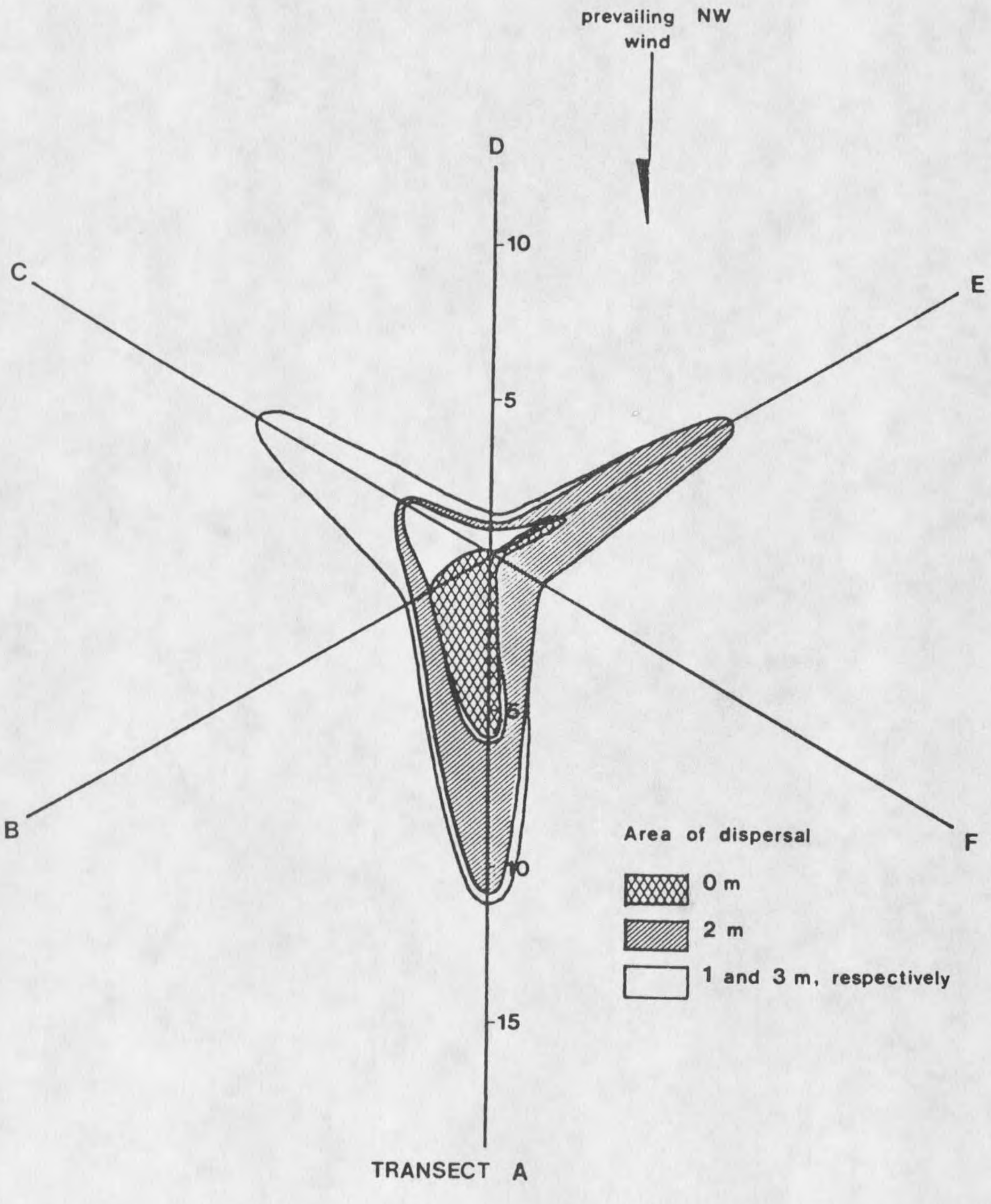

Figure 14. Mean numbers of plains silver sagebrush seed per plate dispersed from a parent plant in six directions at four distances (0, 1, 2, 3 m). Date of dispersal was from November 17-19. Numbers on axes represent mean seeds dispersed. Areas are a generalized seed dispersal pattern at each successive distance. See Appendix D for example of how this graph was constructed.

Qualitative observations on wind direction and speed were made during each dispersal period. The resulting changes in wind direction seemed to correlate well with dispersal patterns that were observed. Although the prevailing wind was from the northwest, changes did occur according to weather variation and topographical influences. All three study sites were located in bottomlands that are dissected to varying degrees. Local wind patterns and fluctuations were naturally established in these situations that contributed to dispersal differences between dates. These local winds would also tend to be in consistent patterns, although in varying degrees of intensity, and they therefore influence the seed dispersal patterns into a three-lobed stellate geometric distribution. While the prevailing winds were generally consistent and of low speed, the changes due to weather and topography tended to be in the form of gusts and with increased velocity. Thus the dispersal patterns observed in this study were not uniform on each date. The transect (A) under the most direct influence of the prevailing wind displayed the characteristic pattern of having the largest numbers of seeds next to the parent plant and smaller amounts at greater distances. The other two major regions of seed dispersal were the result of what tended to be rather consistent weather and topographic influences that were repeated in varying degrees of intensity during each sampling interval.

This type of distributional pattern of dispersed seed has not been described in the literature on sagebrush and probably is the result of the sampling technique. Most of the research on dispersal of sagebrush is observational in nature or was studied in less detail and with smaller numbers and periods than this study provided.

Germination Responses

Response to Individual Factors

All main factors, except stratification, had highly significant ($p < .01$) effects on germination response. These included: date of seed collection, light and dark, temperature, and osmotic potential. Most interactions that did not include stratification as a factor were also highly significant ($p < .01$). These included: (1) light/dark and date of seed collection, (2) temperature and date of seed collection, (3) light/dark and temperature, (4) temperature and osmotic potential, (5) light/dark and osmotic potential, (6) light/dark, temperature, and date of seed collection, (7) light/dark, temperature, and osmotic potential, (8) temperature, osmotic potential, and date of seed collection, and finally (9) light/dark, temperature, osmotic potential, and date of seed collection. Means were separated and ranked by relative importance in regards to these significant responses. Resultant percentages for individual main effects and two-way interactions are summarized in Table 1. For the three way (Table 2) and four-way interactions, no rankings were possible and only general patterns could be observed.

Date of seed collection affected germination percentages. The seed that was collected in the winter had higher germination totals (35%) than that obtained from seeds collected in late fall (24%). Dark germination was generally preferred over light in the first and third collection dates, but no significant difference was shown on the second collection. However, germination in light or dark was higher in

Table 1. Means[1] from individual main effects and separate combinations of two-way interactions where significance (p .01) was found. For factorial ANOV see Appendix C. Letters only apply in individual blocks of means.

		Main Factor											
		Light		Temperature(C)			Osmotic Potential(bars)				Date[2]		
Interaction Factor(s)	Treatment(s)	L	D	10	20	30	0	2.5	5.0	7.5	1	2	3
None	-	27^{b}	32^{a}	29^{b}	36^{a}	23^{c}	57^{a}	40^{b}	17^{c}	4^{d}	24^{c}	29^{b}	35^{a}
Light/dark	L			34^{b}	29^{c}	18^{e}	65^{a}	35^{d}	8^{f}	1^{g}	22^{d}	29^{c}	35^{b}
	D			24^{d}	43^{a}	28^{c}	49^{b}	44^{c}	26^{e}	7^{f}	26^{c}	29^{c}	39^{a}
Temperature	10						57^{b}	41^{d}	16^{f}	3^{i}	22^{d}	26^{c}	39^{a}
	20						64^{a}	48^{c}	25^{e}	8^{h}	33^{b}	39^{a}	40^{a}
	30						50^{c}	30^{e}	10^{f}	2^{i}	25^{d}	22^{d}	25^{cd}
Osmotic Potential[3]	0										51^{b}	58^{a}	62^{a}
	2.5										33^{c}	39^{c}	47^{b}
	5.0										12^{f}	15^{f}	23^{e}
	7.5										1^{i}	4^{h}	8^{g}

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[1] Numbers are mean total germination percentages. Means followed by different letters denote significant differences (p .01) from Duncan's multiple range test.

[2] Dates are as follows: (1) late October, (2) late November, and (3) early January. These are dates of seed collection.

[3] No significance (p .01) could be differentiated between dates in regards to osmotic potentials.

Table 2. Means[1] from three-way interactions of main effect combinations where significance (p .01) was found. For factorial ANOV see Appendix C.

		Main Factor(s)																		
		Osmotic Potential(bars)				Date[2]			Temperature & Osm. Potential (C) (bars)											
									10				20				30			
Interaction Factor(s)	Treatment(s)	0	2.5	5.0	7.5	1	2	3	0	2.5	5	7.5	0	2.5	5	7.5	0	2.5	5	7.5
Date	1								50	27	5	.2	59	40	22	2	48	32	10	0
	2								53	41	10	3	73	49	26	7	49	27	9	2
	3								67	57	37	5	63	54	27	14	54	30	10	4
Light/dark & Osm. Potential	L-0					58	69	67												
	D-0					45	47	57												
	L-2.5					28	34	43												
	D-2.5					38	43	51												
	L-5.0					2	9	13												
	D-5.0					22	21	34												
	L-7.5					.1	2	.3												
	D-7.5					1	5	15												
Light/dark & Temperature	L-10	71	48	17	2	24	37	42												
	D-10	42	34	15	3	17	16	38												
	L-20	69	40	6	1	25	33	32												
	D-20	60	55	44	15	38	44	48												
	L-30	54	16	1	0	20	16	18												
	D-30	46	43	19	4	25	27	32												

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[1] Numbers are mean total germination percentages.

[2] Dates are as follows: (1) late October, (2) late November, and (3) early January.

seed from the last collection than either of the two other collection dates. Collection date changed the effect of temperature on germination totals (Table 1). Although 20 C was preferred overall (36%) and 30 C was the least preferred (23%), germination of seeds at 10 C increased substantially as date became later. Seeds of the first collection at 10 C were the lowest germinating (22%) compared to seeds at 20 C (33%). By the third date of collection the importance of 10 C was such that seeds in this temperature regime were germinating at about the same level as those in the 20 C regime (40%). There were no significant interactions between water potential and date of seed collection.

Germination in the dark was higher (32%) than in the light (27%) (Table 1). Highest germination was observed with seeds exposed to dark conditions at 20 C (43%) when light and temperature was analyzed. Seeds undergoing a treatment of 30 C in the light had the lowest germination (18%).

Progressively decreasing osmotic potentials caused significant decreases in germination percentages (57 to 4%) (Table 1). Interaction effects of osmotic potential and light and dark resulted in response reversal as water stress increased beyond 0 bars. Under no water stress, seeds had higher germination totals in the light (65%) than in the dark (49%). However, this relationship reversed at 2.5 bars so that germination in the dark (44%) was greater than in the light (35%). This response continued as osmotic potentials reached 5 and 7.5 bars. Germination percentages decreased as osmotic stress increased, but the decrease was less precipitous for seeds maintained in the dark. Germination reactions to temperature and osmotic potential combinations followed a predictable pattern. Regardless of the osmotic potential, germination was highest in the 20 C regime followed by the 10 and 30 C regimes, respectively.

Stratification had no statistical effect on germination. Sagebrush seeds are generally considered to be nondormant (McDonough and Harniss 1975, Caldwell 1978). Since stratification is normally a dormancy breaker, it might be expected that plains silver sagebrush would not respond to a cold treatment. Sagebrush seeds ripen and disperse late in the fall and early winter. Cold temperatures are common at this time in the Northern Great Plains and might already result in a field induced stratification. This type of response is suggested by the fact that as seed collection date became later, germination percentages increased.

Germination occurred under a variety of conditions, and this response confirmed that sagebrush seeds do not exhibit specific germination requirements. More optimum conditions are favored by seeds, but these conditions are not restricted to narrow requirements.

Rate Response to Individual Factors

All three seed collections exhibited similar rate responses to increasing water stress (Figure 15). However, higher germination percentages were observed as date of collection advanced. The less negative osmotic potentials had faster rates of germination as well as higher germination percentages. Rates of germination were determined by both the speed at which seeds reached the maximum level of

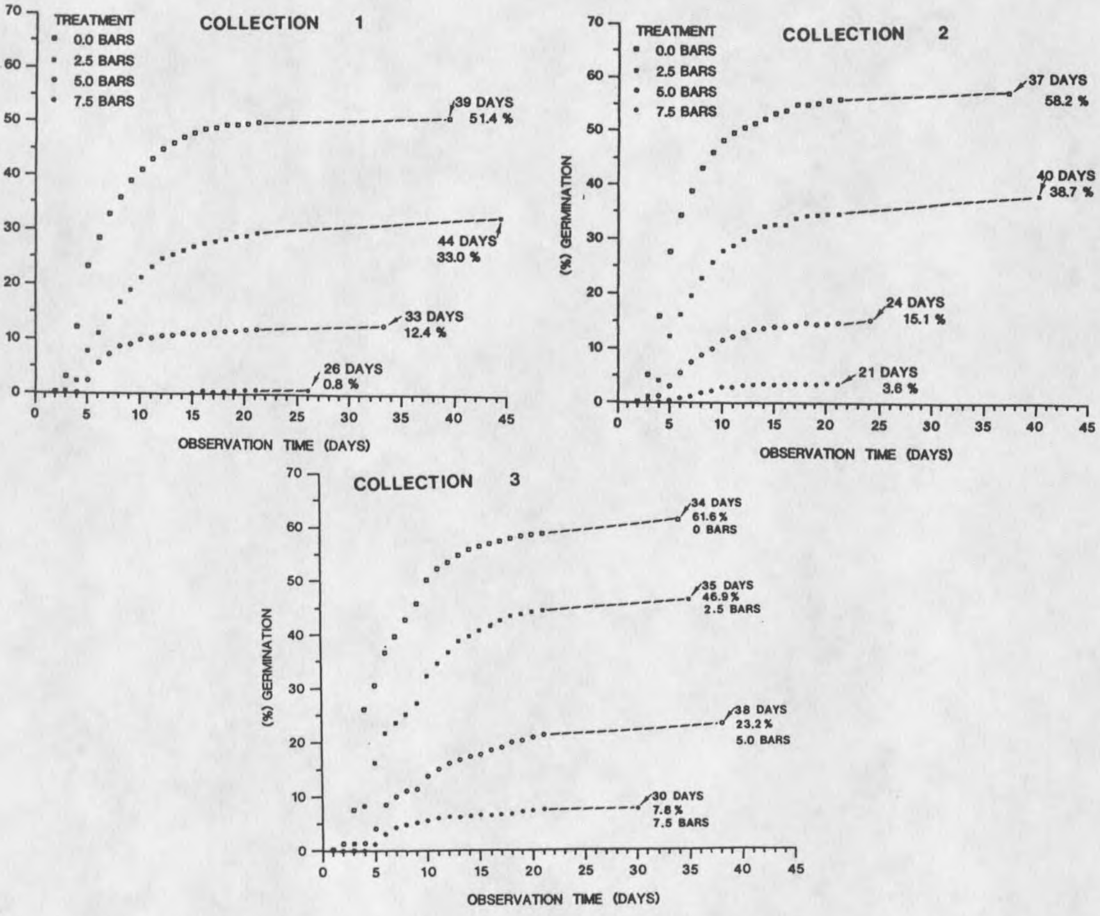


Figure 15. Osmotic potential effects on total germination percentages and rates of germination. Numbers are mean values for all seeds under the four potentials (0, 2.5, 5, 7.5 bars). Three seed collections are presented (late October, late November, and early January).

germination (the steepness of slopes in the following graphs) and days after initiation of germination. As water stress increased, there was a decrease in both amount of seed germinating and rate (slope) of germination. These findings are consistent with the findings of Bewley and Black (1982) and Evans and Young (1982). Plains silver sagebrush seems to be very sensitive to increased water stress and will decrease germination by as much as 1/3 between 0 and 2.5 bars, and by as much as 100 times between 0 and 7.5 bars depending on date of collection (Figure 15). This is comparable to the response found with fringed sagewort as increasingly negative osmotic potentials were encountered (Sabo et al. 1979).

At least three aspects of the seed germination process are affected by water uptake from the soil solution (Evans and Young 1982). They are: (1) imbibition, (2) enzymatic transformation and meristematic activities, and (3) start of growth. As osmotic potential becomes more negative, it becomes harder for the seed to take up water to meet the needs of these three stages. In the preliminary imbibition stage, water uptake is critical because it initializes enzymatic transformation, meristematic activities and finally the start of elongation and emergence of the radicle. In general, increased water stress delays completion of and reduces germination. This is caused by decreased water absorption, disturbed nutrient uptake, abnormal metabolism and reduced growth (Parmar and Moore 1966). Factors such as these undoubtedly contributed to the reduction in germination that was observed in this study under increased moisture stress.

Seed collection date affected the response to all factors and interactions of factors. As seed was collected later, germination was enhanced regardless of other conditions. Although most seed is dispersed in the first few weeks after ripening, seed remaining on the plant probably attains greater maturity. Research on effects of seed ripening or maturity have indicated that later seed collections showed higher germination percentages (Clor et al. 1974, Waller et al. 1980, Krueger and Shaner 1982).

When all factors were considered together, germination was highest at 20 C and lowest at 30 C. However, the effects of temperature on germination changed with respect to seed collection period (Figure 16). Changes were in respect to importance of the 10 C regime. As collection date advanced, highest germination was still observed under the 20 C regime. In contrast, the lowest temperature regime (10 C) became more important in stimulating increased germination. Under this temperature regime, twice as many seeds germinated from the third collection date (40%) as from the first collection date (22%). The fastest germination rates were also recorded in the 20 C regime. Seeds at 10 C had the slowest starting and the longest germination periods recorded. When this germination period is considered, the last collection of seed had no significant difference between the 10 and 20 C temperature regimes. Rates of germination are of value in characterizing seed responses to temperature, although there is often considerable variability due to genetic differences (Bewley and Black 1982). Genetic subpopulations will germinate under different temperature regimes and rates will

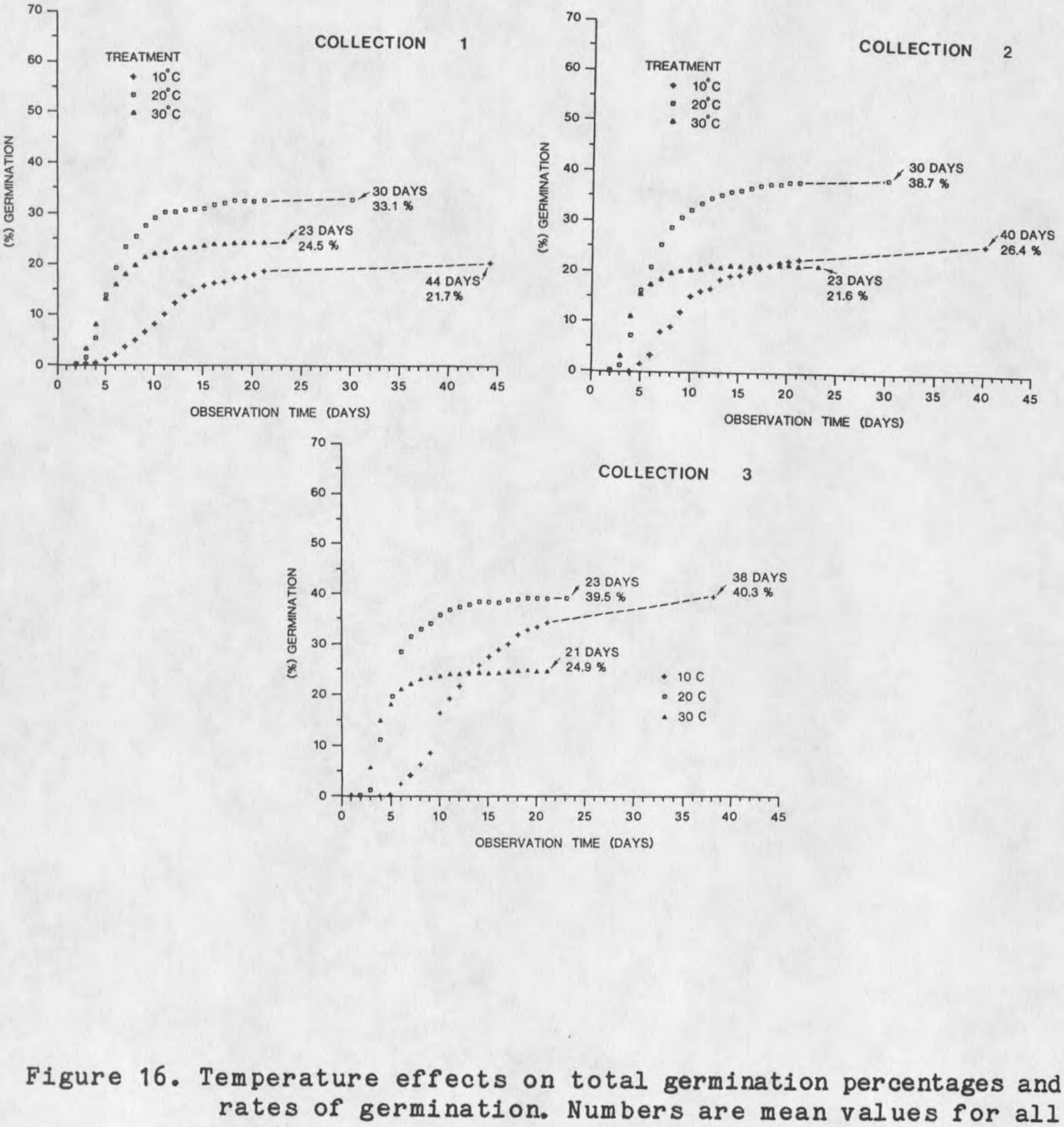


Figure 16. Temperature effects on total germination percentages and rates of germination. Numbers are mean values for all seeds under the three temperatures (10, 20, and 30 C). Three seed collections are presented (late October, late November, and early January).

change with these temperatures. McDonough and Harniss (1975) note that germination time in big sagebrush decreased from 18 to 2 days with increasing temperatures.

One apparent reproductive characteristic in plains silver sagebrush is that seed can germinate over a wide range of temperatures. This is also characteristic of big sagebrush. This characteristic as well as the changing relationship of temperature and seed collection date suggest adaptive features for heterogeneity of seed populations. Caldwell (1978) regards sagebrushes' (most species) ability to germinate over a wide range of temperatures as a competitive advantage over other associated species. A substantiation of McDonough and Harniss' (1975) implication that there are genetic subpopulations of sagebrush with characteristic temperature optima for germination is apparent in the ability of plains silver sagebrush seed to germinate over a wide range of temperatures. This heterogeneity of germination requirements allow seeds to germinate under a variety of environmental conditions that the seed will encounter in the early growing season. This is manifested both in the numbers of seeds germinating and rates of germination in relation to temperature.

Germination responses under light or dark conditions indicated that germination was slightly favored by a dark environment in all collection dates (Figure 17). Rates were not different between the two treatments, although germination periods were generally longer in the dark. In light, this period was from 24 to 43 days while in dark seeds germinated from 38 to 44 days. Differences among and within individual collection dates were small even though germination totals were higher

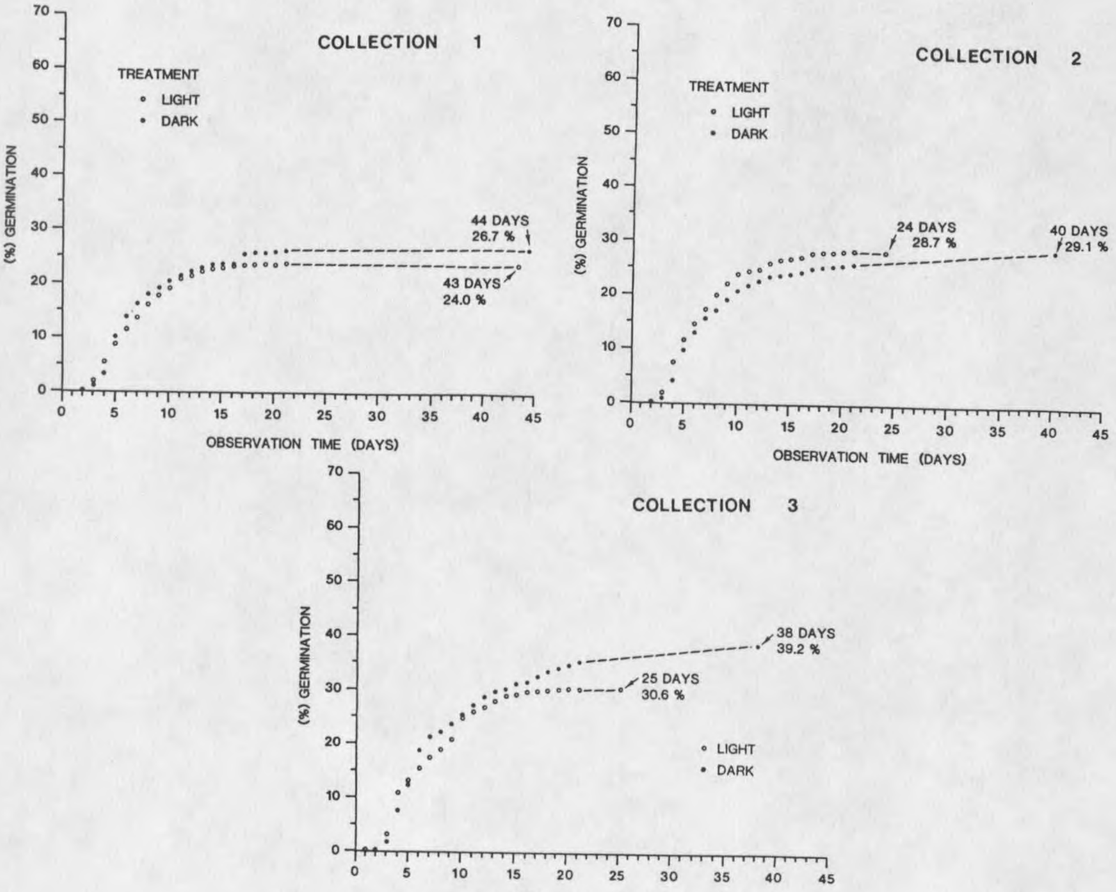


Figure 17. Light/dark effects on total germination and rates of germination. Numbers are mean values for all seeds under the two treatments (light and dark). Three seed collections are presented (late October, late November, and early January).

in seeds from the third collection date. On the first collection, germination was 27 and 24% for dark and light, respectively. On the third collection, seeds in dark had 39% germination while light treated seeds were at 31%.

The effects of light on seed germination is variable depending on species involved and complex interactions with environmental factors such as temperature, water relations and time (Al-Ani et al. 1972, Woolley and Stoller 1978, Cook 1980, Bewley and Black 1982). Light seems to be more important in seeds requiring a dormant period and a dormancy breaking mechanism. Because most sagebrush species are regarded as nondormant, light may not be of critical importance. The evidence for germination responses in other Artemisia species indicates a variable influence. Studies on fringed sagewort and big sagebrush demonstrated significantly more germination with light (Weldon et al. 1957, Beetle 1960, Caldwell 1978, Wilson 1982), but others have shown the opposite response (Sabo et al. 1979). Seed burial and its relationship to light conditions seems to be of major importance in field emergence and survival of plains silver sagebrush (discussed on pp. 107-124).

There were several important environmental interactions that affected germination response to individual factors. These interactions were most easily interpreted by evaluating germination response to any two factors taken together. For example, light and dark treatments were investigated in conjunction with the three temperature regimes. By using this approach, the effects of single factors could be put in better perspective because they were superimposed upon a second variable. Moreover, individual collection dates could also be evaluated in more depth within this context. Thus it became clear that collection date changed the relationships of light and dark within the different temperatures regimes. This is illustrated by Figures 18, 19, and 20 in which light and dark regimes are compared at the three temperatures and for the three collection dates.

In general, dark conditions resulted in higher germination in all three collections. When seeds from the first collection date were germinated under light, essentially no differences could be detected with respect to temperature regime (Figure 18). However, as collection date advanced temperature exerted more of an influence on germination (Figures 19, 20). By the third date, light combined with the 10 C temperature showed significantly higher germination (42%) than either the 20 or 30 C regimes (32 and 18% respectively). The high 30 C temperature resulted in lowest germination from all three dates when light was present. In contrast, dark treated seeds generally showed best germination under the 20 C regime and least at 10 C. Under dark conditions, differences among temperature regimes were commonly 10% or more depending upon collection date. Germination responses did not vary this much in the light. In dark conditions, germination rates (or slopes) were slower and start of germination was usually delayed by three to six days. The total period of germination was also prolonged, especially for those seeds in the 10 C temperature regime where germination occurred at 38 to 44 days. On the third collection, the extended germination period resulted in seed response at 10 C being

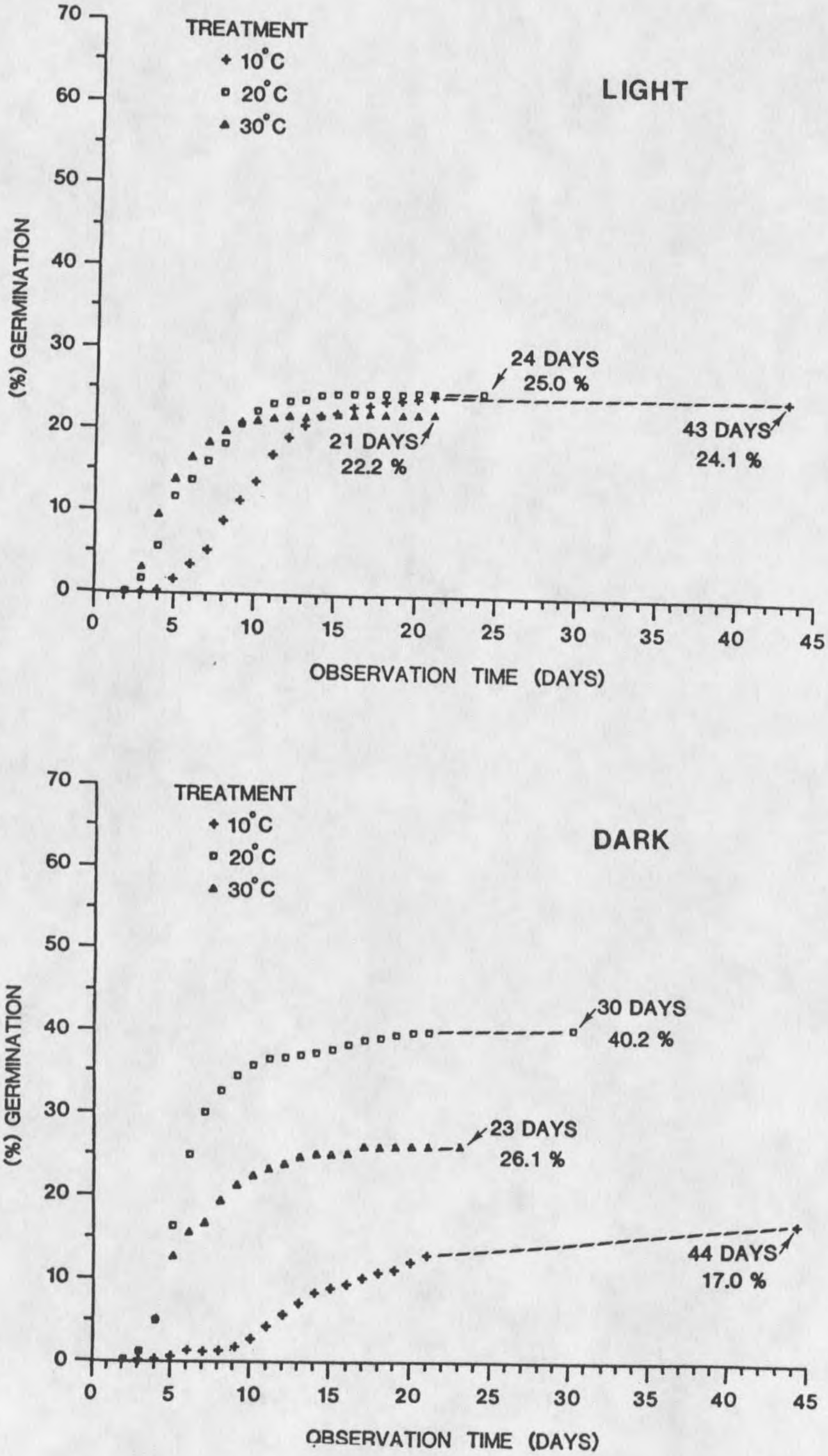
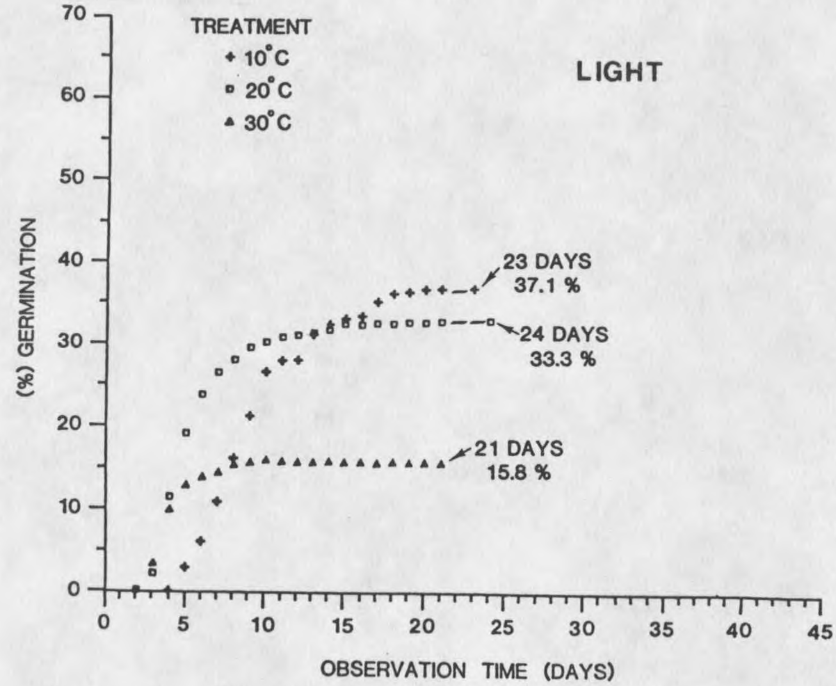


Figure 18. Light/dark comparisons among three temperatures and their effect on total germination percentages and rates of germination. First seed collection (late October) data is presented. Numbers are mean values for all seeds in this collection period.



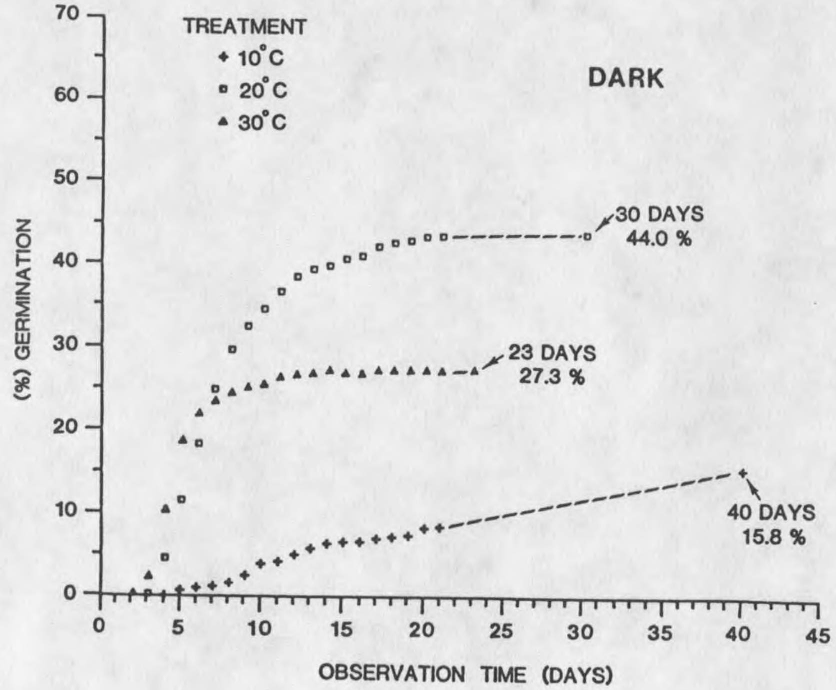


Figure 19. Light/dark comparisons among three temperatures and their effects on total germination percentages and rates of germination. Second seed collection (late November) data is presented. Numbers are mean values for all seeds in this collection period.

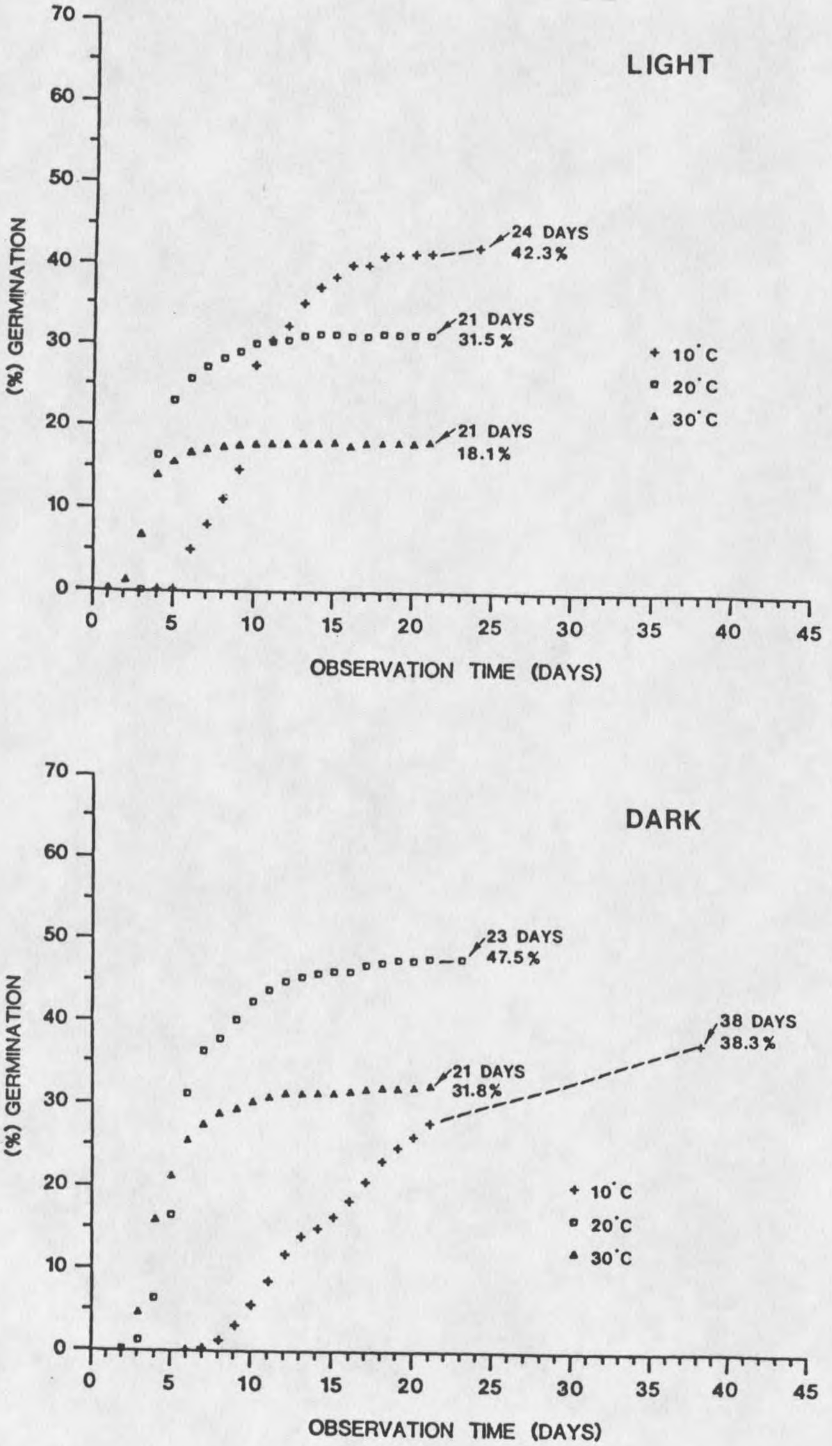


Figure 20. Light/dark comparisons among three temperatures and their effects on total germination percentages and rates of germination. Third seed collection (early January) data is presented. Numbers are mean values for all seeds in this collection period.

slightly higher than that of the 30 C regime but still lower than seed response at 20 C.

My results have demonstrated that plains silver sagebrush seed can germinate under both light and dark conditions. However, light seems to be less effective in inducing germination than dark conditions. Because temperature relationships change according to light or dark treatment, it seems apparent that the interactions of light and temperature can either stimulate or inhibit seed germination. This could be of considerable importance with regards to seed being buried or on the soil surface. During the growing season, temperatures are normally higher and fluctuate more on the soil surface. This means that surface conditions exist that will provide limited germination of those seeds able to respond to variable temperature and light regimes. However, cooler and more stable temperatures exist beneath the soil surface. Since dark conditions also prevail, this provides a more favorable environment for seeds to germinate. The heterogeneity associated with individual germination requirements or sites creates a wide range of environmental conditions to which plains silver sagebrush seems well adapted.

The effects of osmotic potential on seed germination change according to whether light or dark conditions prevail (Figures 21, 22, 23). No significant differences, in regards to these two factors, were observed as seed collection date advanced. At osmotic potentials of 0 bars, germination was higher in the light regime. Germination totals were from 10 to 22 percent higher in light than in dark at this osmotic potential. In this regime, totals ranged from 58

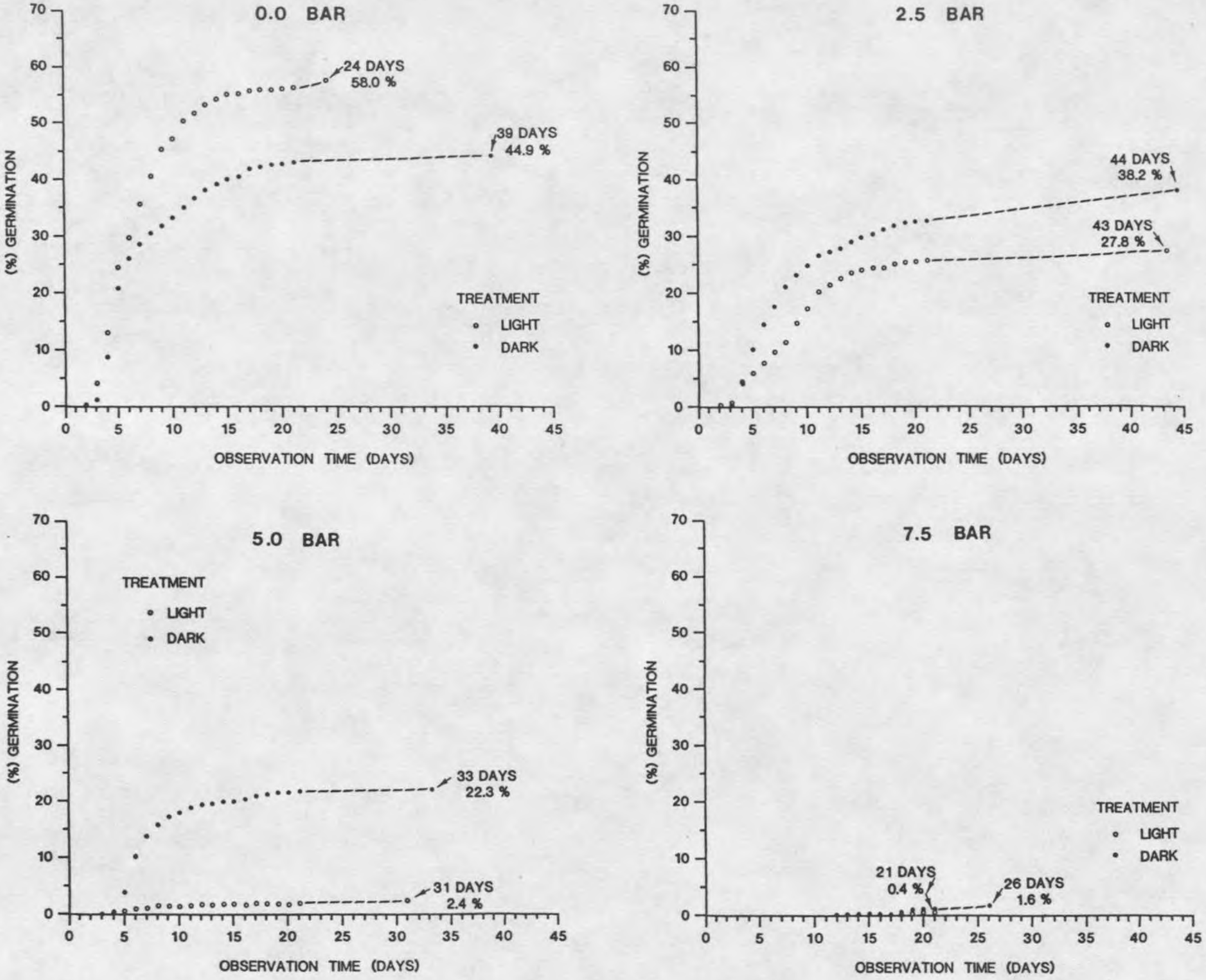


Figure 21. Osmotic potential comparisons between light and dark and their effects on total germination percentages and rates of germination. First seed collection (late October) data is presented. Numbers are mean values for all seeds in this collection period.

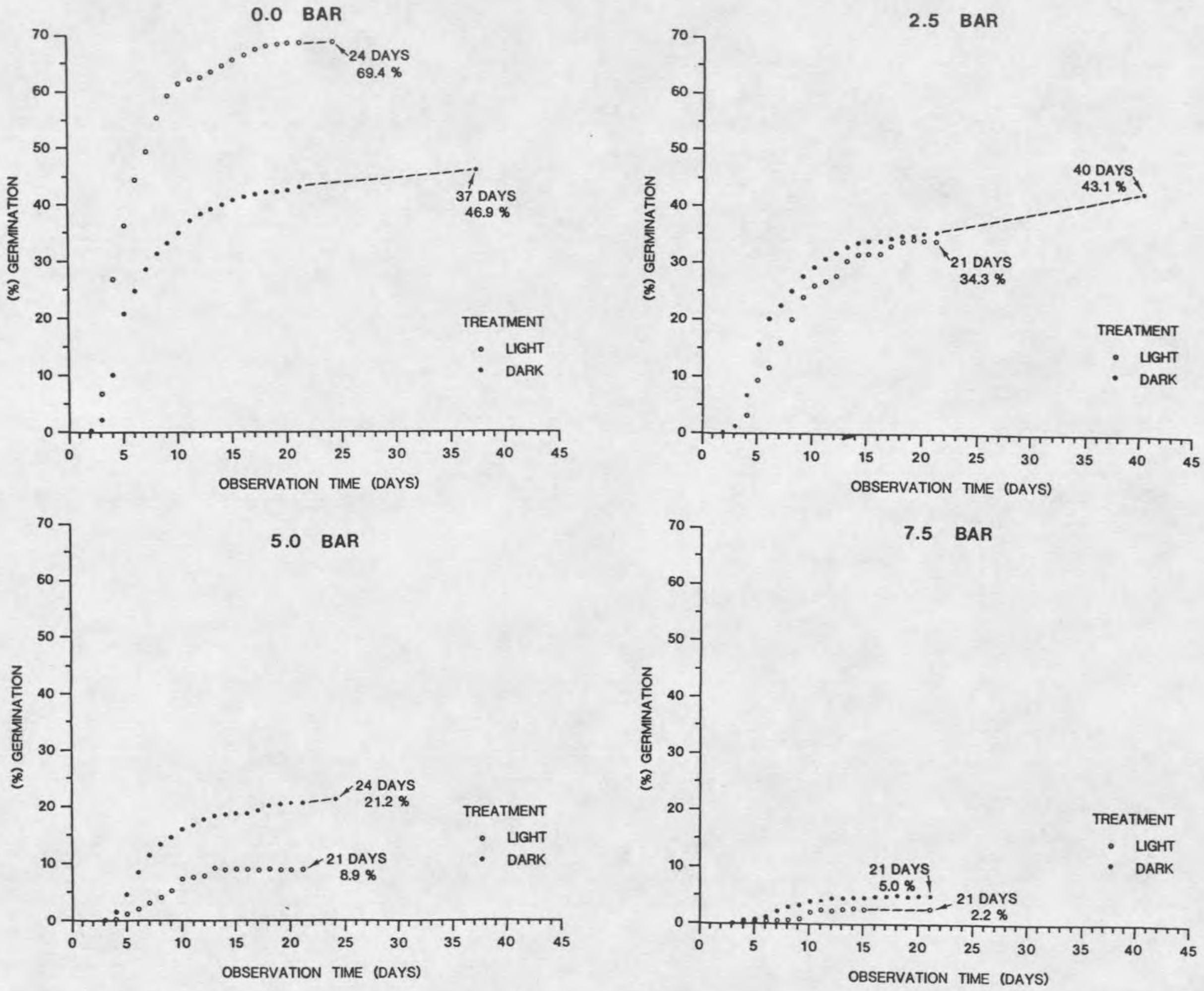


Figure 22. Osmotic potential comparisons between light and dark and their effects on total germination percentages and rates of germination. Second seed collection (late November) data is presented. Numbers are mean values for all seeds in this collection period.

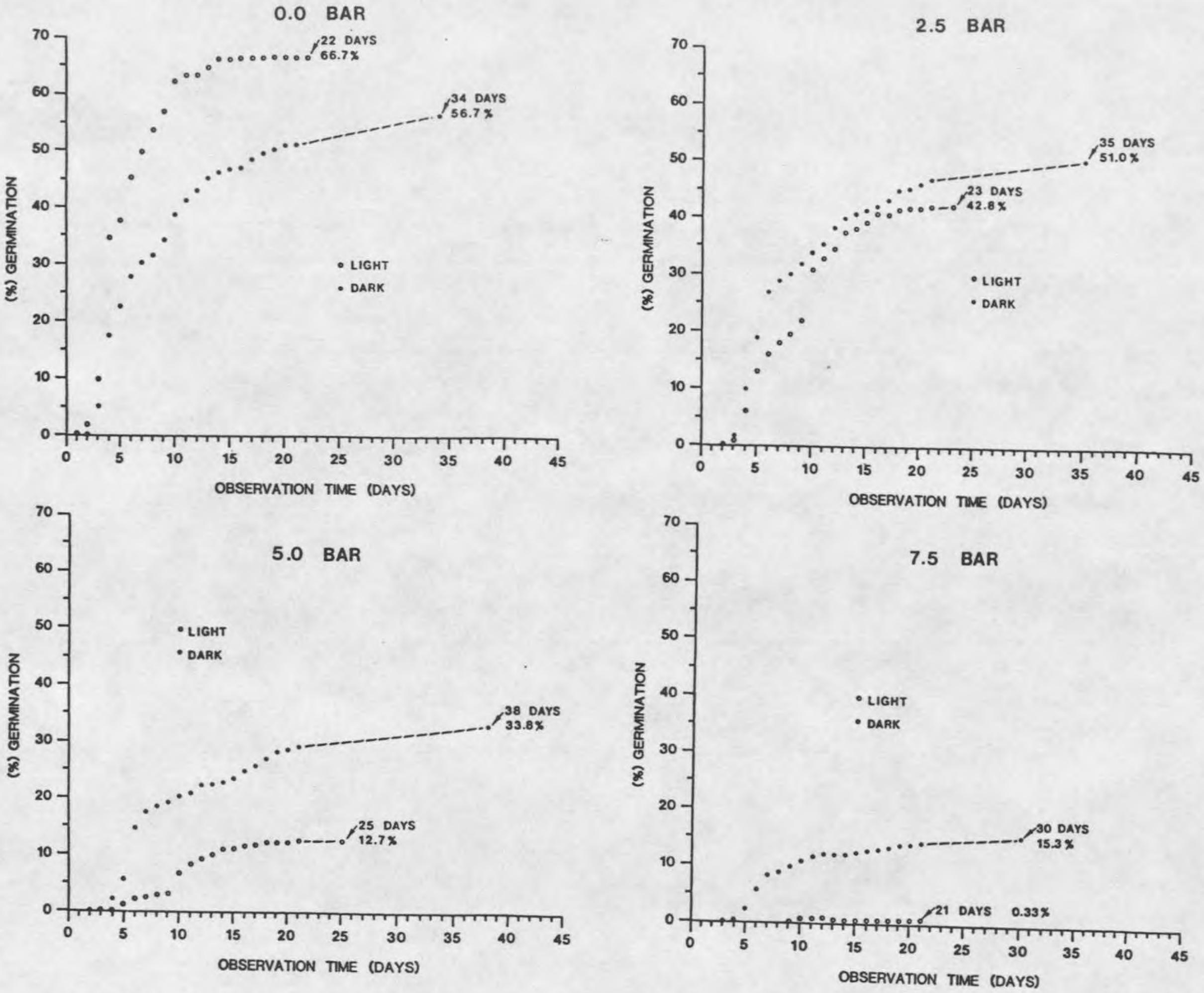


Figure 23. Osmotic potential comparisons between light and dark and their effects on total germination percentages and rates of germination. Third seed collection (early January) data is presented. Numbers are mean values for all seeds in this collection period.

to 69% in the light and 45 to 57% in the dark depending on date of collection. When seeds are located on the soil surface where light is generally a constant factor, germination would be favored only when water is freely available. This relationship was reversed at 2.5 bars so that dark conditions were slightly favored, although germination periods were lengthened. Differences of around 10% were noted here in all collection dates between seeds in dark and those in the light. Response differences to light and dark regimes became greater as water stress increased from 2.5 bars to 5 and 7.5 bars. Dark conditions seemed to ameliorate the effect of increased water stress on seeds. Germination under dark conditions at these more negative osmotic potentials was 2 to 30 times greater than that of light conditions. Therefore, germination in later stages of the growing season, when moisture conditions are generally more severe, would be favored in dark environments such as burial in the soil. Germination rates or time to reach maximum germination were not substantially different in any of the regimes.

The germination response that was observed when osmotic potential was considered along with temperature regimes showed that there were differences in germination totals among collection dates and a changing importance of the 10 C temperature regime as collection date advanced (Figures 24, 25, 26). Germination totals increased in all potentials as date advanced and this is especially true for seeds germinating at 10 C. At 0 bars, germination in this temperature regime increases from 50% on the first date to 67% on the third. Germination

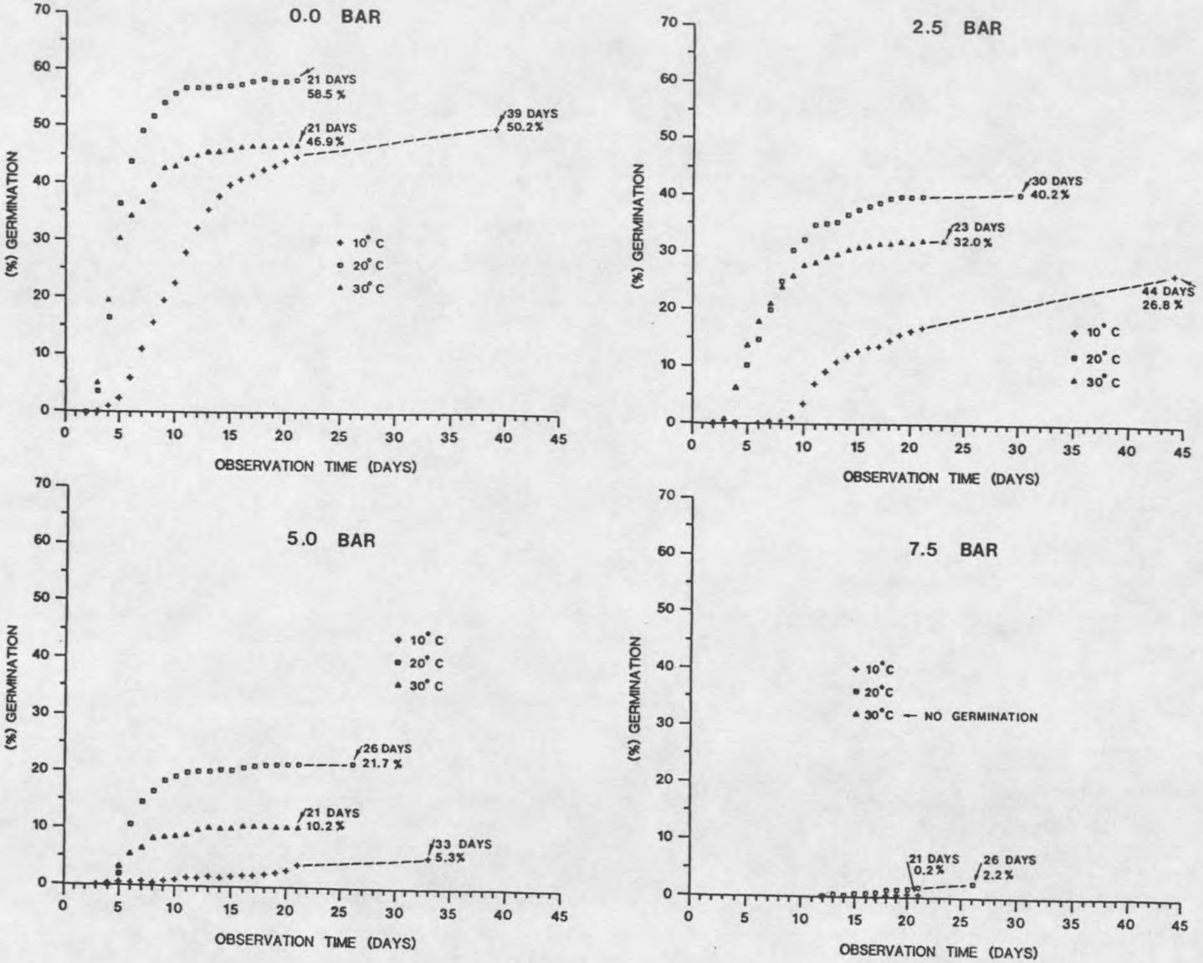


Figure 24. Osmotic potential comparisons among three temperatures and their effects on total germination percentages and rates of germination. First seed collection (late October) data is presented. Numbers are mean values for all seeds in this collection period.

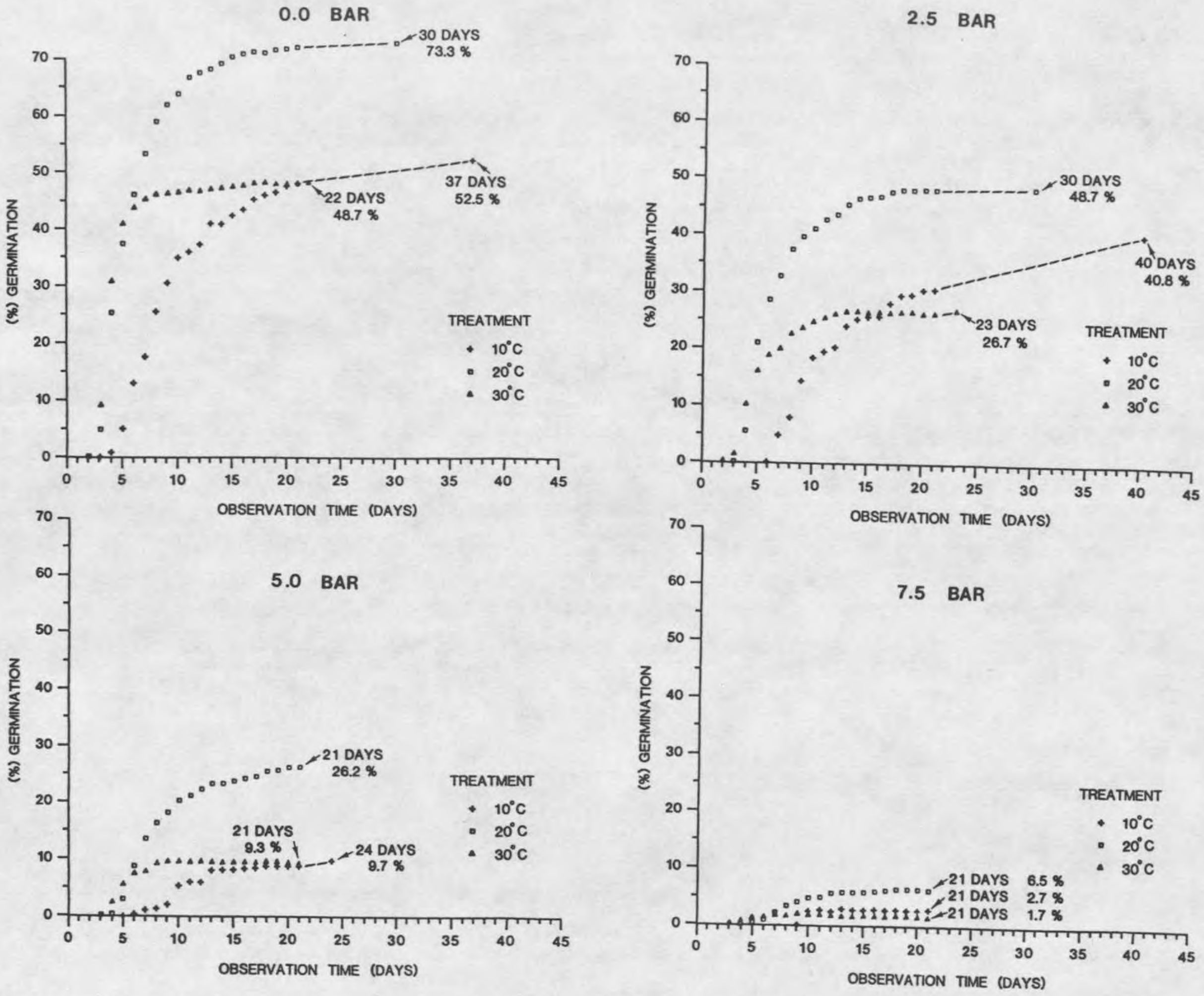


Figure 25. Osmotic potential comparisons among three temperatures and their effects on total germination percentages and rates of germination. Second seed collection (late November) data is presented. Numbers are mean values for all seeds in this collection period.

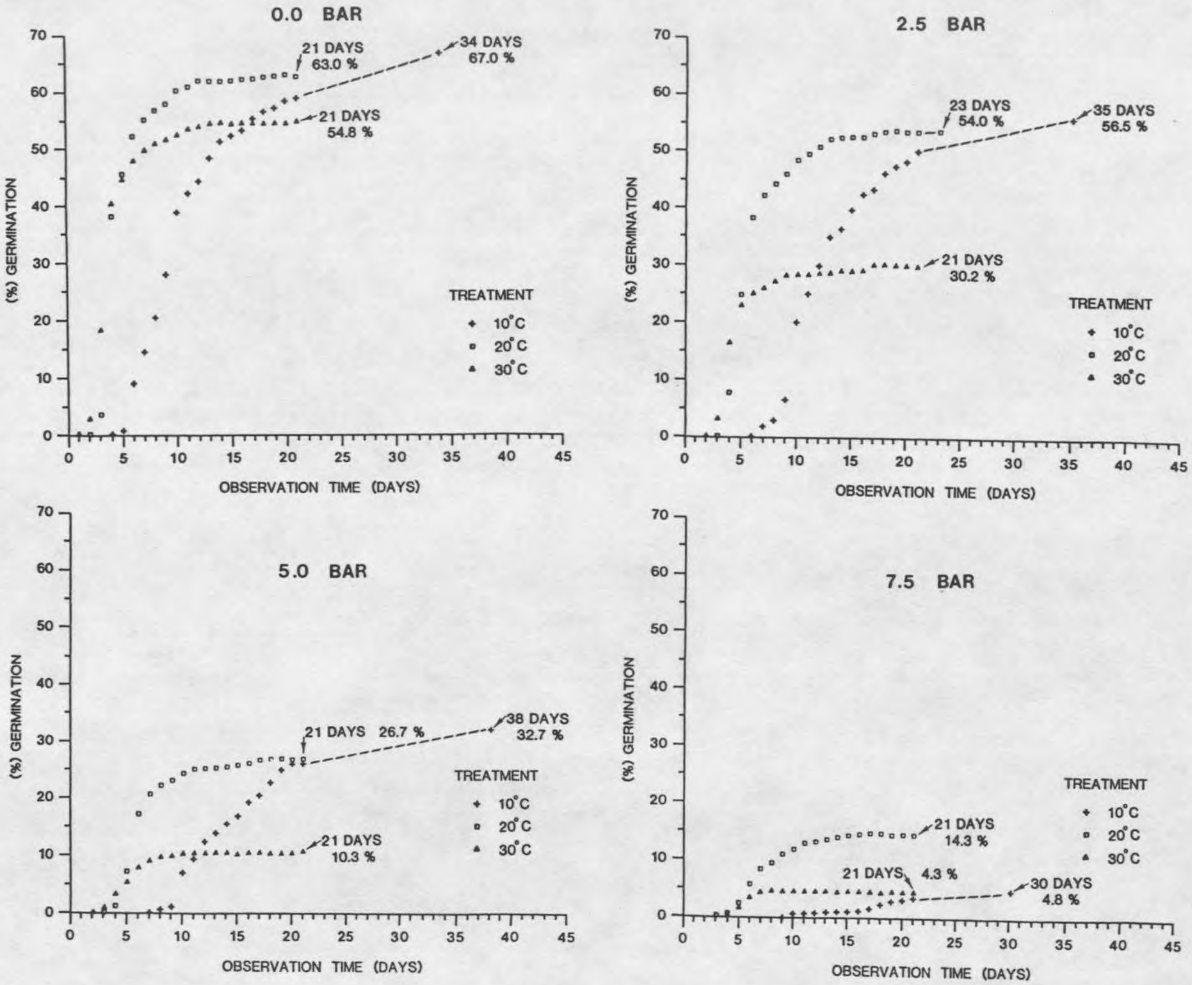


Figure 26. Osmotic potential comparisons among three temperatures and their effects on total germination percentages and rates of germination. Third seed collection (early January) data is presented. Numbers are mean values for all seeds in this collection period.

at 10 C was second or third in importance on the first and second dates in all potentials. However, the third collection showed seeds at 10 C had slightly higher germination percentages than either 20 or 30 C, except at 7.5 bars where it was the second highest. Although germination totals did increase with an advance in collection date, these increases were magnified as potential became more negative. At 0 bars, the increase from the first to last collection was only on the order of 1/15 to 1/10th. At 7.5 bars, this increase was 7 to 14 times the germination on the third collection as in the first. Although the importance of germination in the 10 C regime increased with the advance of collection date, rates had more gradual slopes where the germination potential was reached at a slower pace than in 20 or 30 C. Periods of germination was also extended for seeds at 10 C by 9 to 17 days.

There is a significant relationship between length of time seeds remain on the parent plant and the optimum germination temperature. As length of time (or maturity) becomes greater, germination is enhanced, especially at lower temperatures such as 10 C. This is evident regardless of water stress.

It is apparent that plains silver sagebrush has an ability to germinate under a variety of environmental conditions. However, individual factors and interactions of combinations of factors do significantly inhibit or stimulate germination. Plains silver sagebrush seems to be most sensitive to osmotic potential and to a lesser degree temperature, light conditions and date of seed collection (or dispersal). Stratification could not be detected as having any influence on germination responses. Seeds under no water stress germinated best, especially in conditions of light. The seeds under no water stress were also favored in temperatures of 10 and 20 C. Germination temperatures of 20 C were most favored overall, but seeds at 10 C showed comparable results when collected the later in the season. As water stress increased, dark conditions were a more important stimulant to germination. Date of seed collection or dispersal from a parent plant was important in that it stimulated germination.

Early Seedling Growth

Studies on plains silver sagebrush in growth chambers, the greenhouse and under field conditions confirmed that the environment factors that affected germination also play an important role in determining how many seedlings will emerge, survive and grow. Water availability, temperature and planting depth all affected the degree of seedling success. Depth from which a seedling emerges is affected by light and moisture conditions. Heterogeneity in the seed pool also expressed itself in this work on seedling development.

Temperature Effects on Transplanted Seedlings

Growth chamber studies on the effect of two diurnal temperatures on seedling growth indicated that the higher temperature regime resulted in greatly enhanced growth. Those seedlings in the 32/21 C treatment had significantly more growth in terms of height, number of leaves, and cover expressed by two horizontal axes (Figure 27). Height in the warm regime (32/21 C) responded immediately and sustained rapid growth for more than three months. In contrast, seedling height in the cool regime (21/10 C) did not markedly change for two months. As a consequence, height in the warm regime (80 mm) was more than twice that of that of the cool regime (38 mm) at the end of the study. Numbers of leaves increased (both regimes from around 12 leaves) in the warm regime at a greater rate than those in the cooler regime so that at the end of the study, those seedlings in the 32/21 C regime had about three times as many leaves (180 and 70 leaves). Although the

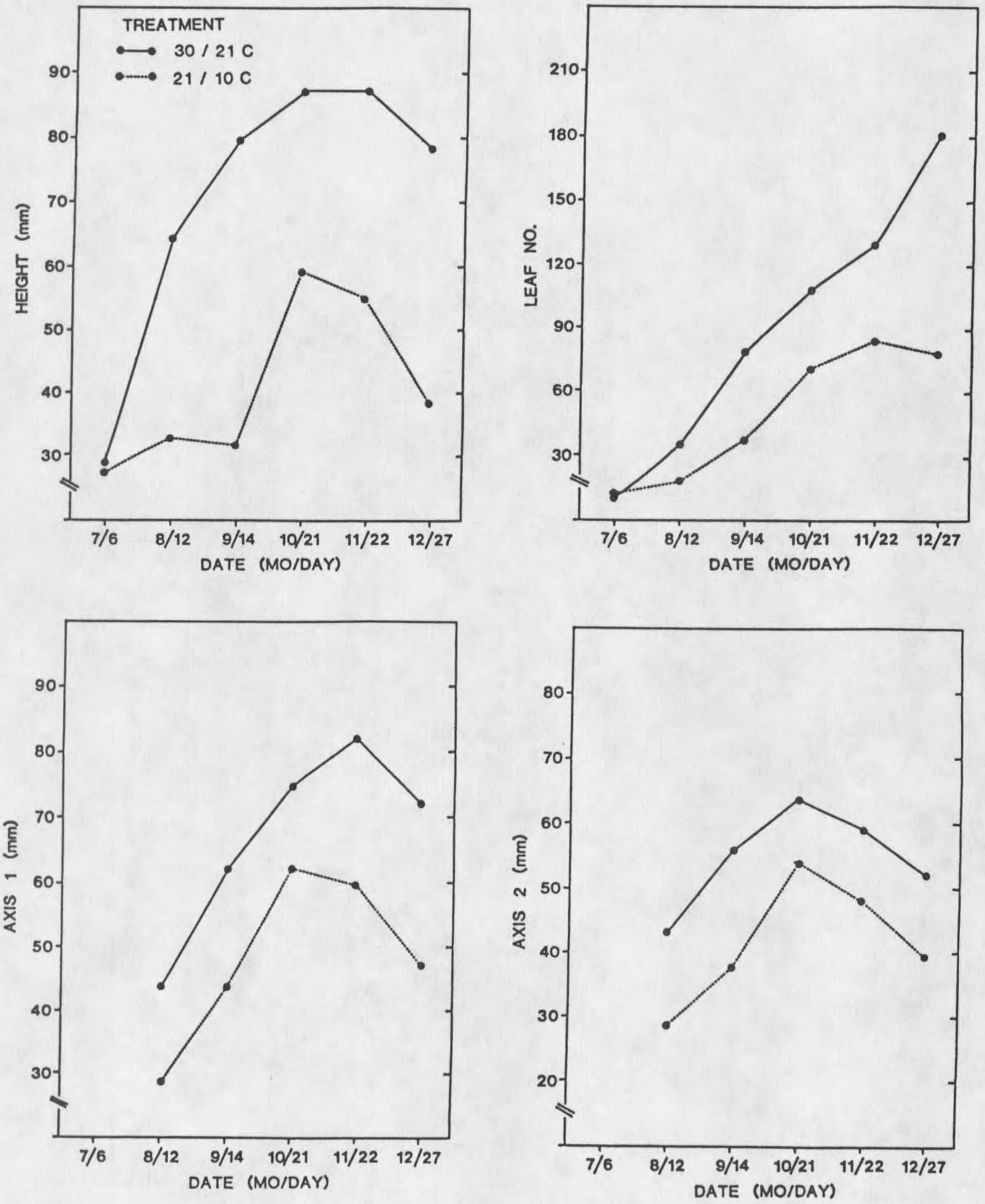


Figure 27. Temperature effects on seedling growth. Four growth parameters are presented: height, number of leaves, and two horizontal cover estimates.

horizontal axes demonstrated the same response of greater growth in the warmer regime, the differences were not as great as the previous two parameters. For three months, the increases were steady, but afterwards there was a decrease in both horizontal axes.

Results for growth in terms of leaf area and root/shoot biomass reflected the same trend, but differences between regimes had different characteristics (Figure 28). Leaf area growth in both regimes increased substantially, but two characteristics were readily apparent. First, leaf area increased in the cooler regime (21/10 C) at the same rate as that of leaf area in the warm regime. However, growth was delayed by a month in the cooler regime and peaked at about the same level as that in the 32/21 C regime. Seedling leaf area declined after three or four months with that of the cooler regime at a steeper rate than in the warmer regime. Leaf area was significantly higher in the warmer regime in every sampling period except the next to last one.

Root biomass in both treatments was significantly higher than shoot biomass in the respective temperature regimes (Figure 28). Root and shoot biomass in the 32/21 C regime increased throughout the experiment, whereas root and shoot biomass in the cooler regime increased steadily until the last date when a precipitous decrease was observed. Overall, the tissue weight in the warmer regime for both roots and shoots was greater than respective root and shoot biomass at the cooler regime. No statistical differences were found among root biomass in both regimes except at the end of the study at which time seedlings at 32/21 C showed about 30% more root biomass due to a steep

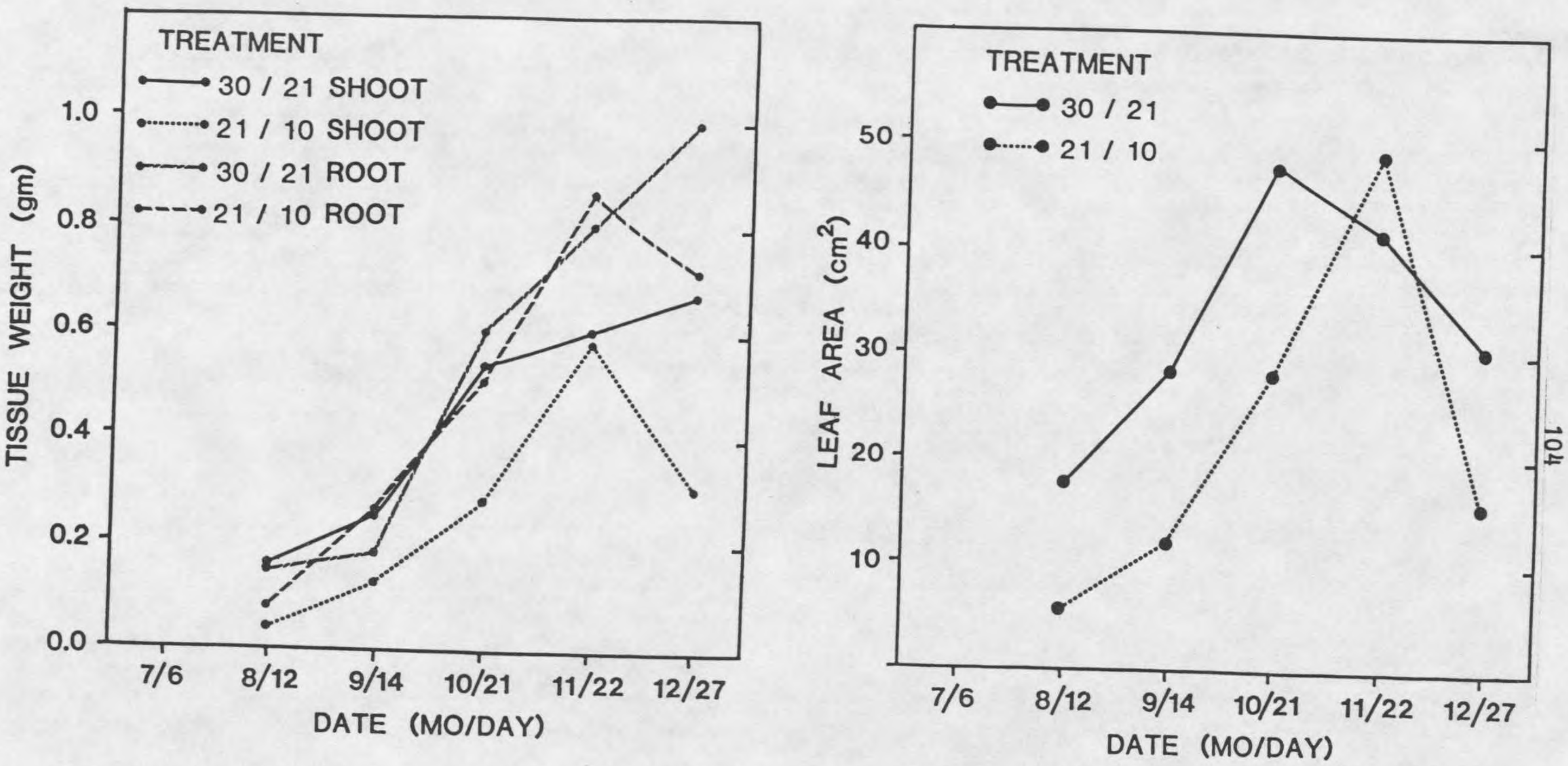


Figure 28. Temperature effects on seedling growth. Two growth parameters are presented: root and shoot growth, and leaf area.

decline in biomass at 21/10 C. Measurements of shoot biomass showed a significant difference on all sampling periods except for the next to last one. At this time shoot biomass at 21/10 C responded similarly to that of root biomass in this regime. There was a steep decline in biomass on the last date. At the end of the study shoot biomass in the warmer regime was twice that of shoot biomass in the cooler regime. Root to shoot ratios increased throughout the experiment (Table 3), with greater shoot growth apparent the first two recording periods for seedlings in the warm regime. Root/shoot ratios changed from 0.94 for the warm regime and 1.8 for the cooler regime to 1.49 and 2.4, respectively. Ratios of root biomass to shoot biomass were higher for seedlings in the cooler regime, with the difference between treatment ratios apparently being due to the greater initial shoot growth for seedlings in the warmer regime.

Table 3. Root to shoot ratios for seedling growth under two temperature regimes. Ratios are presented by temperature regime and sampling date.

	Root/shoot ratios[1]				
	Sampling date				
Temperature regime[2]	8/12	9/14	10/21	11/22	12/22
32/21 C	.94	.72	1.13	1.33	1.49
21/10 C	1.80	2.25	2.14	1.50	2.43

[1] Root and shoot ratios were determined by oven dry tissue weights from four seedlings taken from each temperature regime at each sampling period.

[2] Temperature regimes were regulated for a 12 hour period at each temperature in growth chambers.

Most growth parameters exhibited a positive growth relationship initially that became negative towards the end of the five and one half month study (Figures 27, 28). The only exceptions were the number of leaves at 32/21 C and root and shoot biomass at the 32/21 C regime. In general, growth curves started declining earlier in the lower temperatures than for the higher temperature regime. The only exception was for leaf area where the seedlings in the cooler regime peaked later and then declined sharply. The mechanics for the negative growth was most likely the loss of larger, earlier growth leaves and replacement by smaller leaves.

Growth of seedlings was strongly influenced by ambient temperatures. However, optimum germination temperatures were lower than those found to be the most favorable for seedling growth. This seems to correspond well with environmental temperatures likely to be encountered during the course of the growing season. As previously discussed, germination was most successful at 10 or 20 C (see pages 84-86), while growth of seedlings was more successful at daytime temperatures of 32 C (nighttime 21 C). Seeds germinate and emerge early in the growing season when ambient temperatures are normally lower than those in the summer growing months.

Greenhouse Seeding

Seedling emergence occured at depths of 0, 0.5 and 1.5 cm, but none was observed at the deepest depth of 2.5 cm (Figure 29). The greatest emergence took place at the soil surface with several seedlings never making it past the cotyledon stage. For the two

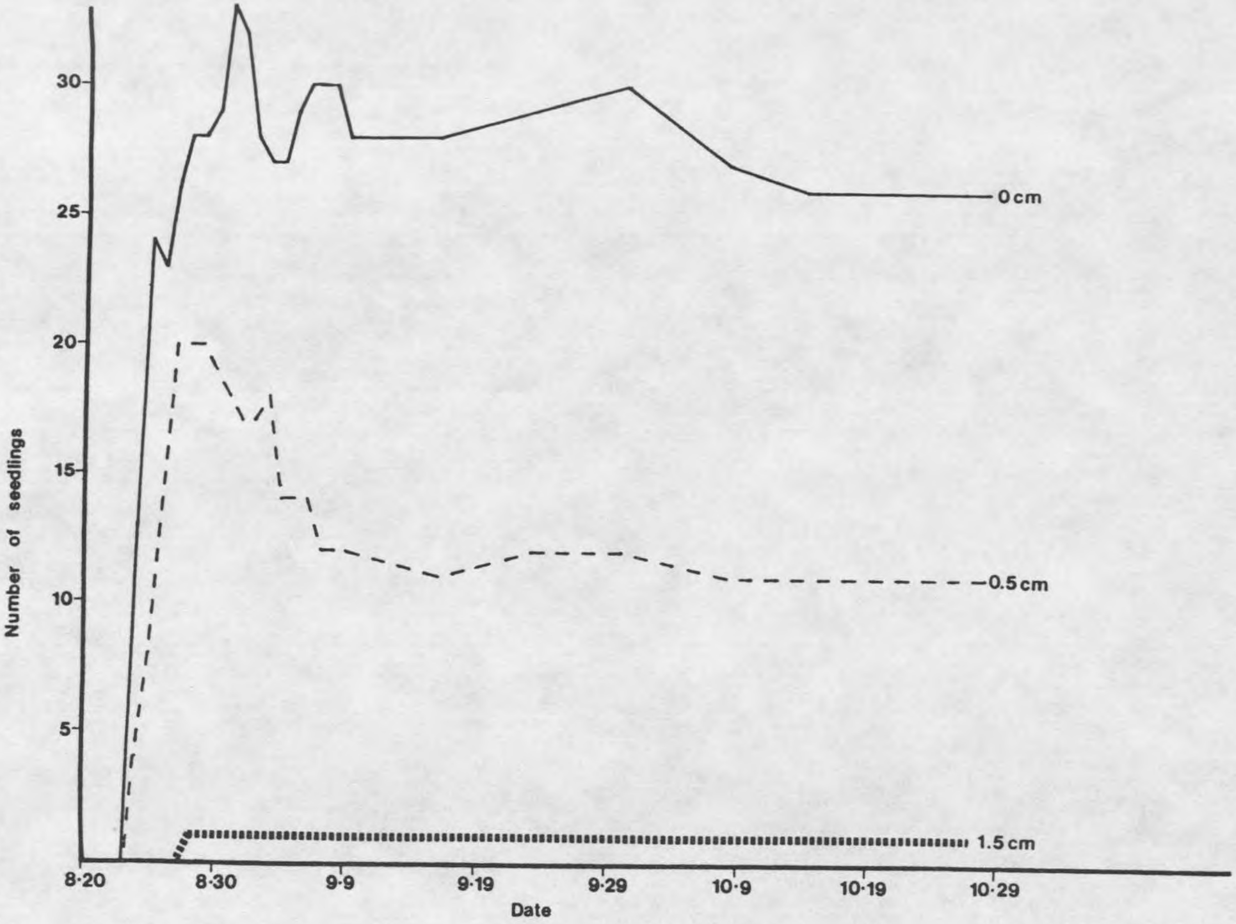


Figure 29. Emergence and survival of greenhouse seedlings at three depths of burial.

shallower depths of burial (0 and 0.5 cm), survival was very similar in terms of having an initial peak of emergence, a die-off of seedlings and then a stable number surviving the study. A large flush of seeds germinated and emerged in the first three weeks. The greatest number of emerged seedlings at any one time was 33 at the soil surface, although a total of 37 (of 100) emerged over the entire study period. This same pattern was observed at 0.5 cm, but with lower total numbers. The highest number of emerged seedlings at this depth was 20, although 22 emerged over the entire study period. Only one seedling emerged from the 1.5 cm depth. Those seedlings that did not establish an adequate root system died shortly after emerging. This left a rather stable number which survived throughout the rest of the trial. This period between germination and stabilization in the growth environment is probably the most critical in the life of the plant and is the period where most mortality has been observed (Eddleman 1979, Evans and Young 1982).

Water relationships probably best explain the high number of germinating seeds and establishing seedlings on the soil surface. In this study water stress was minimized so that light presented a favorable environment in which to germinate (see page 92).

Growth measurements established that those seedlings surviving initial emergence from the 0.5 cm depth grew higher (19 to 22 mm greater) and had more leaves (11 to 14 greater) than those surviving seedlings from the 0 and 1.5 cm depths (Figure 30). The seedling from 1.5 cm showed the least growth in these two growth parameters. Seedlings emerging from 0.5 cm exhibited more lateral

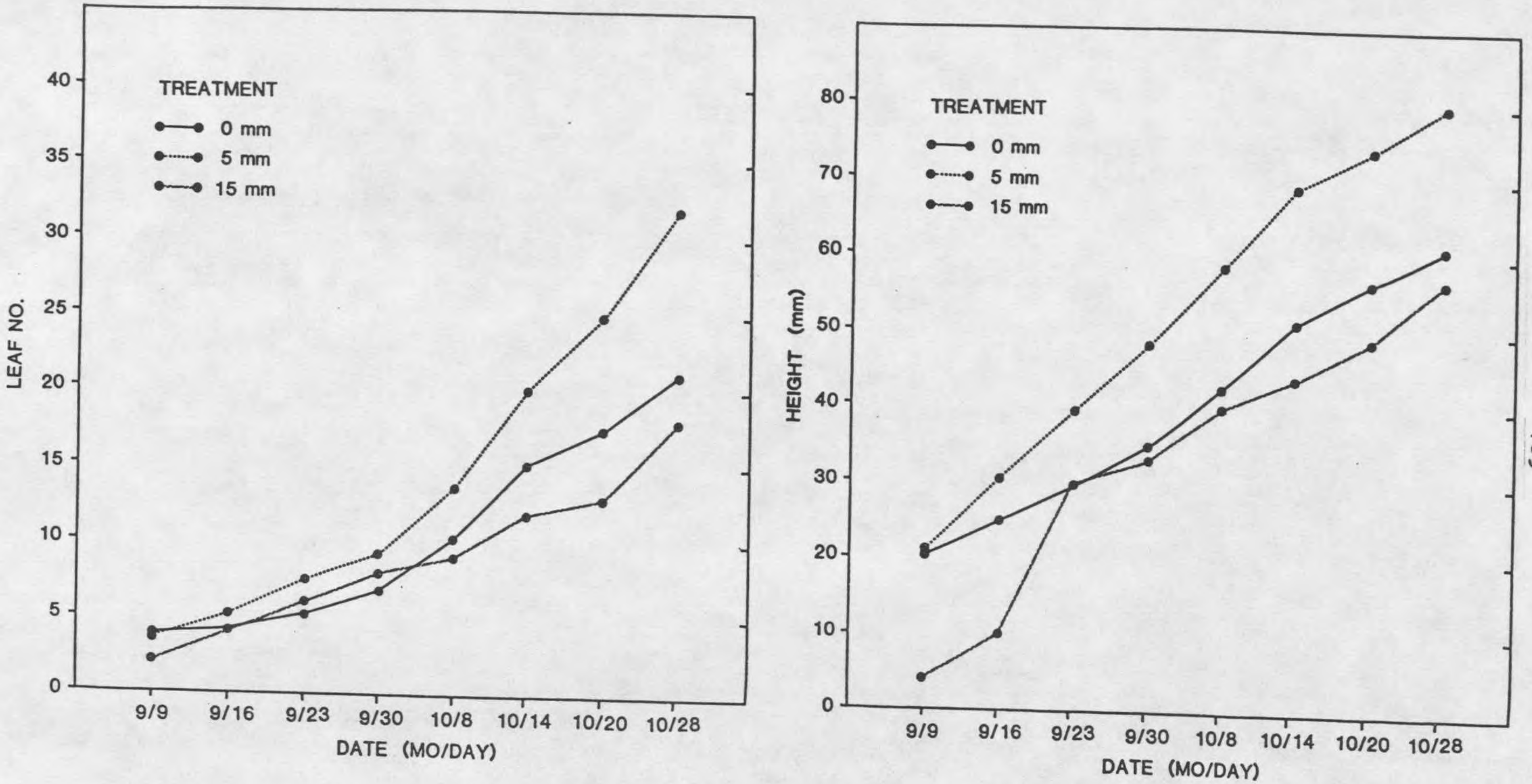


Figure 30. Growth parameters in the greenhouse as affected by depth of seed burial. Number of leaves and height of seedlings are presented.

growth than seedlings from the other two depths (Figure 31). The lowest amount of growth in these two measurements were found in seedlings that were initially on the soil surface although the seedling from the 1.5 cm depth started with the least. In general, the one seedling that emerged from 1.5 cm had similar growth characteristics as seedlings from at the soil surface. The enhanced seedling growth that was measured from seeds buried 0.5 cm deep was probably due to more favorable germination conditions as well as better root growing conditions. Seeds germinating below the surface are surrounded by the soil matrix and therefore have a constant soil contact. This results in more favorable moisture and a greater initial nutrient base from which to draw. Those seedlings that can establish a working root system by the time the cotyledons are above the soil surface already have a substantial advantage for continued growth. This is illustrated by the greater growth exhibited by seedlings establishing from 0.5 cm.

Field Seeding

Emergence of plains silver sagebrush in the field totaled about 1.2 percent of the seeds planted. Of those seedlings that emerged, only about 11% survived the summer. Seedlings were most abundant from the 0.5 cm depth than from the other planting depths (Figure 32). At the highest level of emergence, there were 85 seedlings from the 0.5 cm depth and 59, 52 and 17 seedlings respectively from the 0, 1.5 and 2.5 cm depths. Those germinating on the surface and emerging from 1.5 cm were nearly equal in number. This relationship was maintained

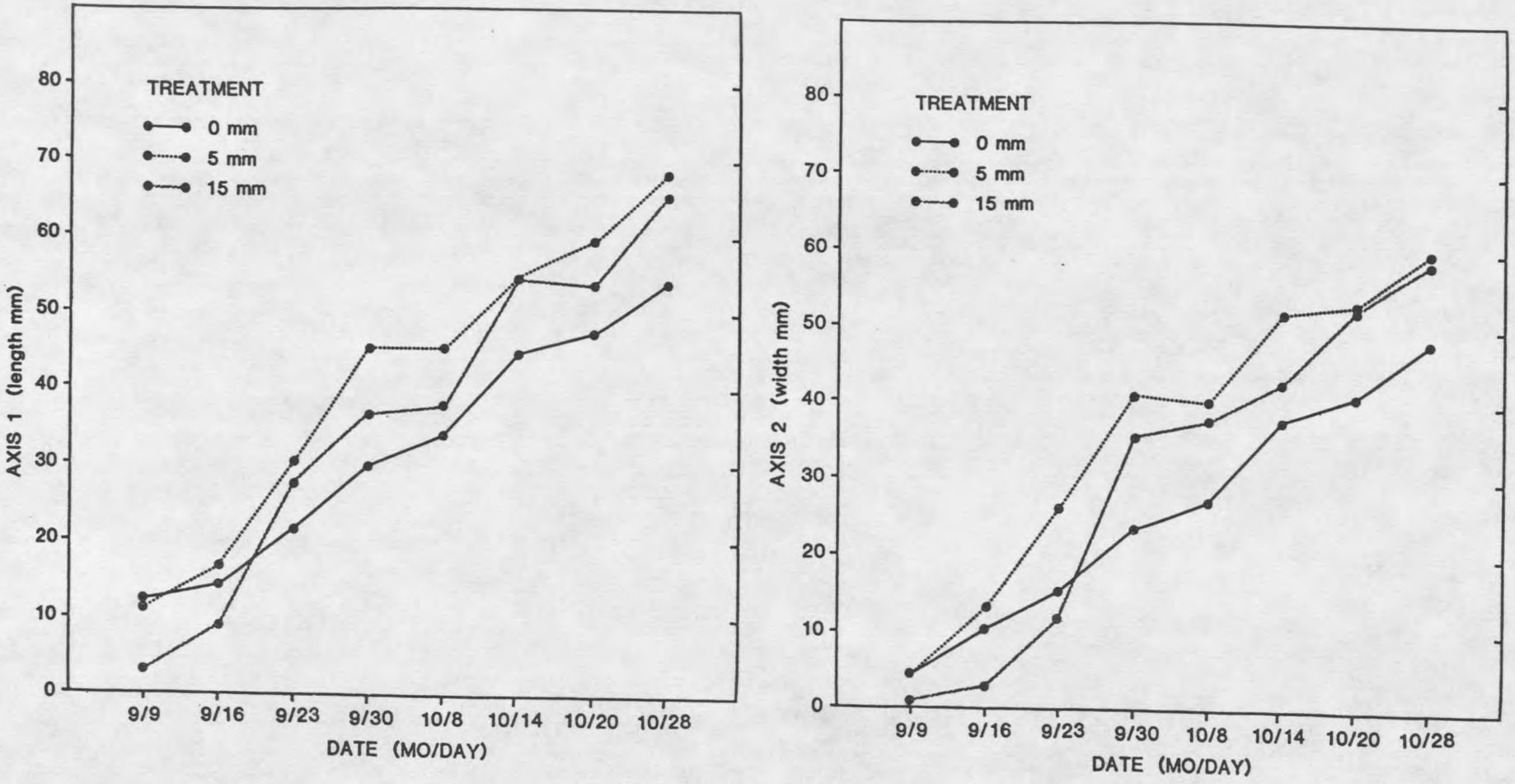


Figure 31. Growth parameters in thee greenhouse as affected by depth of seed burial. Horizontal growth of seedlings by length and width are presented.

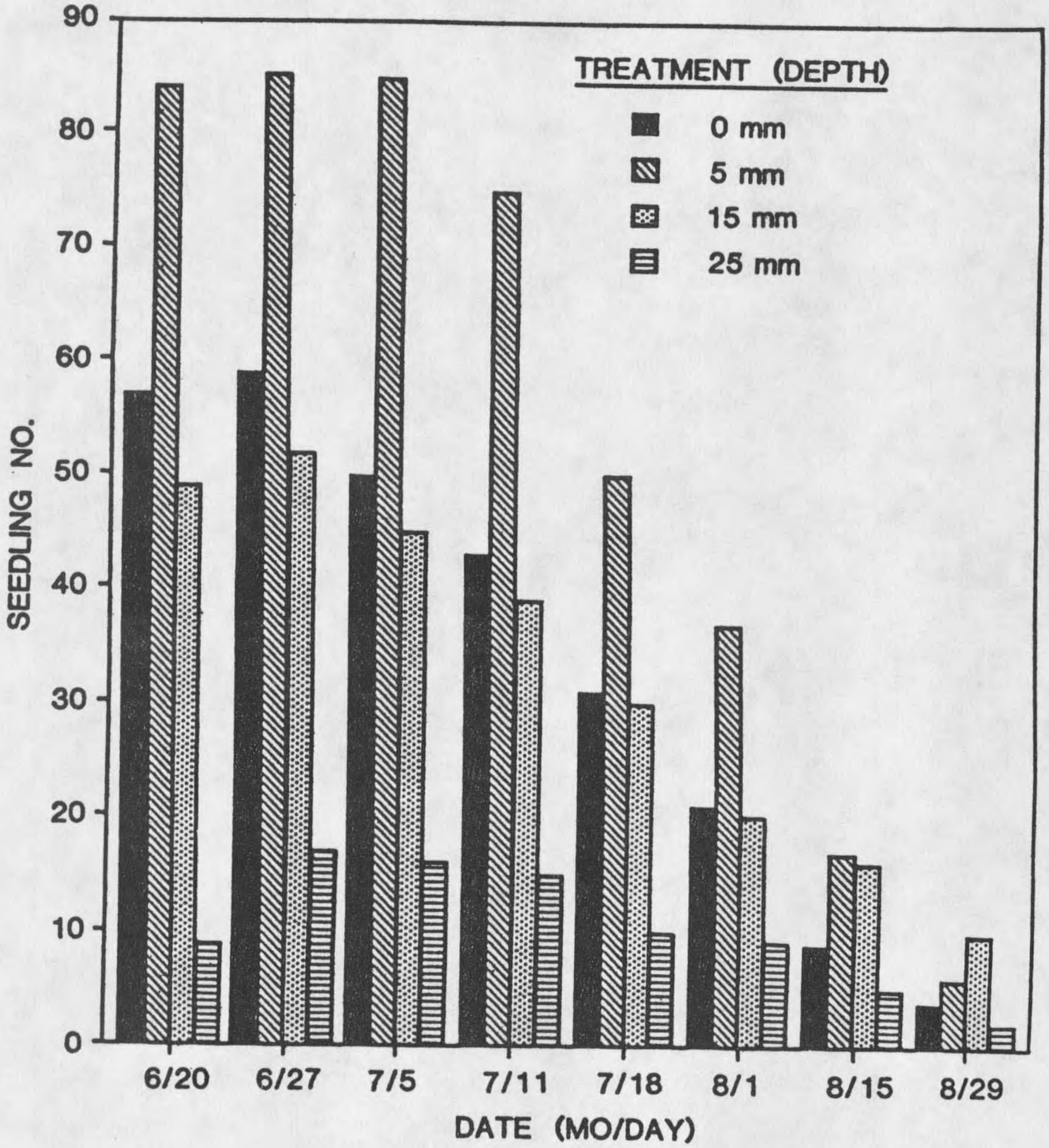


Figure 32. Seedling numbers present throughout summer of 1983 after emerging from four planting depths (0, 5, 15, 25 mm).

throughout the study period except on the last two recording dates. The number of seedlings that survived from 1.5 cm was significantly higher (60% greater) than those surviving from the soil surface on the last date. Emergence from 2.5 cm was noted, but was significantly lower than any of the other depths. Emergence from this depth was 12 to 20% of the emergence from the other depths. After the first of July, seedling mortality was considerable. In addition, significant differences in mortality rates were observed among the various treatment depths. In general, greater mortality was observed where there was the largest number of seedlings. The greatest seedling mortality occurred with plants that emerged from 0.5 cm, and the second highest mortality was observed on plants that were seeded on the surface. Seedlings that emerged from the two deepest depths had lower mortality rates.

Distinct differences in seedling growth were measured in response to seeding depth, but the calculated variance among observations was so high that statistical significance could not be established. However, identifiable response patterns could be discerned. Growth, except for height, responded more under a watering treatment. Planting depth also played a role in growth patterns with burial being slightly favored. These relationships were still apparent when depth and water treatments were analyzed together.

Weekly water applications significantly influenced both emergence and survival of seedlings (Figure 33). Emergence was approximately twice as great in the watered sections as in the nonwatered sections. Survival was also enhanced under the water treatment. Whereas only 2.6

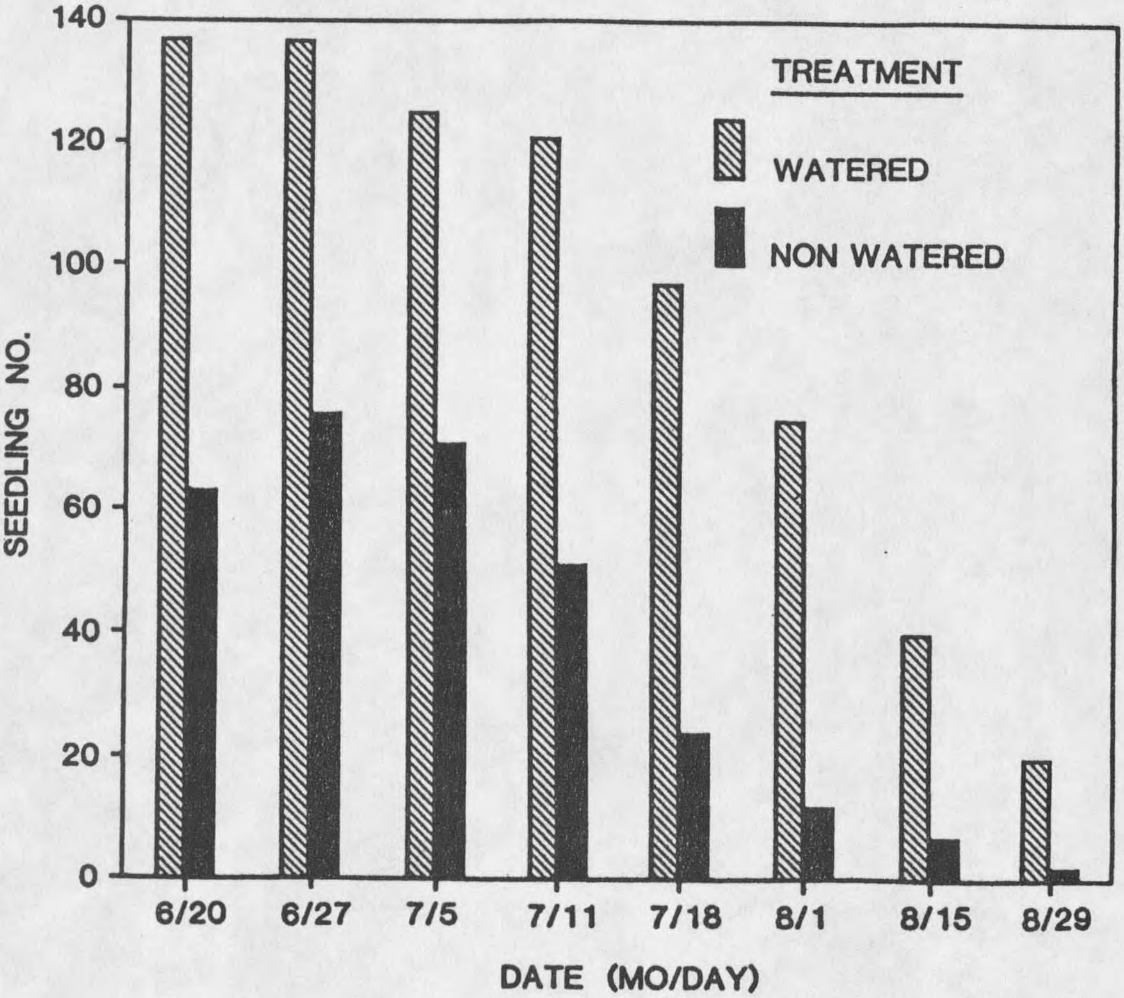


Figure 33. Numbers of seedlings present throughout the summer of 1983 after receiving one inch of water per week or no additional water.

percent of the seedlings survived the summer in the nonwatered treatment, 14.6% made it through the season with additional water.

Supplementary water affected growth characteristics of seedlings in that watered plants became somewhat larger than those grown under ambient conditions (Figure 34). However, differences were small and no statistically significant relationships were found within any of the growth parameters that were measured. Except for seedling height, watered plants were always larger than those that received no additional water. The height of nonwatered plants was less than watered plants for the first four weeks although this relationship reversed itself later. Numbers of leaves and the two horizontal axes were greater on all dates for watered plants.

Analysis of results of planting depth treatments showed that there was generally more growth in seedlings that grew from buried seed than from seed planted on the soil surface (Figure 35). However, only limited growth was observed in any treatment over the summer. The greatest seedling growth occured at planting depths of 0.5 and 2.5 cm.

No significant differences in seedling growth were detected when water and depth treatments were evaluated concomitantly. However, these findings were complicated by total mortality for 0 and 2.5 cm seedlings that were not watered. In general, those seedlings that originated from the 0.5 and 2.5 cm planting depths had the highest relative growth and seedlings that originated at the surface had the lowest (Figures 36, 37). Here too, only limited growth was observed in

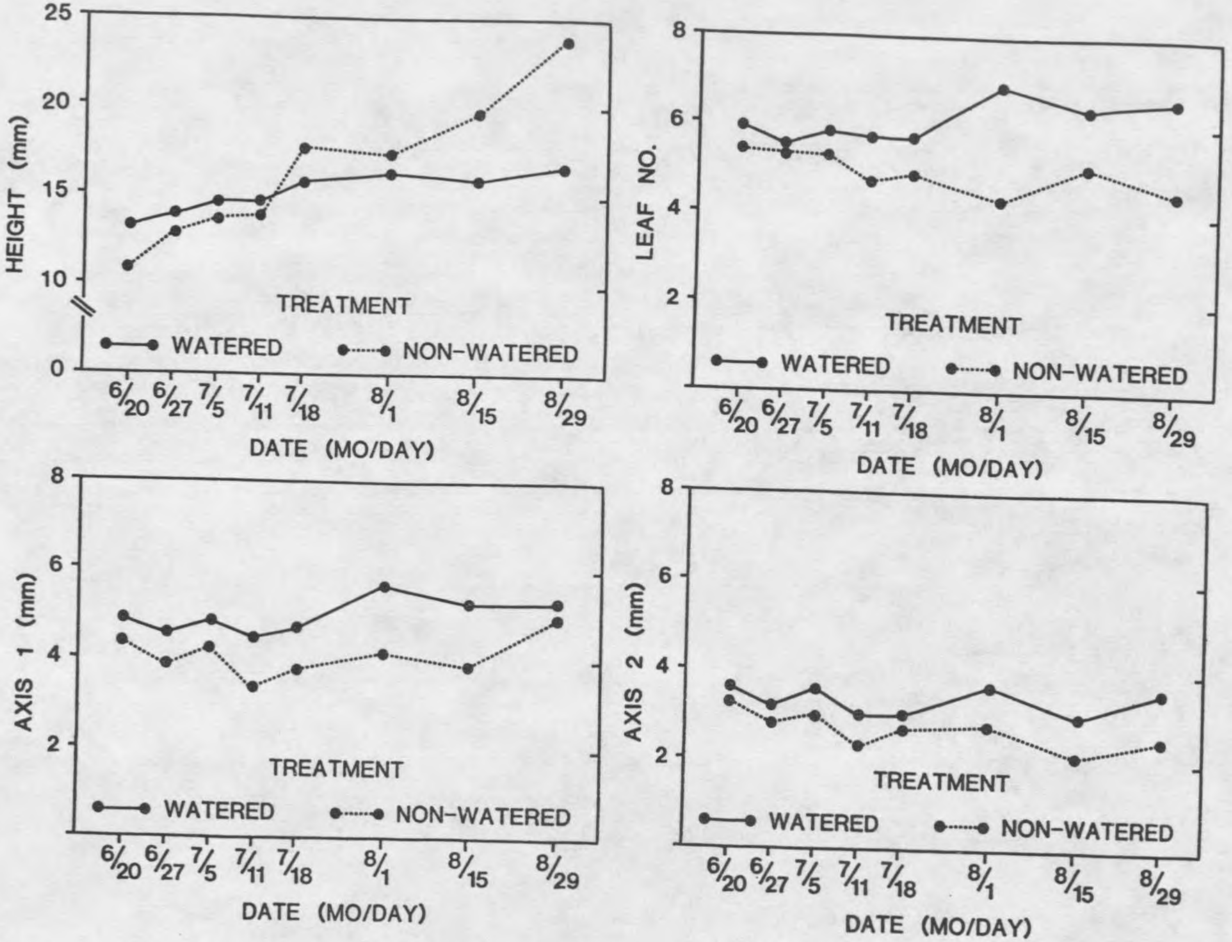


Figure 34. Four growth parameters of seedlings under field conditions. Graphs present relationships of seedlings receiving one inch of water per week or not.

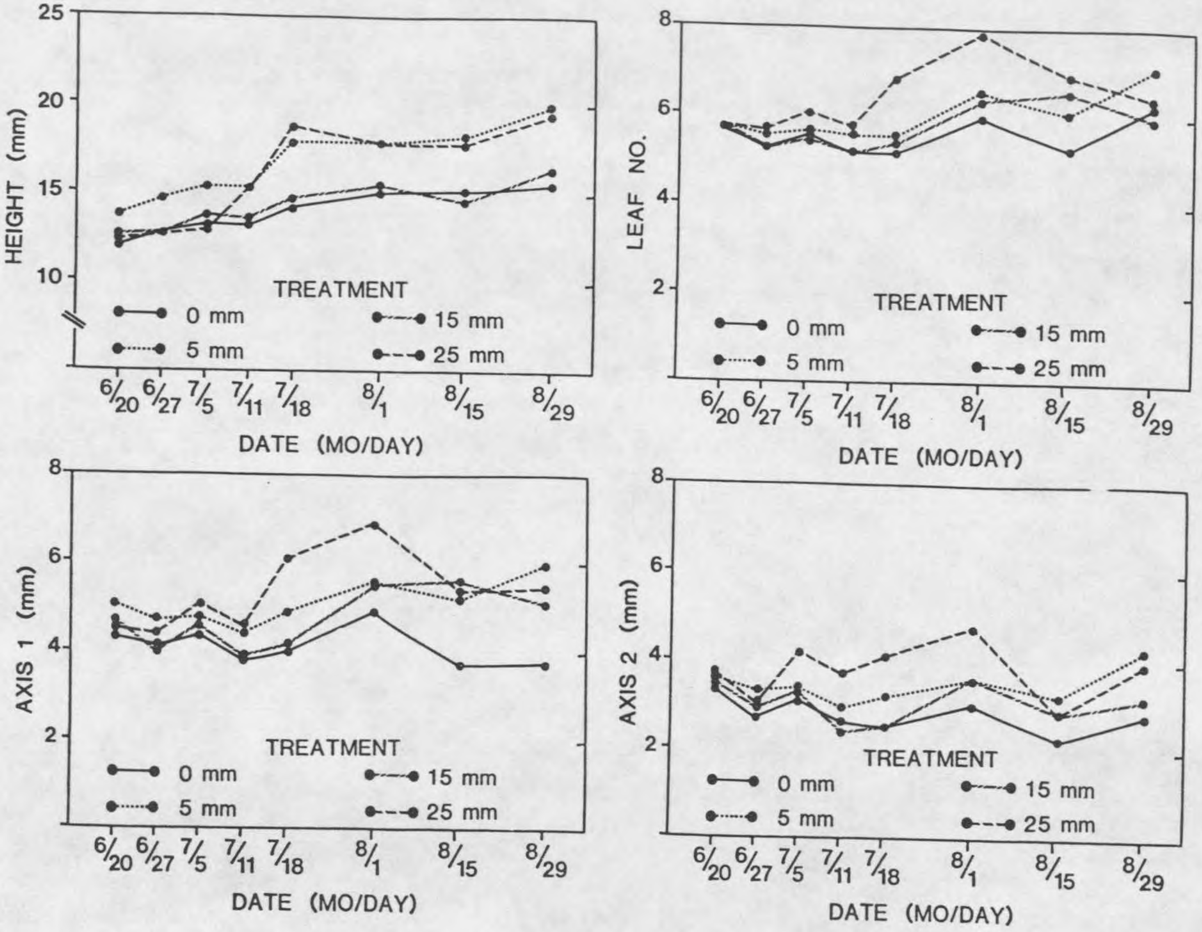


Figure 35. Four growth parameters of seedlings under field conditions. Graphs present relationships of seedlings planted at four depths.

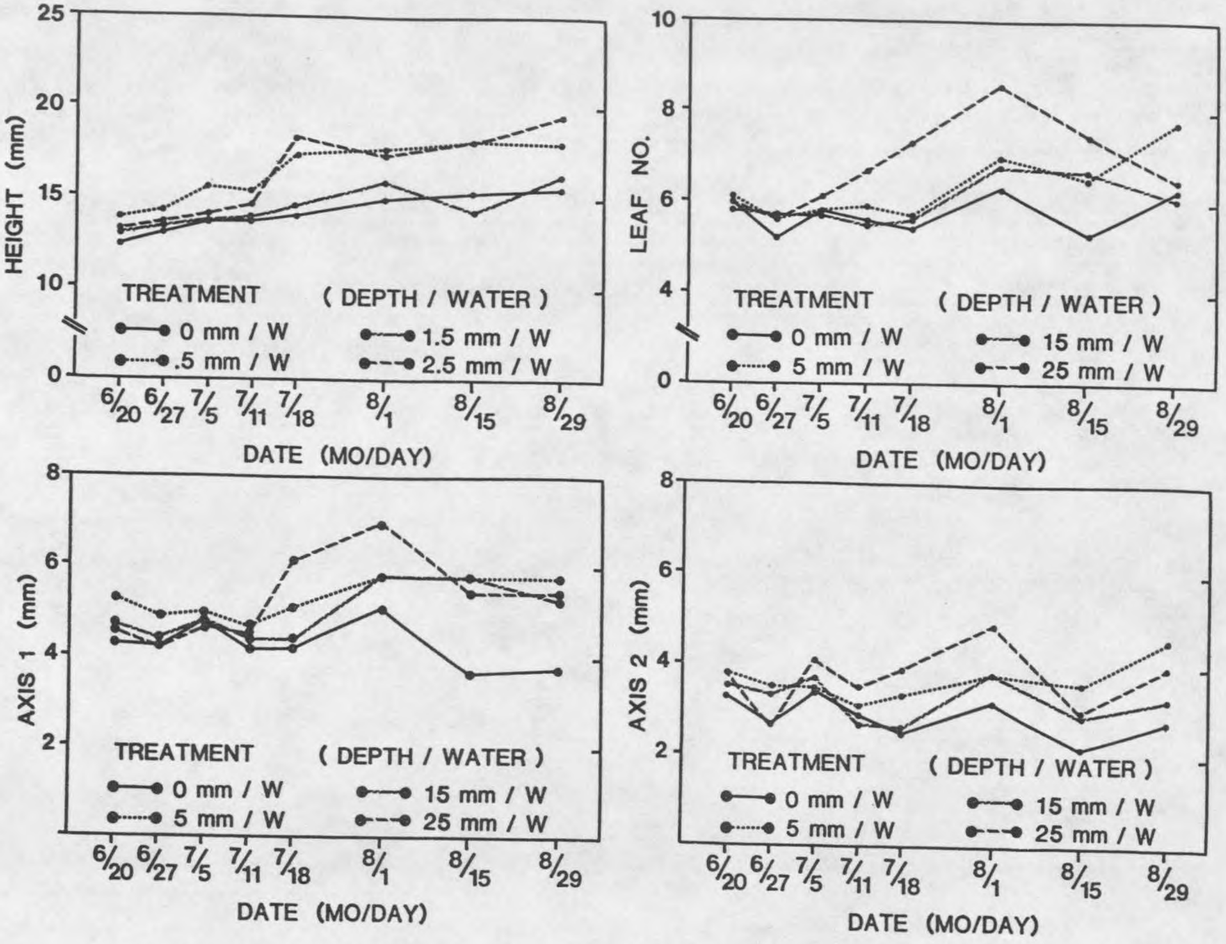


Figure 36. Four growth parameters of seedlings under field conditions. Graphs present relationships of seedlings planted at four depths and receiving one inch of water per week.

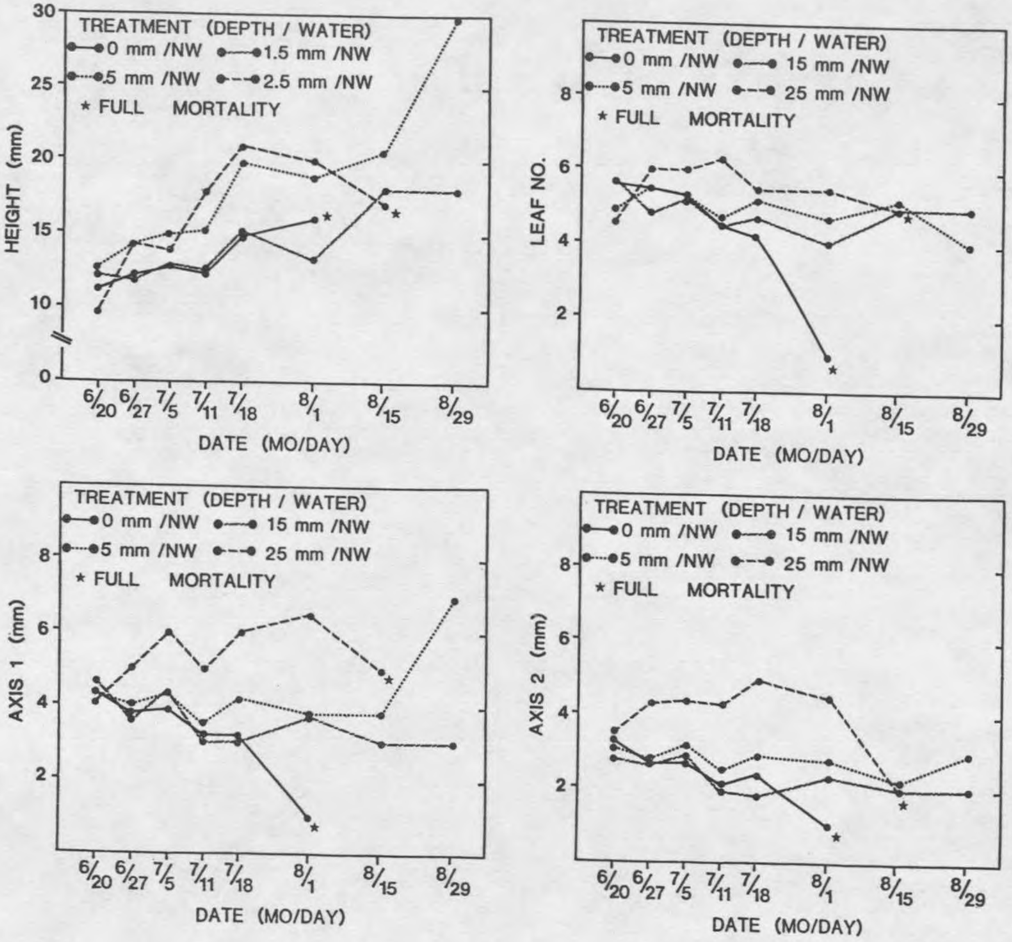


Figure 37. Four growth parameters of seedlings under field conditions. Graphs present relationships of seedlings planted at four depths and receiving no added water.

any treatment over the summer. Measurements for the nonwatered seedlings tended to be more widely spaced than those for the watered seedlings.

The environment immediately surrounding a seed determines whether it receives the conditions, resources and stimuli needed for germination (Harper 1977). This environment also plays a key role in determining if the seedling will survive and prosper. In this study, a more favorable field environment was present for buried seed. Additional water should have improved the environment for emergence and survival. However, the effect of burial and additional water on growth parameters was not always easily determined. This can perhaps be attributed to a moderate drought that occured during the study period. Below average precipitation and abnormally high temperatures were characteristic of the 1983 growing season (see Appendix A), and this apparently resulted in an inhibition of growth in all seedlings. As a consequence, seedling responses in the growth chambers and greenhouse phases of this study could not be directly related to field responses. High mortality of field seedlings also made analysis of growth characteristics difficult.

When seed from the parent plant is buried, it is in a more advantageous environment unless buried too deep. The small size of plains silver sagebrush seed limits the depth to which it can be buried. It was likely that those seeds emerging from 2.5 cm were slightly larger and therefore had sufficient food reserves to reach the surface, while smaller ones were incapable of this response. The same properties were undoubtedly present in those seedlings emerging from the 1.5 cm depth. The seedlings that emerged from these greater depths had much lower mortality rates. This may indicate that these plants established deeper and more extensive root systems that were able to take advantage of favorable moisture conditions.

Although seedlings at the surface and at shallow depths were able to take advantage of earlier, more opportune moisture conditions, they soon lost this advantage as drought conditions were encountered. As the season progressed, their shallower and less developed root systems would be more susceptable to drought than those of deeper rooted seedlings. This was evidenced by both the higher mortality rates in seedlings from the two shallower depths and the effect of added water on emergence and survival (Figures 32, 33).

Sagebrush communities typically have very few seeds germinating in the field despite a large seed production each year (Evernari et al. 1971, Hazlett and Hoffman 1975, Cook 1980, Harvey 1981). Contributing factors to this phenomena include: soil matric potential and its effect on wetted contact between seed and soil (Collis-George 1966), early death of seedlings (Eddleman 1979), seasonal climatic conditions and plant age (Nosova 1973, Evans and Young 1982), soil moisture relationships and litter (Beetle 1960). All these factors affected outcomes in this experiment. However, moisture conditions, as manifested by climatic conditions (especially drought), seemed to be the major influence on seedling success.

Sprouting and Seedling Establishment

Two studies were conducted to evaluate the sprouting nature of plains silver sagebrush. The degree to which the shrub relies more on vegetative reproduction than seedling establishment was evident in both the transect study and the isolated plant excavations.

Transect Excavations

Differences between numbers of sprouts and individuals arising from seedlings were evident in all six study areas and the five transects within each site. Measurements of above and belowground vegetative parts revealed differences in ages, biomass and horizontal space occupied. It was apparent that an elaborate subsurface rhizome system exists that is commonly older than aboveground shoots and stems. Plants that originated from vegetative sprouts outnumbered individuals originating from seed. Distinctions could not be made for site or disturbance influence on ratios of sprouts to seedlings within communities.

Plants were separated into two categories based on a determination as to whether the plant originated from a seed or was a sprout originating from an established plant. Plants found without connections to another plant were considered as originating from a seed. This first group included some plants with aboveground material that had originated from older plants that had been topkilled. The second category included two distinct groups based on morphology of the rhizome system. This category included those plants that were a series of sprouts along a single rhizome that usually terminated with a stump that was dead or decadent. The second group included those plants that had a definite rhizome connection to a healthy parent plant. In most cases a series of sprouts or a single plant was usually connected by a rhizome to another lateral rhizome from a large, established parent plant. Graphic examples of the three cases described above are displayed in Figures 38, 39 and 40. Figure 38 demonstrates how a seedling generally appeared. Figure 39 shows an example of a series of sprouts originating from an older stump or plant. Finally, Figure 40 exhibits how a single sprout could be attached to a lateral rhizome from a parent plant.

There were significant ($p < .05$) age differences between above and belowground vegetative organs. Ages of plant stems, taproots and rhizomes are summarized in Table 4. Aboveground stems were 3 to 5 years younger than taproots and associated rhizomes. Parent rhizomes with directly connected sprouts were clearly the oldest. However, taproots and rhizomes without directly connecting rhizomes to a parent plant were not significantly different from one another.

Lateral extension of rhizomes and rhizome systems was great in comparison to aboveground heights (Table 5). Aboveground size and age correlated well and this relationship was an appropriate criteria for selecting plants for this study. Deviation from the general pattern was due to inclusion of all stems along the rhizome system, not just the individual plants that were marked for study. Rhizome length was about 2 1/2 times that of plant height when sprouts were connected to parent plants. Lateral spread of the rhizome system was approximately

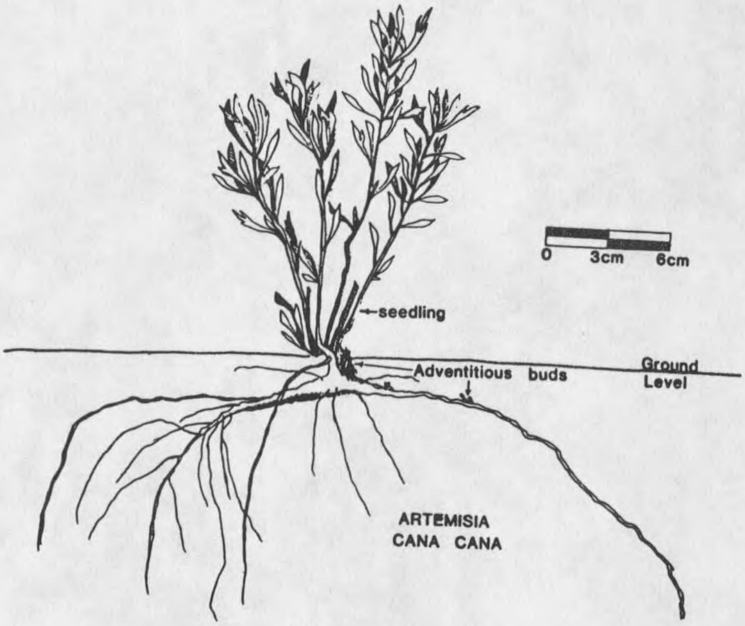


Figure 38. Graphic example of an excavated seedling. Demonstration of common appearance of a seedling.

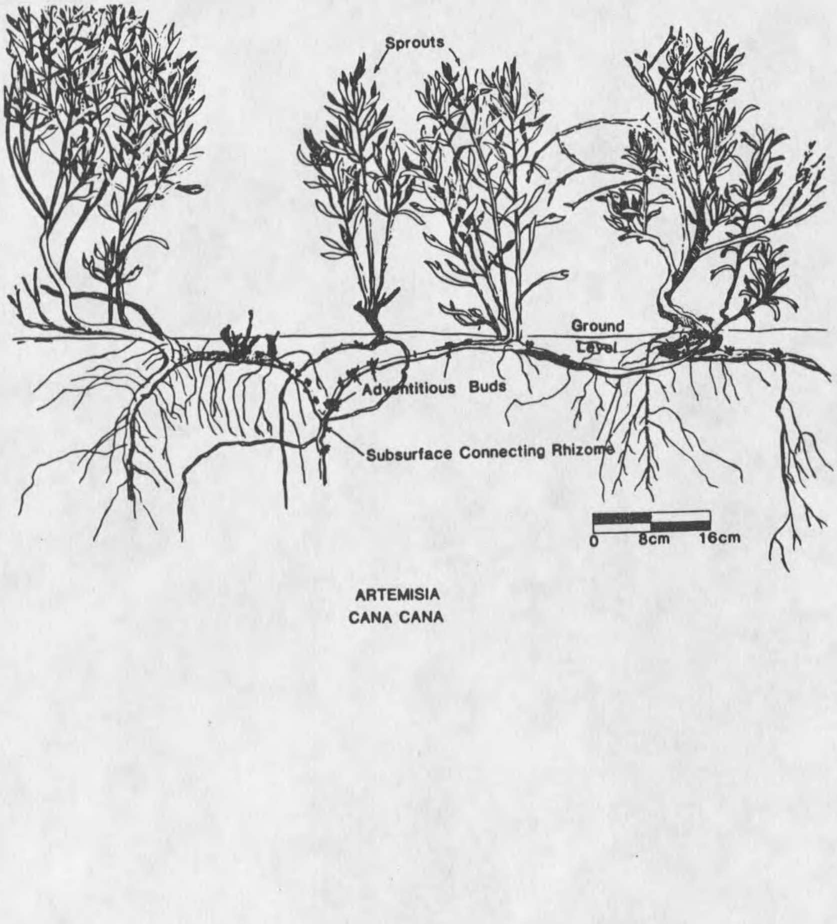


Figure 39. Graphic example of excavated sprout connected to a parent plant. Demonstration of common appearance of a rhizome system with associated sprouts in a series. Original or oldest material is on far right.

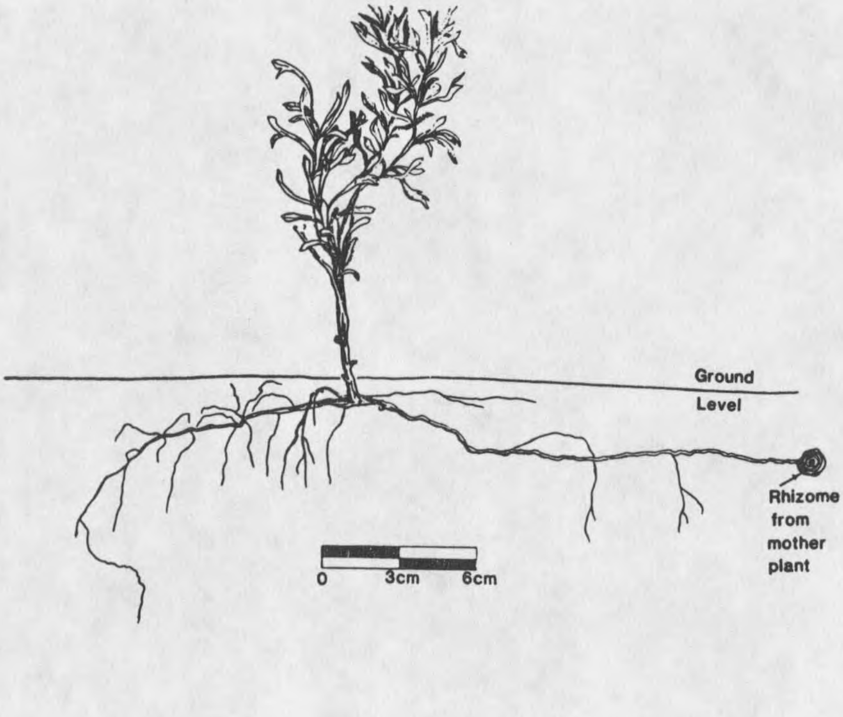


Figure 40. Graphic example of an excavated sprout connected to a parent plant. Demonstration of common appearance of a sprout connected to a parent plant by way of a rhizome from that plant.

Table 4. Age relationships of above and belowground parts of plains silver sagebrush. Sizes of stems and rhizomes are summarized in Table 5.

Plant part measured	Average age(years)	Standard deviation	Number of samples[2]
Stems	3.4^{a}[1]	1.97	204
Taproots	6.9^{b}	3.1	28
Parent rhizome or stump[3]	8.8^{c}	3.7	68
Rhizome system[4]	6.0^{b}	2.5	128

[1] Significant mean differences are denoted when followed by different letters ($p<.05$).

[2] Sample numbers varied due to a variety of situations present in individual excavations.

[3] Rhizome originating from a parent plant (or dead stump) to which sprout was directly connected.

[4] Rhizome sections other than those defined in 3 above.

Table 5. Growth relationships of above and belowground parts of plains silver sagebrush.

Measurement description	Mean (cm)	Range (cm)	Number of samples[2]
Plant (sprout) height	32^{a}[1]	11-59	155
Lateral distance to parent connection[3]	78^{b}	14-277	61
Lateral spread of rhizome system[4]	105^{c}	11-369	90

[1] Significant mean differences are denoted when followed by different letters ($p<.05$).

[2] Sample numbers varied due to a variety of situations present in individual excavations.

[3] Lateral distance from parent plant or rhizome to nearest sprout on rhizome system expressed as a mean of all plants with this growth habit.

[4] Total lateral extent of all rhizomes in an excavation expressed as a mean of all plants with rhizome systems.

3 1/2 times that of plant height. Considerable variation existed in both measurements. The maximum measurements for both instances were 277 cm and 369 cm, respectively. The minimum measurements were 14 cm and 11 cm, respectively. Total lateral spread of rhizomes usually exceeded the distance of a sprout to a connecting rhizome. However, in some cases this distance was similar. Daughter plants were, in general, located considerable distances from parent plants or rhizomes.

The relative frequencies of occurance for distances encountered from parent plants or rhizomes to daughter plants are summarized in Table 6. The largest proportion (59 percent) of rhizomatous connections between parent and daughter plants were from 50 to 100 cm in distance. The second highest proportion (20 percent) was in those rhizome connections between 0 and 50 cm, with the 100-150 cm category being close to this with 15 percent.

Plants arising from rhizomes were more abundant than those that grew from seedlings (Table 7). Approximately 63 percent of the excavated plants were connected by rhizomes to an established plant or rhizome system. About 37 percent were individuals with no connections to any other plant or rhizome. Statistical analysis confirmed that this difference was significant (p< .025). However, one of the six sites, Lignite Creek, showed an opposite trend. The presence of extremely clayey and extensive gravelly soils in the study area might explain the preponderance of nonconnected individuals. Water relationships would be more unfavorable in both soil conditions. Therefore, taprooting plants might have an advantage in these

Table 6. Frequency of occurance for distances encountered from parent plants or rhizomes to daughter plants of plains silver sagebrush.

Distance to parent (cm)	Study sites 1	2	3	4	5	6[1]	Total category numbers
0-50	-	2	4	2	3	1	12
50-100	7	3	8	7	4	7	36
100-150	-	1	2	1	3	2	9
150-200	2	-	1	-	-	-	3
200+	-	-	-	1	-	-	1
Totals	9	6	15	11	10	10	61[2]

[1] Site numbers correspond to names as follows: 1-Lower Flood, 2-Lignite Creek, 3-Paddy Faye, 4-Lower Black Springs, 5-Moon Creek, 6-Yellowstone River pastures.

[2] This number does not include plants with rhizome systems that originated from a dead stump and was included in a series of sprouts and rhizomes.

Table 7. Plant excavation results. Summarization of numbers of individual plants in each study site falling in one of two categories: having rhizomatous connections or not[1].

Category	Study site[2] 1	2	3	4	5	6	Category totals
Rhizomatous[3]	7	15	13	13	14	13	75[a]
Nonrhizomatous	13	5	7	7	6	7	45[b]

[1] Significance was tested ($p<.025$) between categories with Students t-tests. All sites showed significant differences.

[2] Study sites correspond to names as follows: 1-Lignite Creek, 2-Lower Flood, 3-Paddy Faye, 4-Lower Black Springs, 5-Moon Creek, 6-Yellowstone River pastures. Lower Flood, Lower Black Springs and the Yellowstone River pastures were considered disturbed. The others were not.

[3] Rhizomatous plants included all individuals having rhizome systems either from healthy parents or well-defined rhizomes and those that were members of a series of sprouts usually originating from dead stumps.

circumstances in reaching deeper, more favorable conditions, over more shallow, rhizomatous individuals. Significant differences ($p < .05$) were not found among sites according to Chi-square analysis. All sites, except Lignite Creek, had about equal proportions of connected sprouts and separate plants. The Lignite Creek data accounted for ninety percent of the variability among sites. Comparison of the three disturbed sites with the three undisturbed sites revealed no significant differences ($p < .05$).

Several factors might explain why vegetative reproduction was common in these silver sagebrush communities. Evolution plays a key role in understanding why a particular plant or community reacts to external forces as they do (Cook 1983). Benefits of vegetative reproduction include: (1) an enhanced ability to utilize unevenly distributed resources, and (2) an increased competitive ability to invade other areas. In addition, sprouts are better able to resist invasion of other seedlings while reducing the probability of genet extinction. This is accomplished by spreading the risk among many genetically identical individuals. An evolutionary strategy such as this is therefore consistent with the findings of Abrahamson (1980), who reported that increased environmental severity generally shifted emphasis to vegetative reproduction.

The sprouting nature of silver sagebrush may be indicative of the habitat in which it is encountered. Being located predominantly on flood plains and bottomlands, the plant is continually under the influence of disturbances such as deposition from flooding and ice scraping in winter. Fire may also have played a role in the evolution of the taxon's resprouting characteristics. Plant production is generally higher in the bottomlands, both in herbaceous and woody growth, and this would presumably contribute to higher fuel loads for natural and man-induced fires. Consequently, fire would be more intense and more prone to carry in such ecosystems. Silver sagebrush is a vigorous sprouter and this is most likely the result of the evolutionary influences of recurring cyclic or periodic disturbances.

Utilization of limited resources through lateral extension of rhizomes would appear to be a competitive advantage over establishment by seeds. More abundant herbaceous vegetation in the mesic environments of floodplains produces greater competition for sagebrush seedlings. Vegetative sprouts may compensate for this disadvantage by more rapid morphological development. Sprouts are associated with a larger, more available nutrient and carbohydrate reserves from established roots and shoots, thus increasing life expectancy of the genet (Abrahamson 1980). Although not rare in the communities studied, seedling establishment was found in only one third of the plants that were excavated. This relatively low occurance is perhaps attributable to disadvantages associated with germination requirements, seedling emergence and survival, and subsequent competition from established plants. Whereas seedlings must draw upon their own resources, sprouts proliferate by utilizing established shoot and root resources.

Environmental factors, especially drought, might best explain differences in ratios of sprouts and seedlings. Eastern Montana is under the constant embrace of drought cycles. For example, a three year drought extending from 1979 through 1981 preceded the wet year of

1982. This latest drought coincided with the ages of the majority of the plants picked for this study (mean of 3.4 years). The relatively moist year preceding this drought of 1979-1981 and the wet year of 1982 was apparently the source for most of the nonconnected individuals. Sprouts were, in general, on either side of the spectrum, especially the older individuals. This particular drought was probably the greatest influence on whether a sprout or seedling was observed. There does seem to be a stratification in silver sagebrush communities and is in relation to occurance of wet years and dry years, with seedlings being favored in wet years.

The relatively cool growing season of 1982 was associated with relatively high precipitation. Numerous seedlings and a few sprouts were produced in this year. The dry, warm growing season of 1983 produced few seedlings and an abundance of sprouts. It was observed that few seedlings from 1982 survived the second season. It would therefore appear that the mode as well as the success of reproduction is strongly related to climatic regime. These general observations, combined with this shrub's ability to sprout under stress, suggest that drought conditions might produce sufficient stress to favor vegetative reproduction. This overriding importance of drought stress on reproductive strategy might also explain why differences could not be found between and within disturbed and undisturbed study sites.

Isolated Plant Excavations

The extensive sprouting nature of plains silver sagebrush was readily apparent after complete excavations had been completed on the areas surrounding two large, isolated plants. In addition, it became clear that most roots consisted of a shallow, underground network of rhizomes. Maps of the excavations established that plains silver sagebrush possesses a highly complex root system (Figures 41, 42) that may include several smaller, independent systems (Figure 43).

Root excavations revealed that older well-established plants consisted of not one, but an aggregate of several individual systems or plants (Figures 41, 42). There was considerable diversity in degree of rhizome system complexity. Individual clones had as many as 52 sprouts and as few as one (Figure 43). No evidence was found to indicate that all individual clones were of the same genet. That is, no common root connections could be traced. However, this does not exclude the possibility that they might have been connected and later separated after death of connective rhizomes.

Excavations established that rhizomes can extend and sprout at least three meters away from the parent plant. Therefore, a large number of progeny can potentially arise from one genetic individual. A dendritic pattern was characteristic of this type of horizontal rhizome expansion, with size classes decreasing in general concentric circles away from the main canopy. That is, sprouts decreased in size as distance from the plant increased.

One of the factors that might help explain distribution patterns in field populations of plains silver sagebrush would involve utilization of soil moisture and nutrients. Allelopathy might also play a role. A spatial relationship is frequently identifiable in which rhizomes will grow into areas that are not already occupied by

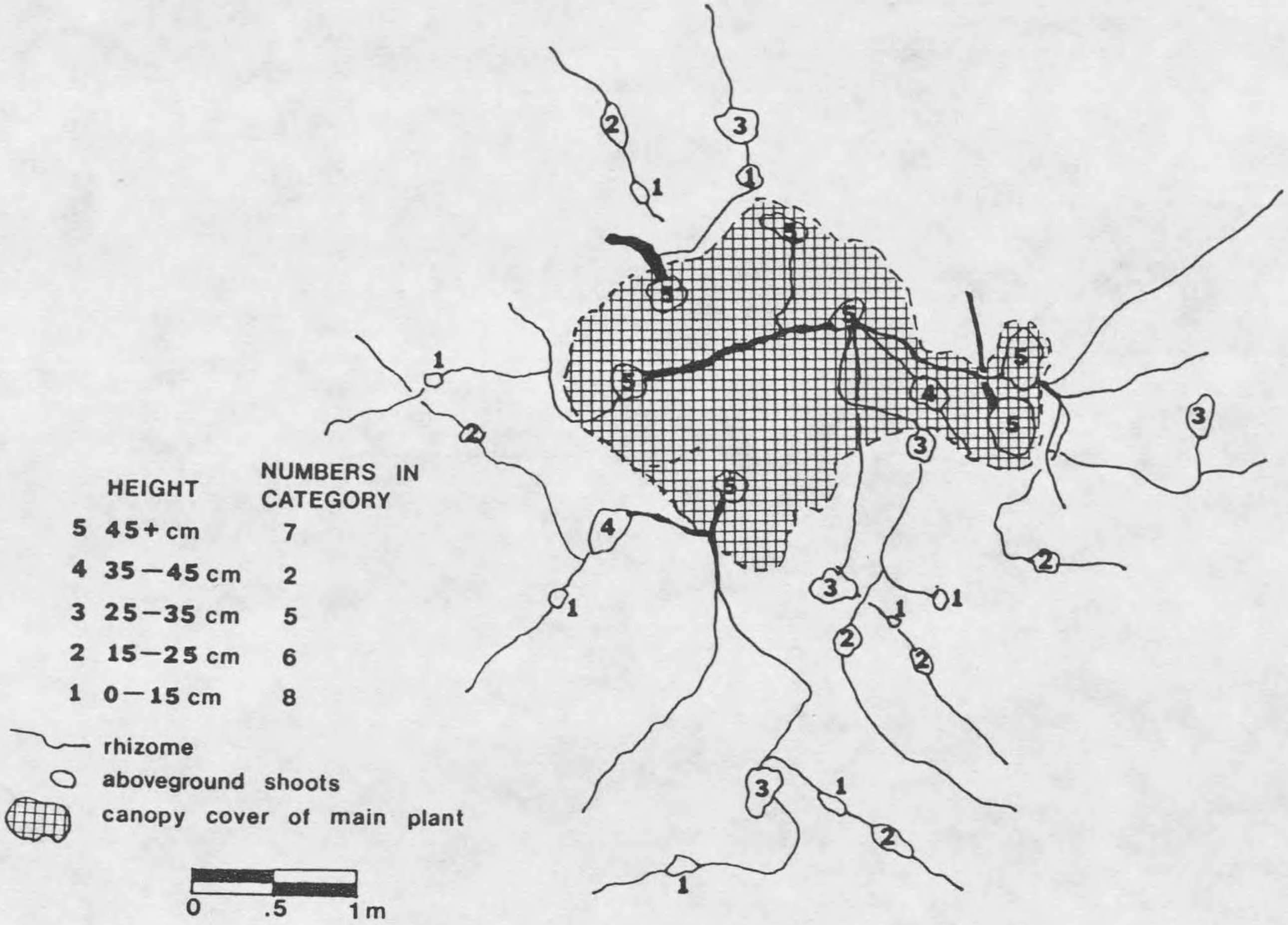


Figure 41. Map of first large, isolated plant excavation. All aboveground shoots are shown individually and numbered according to stature. Rhizomes are shown as lines with thickness relative to size.

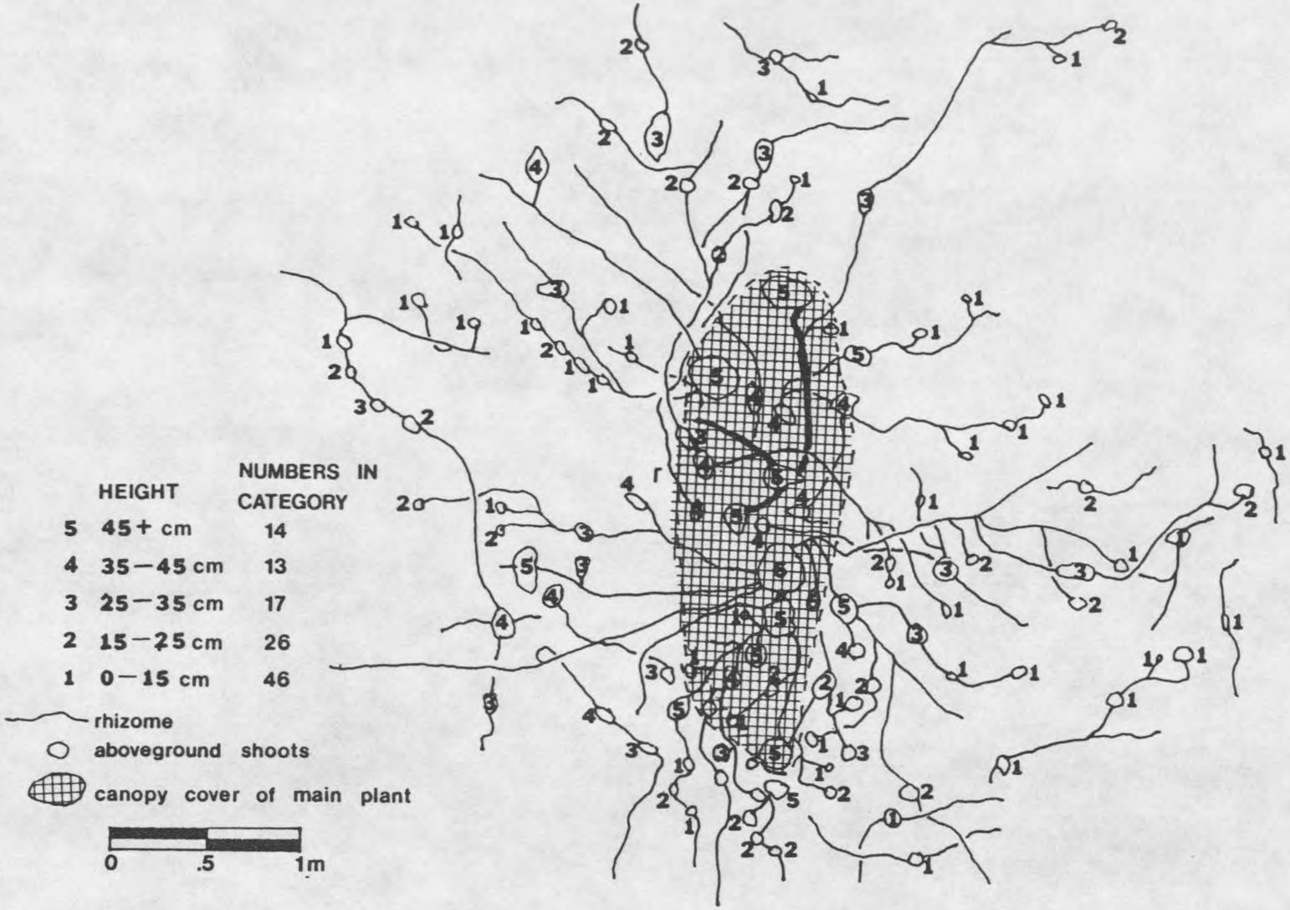


Figure 42. Map of second large, isolated plant excavation. All aboveground shoots are shown individually and numbered according to stature. Rhizomes are shown as lines with thickness relative to size.

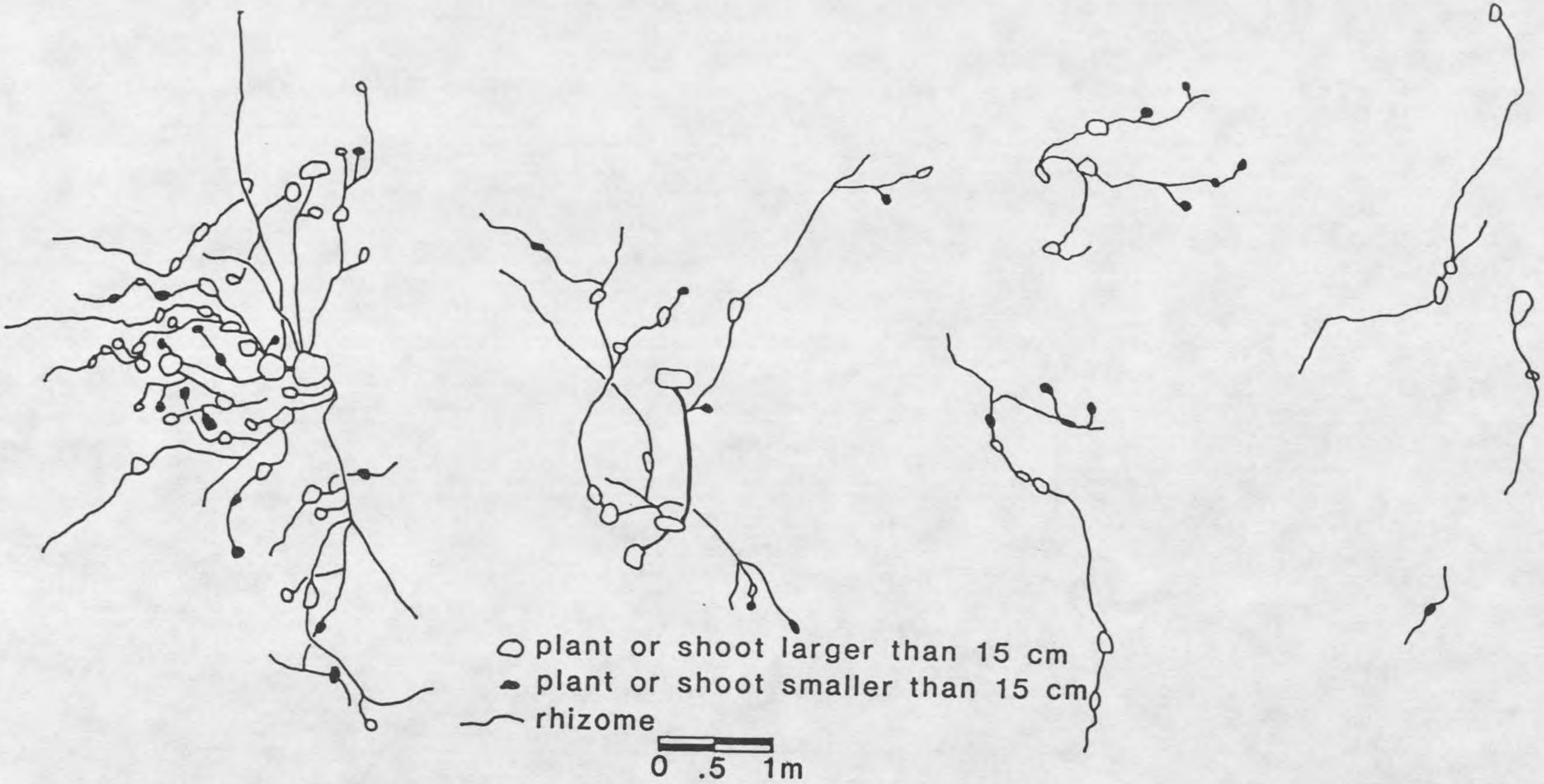


Figure 43. Example of degrees of complexity in rhizome systems. This example was obtained from a separation of excavation mapped and presented in Figure 42.

other sagebrush plants. Limited nutrients and soil moisture exert a dominant impact on a plants ability to survive and prosper. Abrahamson (1980) predicts that when population density is low in clonal type plants, vegetative reproduction would be more advantageous, thereby enhancing genet spread and occupation. Such a situation exists in many plains silver sagebrush communities where sparse plant populations are common.

Competition for available resources seems to be the major influence on determining where a plant can become established (Noble et al. 1979, Cook 1983). In communities where competition for resources is great, clonal establishment might be at an advantage when expanding a plant's area of establishment. This is largely due to the ability to draw upon nutrients and reserves from established roots and shoots. Spatial arrangements in plains silver sagebrush communities can be mostly explained by competitive stress that limits densities in any one area and influence where a rhizome can grow.

Allelopathy is a feature in sagebrush communities that could perhaps play a role in determining spatial patterns. Leachates from leaf material would probably not affect rhizome formation and growth, because rhizomes are generally located in the 8 to 30 cm zone. Studies have shown that certain hydrophilic metabolites exuded from rhizomes can permeate the immediately surrounding soil (Numata et al. 1975, Hale 1982, Melkania et al. 1982), thus influencing nearby development either by seedlings or rhizomes. However, no such findings are reported for plains silver sagebrush.

SUMMARY

This study was designed to gain a better appreciation of plant population dynamics. Specifically, it investigated reproductive characteristics and mechanisms important in plains silver sagebrush. In particular, studies examined: (1) seed dispersal from individual plants and among sites, (2) factors affecting germination, (3) emergence, growth and survival of seedlings under controlled and field conditions, and (4) whether the primary origin of individual plants was from seed or vegetative sprouts.

Wind appears to be the most influential factor in the dispersal of achenes from plains silver sagebrush plants. A definite three-directional distribution of dispersed seed was found. The largest proportion of seed was dispersed in line with the prevailing northwest wind, but secondary areas of seed deposition were also found at 120 degrees on either side of the primary one. The mechanism for this type of distribution is basically unexplained. Dispersal in these secondary directions was, at times, more prevalent depending on date and associated winds (or storms). Most seed was dispersed close to, or under, the shrub. However, in at least one case the largest proportion of seed was dispersed at three meters. In this instance, seed was evenly dispersed from the plant out to three meters, and there was no steady decrease of dispersed seed, until the three meters distance was reached. Seed numbers then dropped off sharply.

There were no major differences in dispersal patterns among the three study sites, but plant phenology seemed to be variable so that the majority of seed fell at different times depending on site. At one site, dispersal was evenly distributed throughout the study period due to differences in phenological development.

Plains silver sagebrush seed can germinate under a variety of environmental conditions, but certain situations did favor higher germination percentages. Stratification had no effect on germination success, probably due to seed not being dormant and therefore not requiring the dormancy breaking cold treatment. Possibly some stratification was inherently present because of cold temperatures during the late fall and early winter when seeds were collected from the field. Date of seed collection, light and dark regime, temperature and water stress had important influences on germination success, but sagebrush seeds were not noted to have specific germination requirements.

Higher germination percentages were observed in later seed collection periods. Seeds in complete dark germinated better than in light except when they were under no water stress. Temperatures of 20 C were generally most favorable for germination. However, on the last seed collection, seed germination at 10 C was not different than at 20 C. Rates of germination increased with higher temperatures. Germination percentages and rates dropped off steeply under the influence of more negative osmotic potentials. Light-affected seeds in the 10 C temperature regime showed favorable germination, but under dark conditions, 20 C became more important with slower rates than in light. Heterogeniety in the seed population was probably the most important variable explaining the results of this study on germination. As combinations of factors such as temperature, osmotic potential or light changed, this heterogeniety allowed seeds to germinate.

After seeds have germinated, the environment that the seedling is subjected to determines seedling success. Temperature was found to be important in the growth of seedlings. Higher temperatures that had adverse effects on germination were favored in seedling growth. This might be expected because higher temperatures are normally present in the later stages of the seedling growing season. Seedling response was enhanced by the addition of supplementary water. More seedlings emerged, and survived through the summer. Seeds that had been planted at 5 mm produced the most seedlings in the field (85), while those at the surface and at 15 mm produced about the same numbers (59 and 52 respectively). Mortality was greatest among seedlings emerging from 5 mm and the least for those emerging from 15 and 25 mm.

Seedling growth was relatively unaffected by additional water, but patterns could be discerned. Watered seedlings showed somewhat greater growth, especially from the 5 and 25 mm planting depths. Burial places the the seeds in a less severe environment in terms of temperatures and water stress. Despite the large numbers of seeds that were planted, very few seedlings emerged in the field (1.2 %), and of these only 11 percent survived the summer.

The degree to which plains silver sagebrush relies on vegetative reproduction was established by root excavations. Plains silver sagebrush in almost all cases showed some degree of rhizomatous growth even among small seedlings. However, most excavated individuals turned out to be sprouts from an already established plant. Ages of aboveground shoots were younger than any belowground roots or rhizomes, while the oldest plant segments were parent rhizomes to which individual plants were connected. Most growth was below ground and was represented by subsurface lateral extension of rhizomes and rhizome systems. On average, this lateral spread was 3 1/2 times that of the shoot height. The largest proportion of rhizomatous connections to parent plants or rhizomes were from 50 to 100 cm in distance. No differences could be found among sites or between disturbed or undisturbed sites. This was most likely due to drought conditions overriding any effect of disturbance as far as an influence on growth habits.

In excavations of large, isolated plants the large degree to which sprouts arise from rhizomes was evident. These "individual" plants were composed not of one, but an aggregate of clonal systems indicating a great potential for vegetative reproduction.

LITERATURE CITED

LITERATURE CITED

Abrahamson, W. G. 1980. Demography and vegetative reproduction. In: Demography and evolution in Plant Populations, ed. O. T. Solbrig, pp. 89-106. Oxford: Blackwell Scientific Publications.

Al-Ani, T.A., M.M. Al-Mufti, and F.M.R. Al-Cherchafchy. 1972. Germinability of some native range species of Iraq. In: First Scientific Conference, Scientific Research Foundation, General and Agricultural Sciences. Baghdad. pp.234-242.

Anderson, J.E., and K.E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangelands in southeastern Idaho. J. Range Manage. 34(1):25-29.

Ashmun, J.W., R.J. Thomas, and L.F. Pitelka. 1982. Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. Ann. Bot. 49:403-415.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.

Bartolome, J.W., and H.F. Heady. 1978. Ages of big sagebrush following brush control. J. Range Manage. 31(6):403-406.

Beetle, A.A. 1960. A study of sagebrush - section Tridentatae of Artemisia. Wyo. Agr. Exp. Sta. Bull. 368, 83p.

Beetle, A.A. 1965. A third subspecies in the Artemisia tridentata complex. Rhodora 67:405-406.

Beetle, A.A. 1977. Recognition of Artemisia subspecies - a necessity. In: Proceedings 6th annual Wyoming Shrub Ecology Workshop. pp.35-42.

Berkat, O., and D.D. Briske. 1981. A water potential comparison of three germination techniques utilizing polyethylene glycol 20000. Society of Range Management, 34th annual meeting, Tulsa, Okla. Abstract.

Bewley, J.D., and M. Black. 1982. Physiology and biochemistry of seeds in relation to germination. Vol.2. Springer-Verlag, Berlin Heidelberg New York. 375 p.

Bhadane, N.R., and F. Shafizadeh. 1975. Sesquiterpene lactones of sagebrush: the structure of artecanin. Phytochemistry 14:2651-2653.

Blaisdale, J.P., and W.F. Mueggler. 1956. Effect of 2,4-D on forbs and shrubs associated with big sagebrush. J. Range Manage. 9:38-40.

Bostock, S.J., and R.A. Benton. 1979. The reproductive strategies of five perennial Compositae. J. Ecol. 67:91-107.

Branson, F.A., and R.F. Miller. 1981. Effects of increased precipitation and grazing management on Northeastern Montana rangelands. J. Range Manage. 34(1):3-10.

Caldwell, M.M. 1978. Physiology of sagebrush. In: The Sagebrush Ecosystem: a symposium. Utah State Univ. Logan. pp. 74-85.

Chirca, E., and A. Fabian. 1973. Some allelopathic effects caused by Artemisia absinthium L. Contributii Botanica Universitatea Babes-Bolyai din Cluj. p. 267-276.

Clor, M.A., T.A. Al-Ani, and F. Charchafchy. 1974. Range resources of Iraq. 15. Germination, storage conditions and afterripening of the seeds of Artemisia herba-alba. Institute for App. Res. on Nat. Resources, Iraq. Tech. Bull. No.76. 19p.

Collis-George, N., and J.B. Hector. 1966. Germination of seeds as influenced by matric potential and by area of contact between seed and soil water. Aust. J. Soil Res. 4:145-164.

Cook, R.E. 1979. Asexual reproduction: a further consideration. Am. Nat. 113:769-772.

Cook, R.E. 1980. The biology of seeds in soil. In: O.T. Solbrig (ed.), Demography and the Dynamics of Plant Populations. Oxford: Blackwell Scientific Publications. pp. 107-127.

Cook, R.E. 1983. Clonal plant populations. Amer. Scientist 71(3):244-253.

Cornelius, D.R., and C.A. Graham. 1958. Sagebrush control with 2,4-D. J. Range Manage. 11:122-125.

Cunningham, H. 1971. Soil vegetation relationships of a bitterbrush-sagebrush association in Northeastern Colorado. M.S. Thesis. Colo. State Univ. 83p.

Daubenmire, R. 1975. Ecology of Artemisia tridentata subsp. tridentata in the state of Washington. Northwest Sci. 49:24-35.

Depuit, E.J., and M.M. Caldwell. 1973. Seasonal pattern of net photosynthesis of Artemisia tridentata. Amer. J. Bot. 60(5):426-435.

Dietz, D.R., R.H. Udall, and L.E. Yeager. 1962. Chemical composition and digestibility by mule deer of selected forage species, Cache la Poudre Range, Colorado. Colo. Game and Fish Dep. Tech. Pub. 14. 89p.

Donart, G.B., and C.W.Cook. 1970. Carbohydrate reserve content of mountain range plants following defoliation and regrowth. J. Range Manage. 23:15-19.

Dusek, G.L. 1975. Range relations of mule deer and cattle in prairie habitat. J. Wildl. Manage. 39(3):605-616.

Eddleman, L.E. 1979. Regeneration strategies of mixed-prairie plants. In: (J.R. Goodin and D.K. Northington, ed.) Arid lands plant resources: proceedings of the International Arid Lands Conference on Plant Resources, Texas Tech Univ.

Evans, R.A., and J.A. Young. 1982. Microhabitat variation in relation to weed seed germination and seedling emergence. In: Biometerology in integrated pest management. Academic Press. pp. 421-448.

Evenari, M.L., L. Shanan, and N. Tadmor. 1971. The Negev: the challenge of the desert. Harvard University Press, Cambridge, Mass.

Everett, R.L., R.O. Meeuwig, and R. Stevens. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. J. Range Manage. 31(1):70-73.

Everett, R.L., R.O. Meeuwig, and J.H. Robertson. 1978. Propagation of Nevada shrubs by stem cuttings. J. Range Manage. 31(6):426-429.

Ferguson, C.W. 1964. Annual Rings in Big Sagebrush. Univ. of Arizona Press, Tucson. 95p.

Fernandez, O.A., and M.M. Calwell. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. J. Ecol. 63:703-714.

Friedman, J., and G. Orshan. 1975. The distribution, emergence and survival of seedlings of Artemisia herba-alba Asso in the Negev Desert of Israel in relation to distance from the adult plants. J. Ecol. 63(2):627-632.

Friedman, J., G. Orshan, and Y. Ziger-Cfir. 1977. Suppression of annuals by Artemisia herba-alba in the Negev Desert of Israel. J. Ecol. 65(2):413-426.

Frischknecht, N.C., and L.E. Harris. 1973. Sheep can control sagebrush on seeded range if ... Utah Sci. 34(1):27-30.

Froeming, D.K. 1981. Influences of soil and climate on the climax distribution of selected Artemisia species. In: Soc. of Range Manage., 34th annual meeting, Tulsa, Okla. Abstract.

Gates, D.H. 1964. Sagebrush infested by leaf defoliating moth. J. Range Manage.17:209-210.

Goodwin, D.L. 1956. Autecological studies of Artemisia tridentata Nutt. Ph.D. diss. Washington State Univ., Pullman. 79p.

Gordon, R.A., and H.A. Wright. 1981. Ecological factors influencing common broomweed emergence and survival. Soc. of Range Manage., 34th annual meeting, Tulsa, Okla. Abstract.

Gough, L.P., and J.A. Erdman. 1980. Seasonal differences in the element content of Wyoming big sagebrush. J. Range Manage. 33(5):374-378.

Groves, C.R., and J.E. Anderson. 1981. Allelopathic effects of Artemisia tridentata leaves on germination and growth of two grass species. Amer. Mid. Nat. 106(1):73-79.

Hale, M. 1982. Allelopathic potential of Artemisia vulgaris rhizomes. Plant Physiol. 69(4):23.

Harberd, D.J. 1962. Some observations on natural clones of Festuca ovina L. New Phytol. 61:85-100.

Harberd, D.J. 1967. Observations on natural clones of Holcus mollis. New Phytol. 66:401-408.

Harniss, R.O., and W.T. McDonough. 1975. Seedling growth of three big sagebrush subspecies under controlled temperature regimens. J. Range Manage. 28(3):243-244.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London New York San Francisco. 892p.

Harvey, S.J. 1981. Life history and reproductive strategies in Artemisia. M.S. Thesis. Montana State Univ. 132p.

Hazlett, D.L., and G.R. Hoffman. 1975. Plant species distributional patterns in Artemisia tridentata- and Artemisia cana-dominated vegetation in western North Dakota. Bot. Gaz. 136(1):72-77.

Helmrick, R.H., and R.P. Pfeifer. 1954. Differential varietal responses of winter wheat germination and early growth to controlled limited moisture conditions. Agron. Jour. 46:560-562.

Hoffman, G.R., and D.L. Hazlett. 1977. Effects of aqueous Artemisia extracts and volatile substances on germination of selected species. J. Range Manage. 30(2):134-137.

Howard, G.S., G.E. Schuman, and F. Rauzi. 1977. Growth of selected plants on Wyoming surface-mined soils and flyash. J. Range Manage. 30(4):306-310.

Hussain, F., and H. Khanum. 1982. Phytotoxic potentiality of Artemisia maritima. Pakistan J. Bot. 14:18-19.

Ito, K., K. Ide, and J.Inouye. 1976. Ecological studies and control of mugwort. In: Proceedings of 5th Asian-Pacific Weed Science Soc. Con., Tokyo, Japan. pp. 66-69.

Johnson, A.E. 1982. Toxicological aspects of photosensitization in livestock. N. Nat. Cancer Institute. 69:253-258.

Johnson, K.L. 1978. Basic synecological relationships of the big sagebrush types on the high plains of Montana, Wyoming and the Dakotas. In: The Sagebrush Ecosystem: A symposium. p. 42-49.

Johnson, J.R., and G.F. Payne. 1968. Sagebrush reinvasion as affected by some environmental influences. J. Range Manage. 21:209-213.

Kelsey, R.G., M.S. Morris, and F. Shafizadeh. 1976. The use of sesquiterpene lactones as taxonomic markers in the shrubby species of Artemisia (section Tridentatae) in Montana. J. Range Manage. 29(6):502-505.

Kemperman, J.A., and B.V. Barnes. 1976. Clone size in American aspens. Can. J. Bot. 54:2603-2607.

Krasikova, N.S. 1978. Byulleten' Vsesoyuznogo Nauchno-Issledovatel' skogo Instituta Rastenievodstva imeni NI. Vasilova No. 81:67-82.

Krueger, R.R., and D.L. Shaner. 1982. Germination and establishment of prostrate spurge (Euphorbia supina). Weed Sci. 30:286-290.

Kufeld, R.C. 1973. Foods eaten by Rocky Mountain Elk. J. Range Manage. 26(2):106-113.

Kumar, D., and P.F. Wareing. 1972. Factors controlling stolon development in the potato plant. New Phytol. 71:639-648.

La Tourette, J.E., J.A. Young, and R.A. Evans. 1971. Seed dispersal in relation to rodent activities in seral big sagebrush communities. J. Range Manage. 24:118-120.

Legere, A., and S. Payette. 1981. Ecology of black spruce (Picea mariana) clonal populations in the hemiarctic zone, northern Quebec: population dynamics and spatial development. Arctic and Alpine Research. Vol. 13(3):261-276.

Lovett-Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (Ranunculus repens). I. The dynamics of ramets in contrasting habitats. J. Ecol. 69:743-755.

Mackie, R.J. 1970. Range ecology and relationships of mule deer, elk and cattle in the Missouri Breaks, Montana. Wildl. Monogr. No. 20. 79p.

Mayeux, H.S., and L. Leotta. 1981. Germination of broom snakeweed (Gutierrezia sarothrae) and threadleaf snakeweed (G. microcephalum) seed. Weed Sci. 24:530-534.

McArthur, E.D., B.C. Giunta, and A.P. Plummer. 1974. Shrubs for restoration of depleted ranges and disturbed areas. Utah Sci. 35:28-33.

McArthur, E.D., and A.P. Plummer. 1978. Biogeography and management of native western shrubs: A case study, section Tridentatae of Artemisia. In: Great Basin Memoirs, No. 2. Intermountain Biogeography: a symposium. BYU.

McArthur, E.D., and B.L. Welch. 1982. Growth rate differences among big sagebrush (Artemisia tridentata) accessions and subspecies. J. Range Manage. 35(3):396-400.

McDonough, W.T., and R.O. Harniss. 1974. Seed dormancy in Artemisia tridentata Nutt. subspecies vaseyana Rydb. Northwest Sci. 48(1):17-20.

McDonough, W.T., and R.O. Harniss. 1975. Know your sagebrush - and better your range. Utah Sci. 36(3):99-103.

Melkania, N.P., J.S. Singh, and K.K.S. Bisht. 1982. Allepathic potential of Artemisia vulgaris L. and Pinus roxbingii: a bioassay study. In: Proceedings of the Indian National Science Academy. 48(5):685-688.

Morris, M.S., R.G. Kelsey, and D. Griggs. 1976. The geographic and ecological distribution of big sagebrush and other woody Artemisia's in Montana. In: Proceedings of the Montana Academy of Sciences 36: 56-79.

Mott, J.J. 1979. Flowering, seed formation and dispersal. In: Arid-land ecosystems: structure, functioning and management. Vol. 1. Cambridge Univ. Press. Cambridge London New York Melbourne. IBP pp. 627-645.

Mueggler, W.F. 1966. Vole damage to big sagebrush in southwestern Montana. J. Range Manage. 20:88-90.

Noble, J.C., A.D. Bell, and J.L. Harper. 1979. The population biology of plants with clonal growth. I. The morphology and structural demography of *Carex arenaria*. J. Ecol. 67:963-1008.

Nosova, L.I. 1973. Potential seed productivity of *Artemisia rhodantha*. Botanicheskii Zhurnal. 58(6):899-904.

Numata, M., A. Kobayashi, and N. Ohga. 1975. Studies on the role of allelopathic substances. *In*: Studies in Urban Ecosystems, ed. by M. Numata. pp. 38-41.

Nuttall, T. 1841. *Artemisia* and *Picrothamnus*. Trans. Am. Phil. Soc. II. 7:398, 417.

Olson, K.C. 1982. Effect of precipitation on mixed grass plant communities of Southeastern Montana and its implications for grazing intensity. M. S. Thesis. Montana State Univ. 205p.

Parmar, M.T., and R.P. Moore. 1966. Effects of simulated drought by polyethylene glycol solutions on corn (*Zea mays* L.) germination and seedling development. Agron. J. 58:391-392.

Pechanec, J.F., A.P. Plummer, J.H. Robertson, and A.C. Hall. 1965. Sagebrush control on rangelands. USDA Agr. Handbook No. 277. 40p.

Pijl, L. vander. 1982. Principles of dispersal in higher plants. 3rd edition. Springer-Verlag. Berlin Heidelberg New York. 215p.

Roath, L.R., and W.C. Krueger. 1982. Cattle grazing influence on a mountain riparian zone. J. Range Manage. 35(1):100-103.

Sabo, D.G., G.V. Johnson, W.C. Martin, and E.F. Aldon. 1979. Germination requirements of 19 arid land plants. Research Paper, Rocky Mtn. Forest and Range Exp. Sta., USDA Forest Service, No. RM-210. 26p.

Salisbury, E.J. 1942. The reproductive capacity of plants; studies in quantitative biology. 224p. London, G. Bell and Sons, Ltd.

Scholl, J.P., R.G. Kelsey, and F. Shafizadeh. 1977. Involvement of volatile compounds of *Artemisia* in browse preference by mule deer. Biochem. Sys. and Ecol. 5:291-295.

Shafizadeh, F., and A.B. Melnikoff. 1970. Coumarins of *Artemisia tridentata* ssp. *vaseyana*. Phytochemistry 9:1311-1316.

Sheehy, D.P., and A.H. Winward. 1981. Relative palatability of seven Artemisia taxa to mule deer and sheep. J. Range Manage. 34(5):397-399.

Shetler, S.G., and L.E. Skog. 1978. A provisional checklist of species for Flora North America. Flora North America Report 84. Missouri Botanical Garden. 199p.

Stevens, R., and E.D. McArthur. 1974. A simple field technique for identification of some sagebrush taxa. J. Range Manage. 27(4):325-326.

Stidham, N.D., R.M. Ahring, J. Powell, and P.L. Claypool. 1980. Chemical scarification, moist prechilling and thiourea effects on germination of 18 shrub species. J. Range Manage. 33(2):115-118.

Sturges, D.L. 1977a. Soil moisture response to spraying big sagebrush: A seven year study and literature interpretation. USDA Forest Service Research Paper, RM-188. 12p.

Sturges, D.L. 1977b. Soil water withdrawal and root characteristics of big sagebrush. Amer. Mid. Nat. 98(2):257-274.

Thatcher, A.P. 1959. Distribution of sagebrush as related to site differences in Albany County, Wyoming. J. Range Manage. 12:55-60.

Tisdale, E.W., and M. Hironaka. 1981. The sagebrush-grass region: A review of the ecological literature. Forest, Wildl. and Range Exp. Sta., Univ. Idaho. No. 209. 31p.

Vasek, F.C. 1980. Creosote bush: long lived clones in the Mojave Desert. Amer. J. Bot. 67(2):246-255.

Waller, S.S., D.K. Schmidt, J. Stubbendieck, C.M. Britton, and F.A. Sneva. 1980. Germination of Kochia prostata(L.). Schrad. Society of Range Manage., 33rd annual meeting, San Diego, Calif. Abstract.

Weaver, T.W., and D. Klovich. 1977. Allelopathic effects of volatile substances from Artemisia tridentata. Amer. Mid. Nat. 97(2):508-512.

Welch, B.L., and E.D. McArthur. 1979. Feasibility of improving big sagebrush for use on mule deer winter ranges. In: (J.R. Goodin and D.K. Northington, ed.), Proceedings Arid Land Plant Resources. Texas Tech. Univ., Lubbock.

Weldon, L.W., D.W. Bohmont, and H.P. Alley. 1959. The interrelation of three environmental factors affecting germination of sagebrush seed. J. Range Manage. 12:236-238.

Went, F.W. 1979. Germination and seedling behavior of desert plants. In: Arid-land Ecosystems: structure, functioning and management. IBP. Vol. 1. Cambridge Univ. Press. Cambridge London New York Melbourne. pp. 477-479.

White, R.S., and P.O. Currie. 1983. The effects of prescribed burning on silver sagebrush. J. Range Manage. 36:611-613.

Wilson, R.G. 1982. Germination and seedling development of fringed sagewort (*Artemisia frigida*). Weed Sci. 30:102-105.

Wilson, R.W. 1977. Sagebrush utilization by mule deer and antelope. In: Wyoming Shrublands--proceedings of sixth Wyoming Shrub Ecology Workshop. pp. 25-34.

Winward, A.H. 1980. Taxonomy and ecology of sagebrush in Oregon. Oregon Agr. Exp. Sta. Bull. 642, 15p.

Winward, A.H., and E.W. Tisdale. 1969. A simplified chemical method for sagebrush identification. Univ. Idaho. Sta. Note. No. 11. 2p.

Woolley, J.T., and E.W. Stoller. 1978. Light penetration and light induced seed germination in soil. Plant Physiol. 61:597-600.

Wright, H.A., L.F. Neuenschwander, and C.W. Britton. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities: a state of the art review. USDA Gen. Tech. Rep. No., INT-58. 48p.

Young, J.A., and R.A. Evans. 1972. Population dynamics of green rabbitbrush. In: Proceedings of the Western Society of Weed Science. Vol. 24:13.

Young, J.A., and R.A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weed Sci. 23(5):358-364.

Young, J.A., and R.A. Evans. 1979. Arrowleaf basamroot and mules ear seed germination. J. Range Manage. 32(1):71-74.

APPENDICES

APPENDIX A

PRECIPITATION AND TEMPERATURE DATA FOR THE YEARS 1981, 1982 AND 1983

Summarization of climatic data presented in two tables. Table 7 is the precipitation and temperature averages for the summer months for the years of 1981 through 1983 at Miles City, Montana. Table 8 is maximum temperatures and days above 90 F during the summer months at Miles City.

Table 8. Precipitation and temperature averages by month for the years 1981, 1982 and 1983 at Miles City, Montana.

Year	Month	Precipitation		Departure		Temperature		Departure	
		(in)	(cm)	(in)	(cm)	(F)	(C)	(F)	(C)
1981	January	.05	.13	-.44	-1.12	31.0	-.6	15.6	8.7
	February	.06	.15	-.45	-1.14	27.9	-2.3	6.3	3.5
	March	.28	.71	-.37	-.94	40.7	3.8	10.5	5.9
	April	.20	.51	-1.06	-2.69	51.3	10.8	6.0	3.4
	May	2.87	7.29	.81	2.06	57.1	14.1	.8	.5
	June	2.57	6.53	-.75	-1.91	63.9	17.9	-1.0	-.6
	July	.36	.91	-1.19	-3.02	75.1	24.1	.7	.4
	August	1.12	2.84	-.08	-.20	74.7	23.9	2.2	1.2
	September	.72	1.83	-.47	-1.19	63.8	17.8	3.9	2.2
	October	1.39	3.53	.68	1.73	45.0	7.3	-3.8	-2.1
	November	.78	1.98	.27	.69	37.0	2.8	4.6	2.6
	December	.23	.58	-.25	-.64	21.9	-5.7	-.1	-.1
	ANNUAL	10.63	27.00	-3.30	-8.38	49.1	9.6	3.8	2.1
1982	January	.96	2.44	.47	1.19	1.9	-16.9	-13.5	-7.6
	February	.20	.51	-.31	-.79	17.2	-8.3	-4.4	-2.5
	March	.73	1.85	.08	.20	30.8	-.7	.6	.3
	April	.53	1.35	-.73	-1.85	41.9	5.5	-3.4	-1.9
	May	2.61	6.63	.55	1.40	52.6	11.5	-3.7	-2.1
	June	5.10	12.95	1.78	4.52	63.7	17.8	-1.2	-.7
	July	.69	1.75	-.86	-2.18	73.1	23.0	-1.3	-.7
	August	.61	1.55	-.59	-1.50	74.2	23.6	1.7	1.0
	September	2.23	5.66	1.04	2.64	59.4	15.3	-.5	-.3
	October	1.61	4.09	.91	2.31	46.7	8.2	-2.1	-1.2
	November	.10	.25	-.41	-1.04	28.4	-2.0	-4.0	-2.2
	December	1.01	2.57	.53	1.35	21.4	-5.9	-.6	-.3
	ANNUAL	16.38	41.61	2.45	6.22	42.6	5.9	-2.7	-1.5
1983	January	.26	.66	-.31	-.79	27.7	-2.4	13.6	7.6
	February	.09	.23	-.47	-1.19	34.9	1.6	12.8	7.2
	March	.95	2.41	.36	.91	36.5	2.5	5.2	2.9
	April	.02	.05	-1.35	-3.43	44.9	7.2	0.0	0.0
	May	1.36	3.45	-.95	-2.41	53.7	12.2	-3.1	-1.7
	June	1.56	3.96	-1.19	-3.02	65.7	18.9	-.7	-.4

Table 8. continued.

Year	Month	Precipitation (in)	Precipitation (cm)	Departure (in)	Departure (cm)	Temperature (F)	Temperature (C)	Departure (F)	Departure (C)
	July	1.89	4.80	.37	.94	76.1	24.7	1.5	.8
	August	.33	.84	-.93	-2.36	80.4	27.1	8.1	4.5
	September	1.36	3.45	.28	.71	58.3	15.8	-1.8	-1.0
	October	.26	.66	-.64	-1.63	49.9	10.0	1.5	.8
	November	.43	1.09	-.17	-.43	34.0	1.1	2.0	1.1
	December	.28	.71	-.32	-.81	0.9	-17.4	-20.6	-11.1
	ANNUAL	8.79	22.33	-4.67	-11.86	46.9	8.3	1.6	.9

Table 9. Maximum temperatures and days above 90 F (50.4 C) during June, July and August of 1982 and 1983 at Miles City, Mont.

Year	Month	Maximum Temperature (F)	Maximum Temperature (C)	Days above 90 F (50.4 C)
1982	June	94	52.6	2
	July	99	55.4	11
	August	101	56.6	14
1983	June	100	56.0	3
	July	108	60.5	20
	August	105	58.8	25

APPENDIX B

DISPERSAL ANALYSIS OF VARIANCE TABLE

Summarization of analysis of variance of seed dispersal data in which the six transects and four distances are considered split plots and date of dispersal as a covariant. Sources of variation, degrees of freedom, F-ratio and significance are presented.

Table 10. Summarization of dispersal analysis of variance.

Source of variation	Degrees of freedom	F-ratio	Significance level
Study area	2	.40	.68
Transects (direction)	5	6.58	.0001
Distance from plant	3	11.71	.0
Date of seed drop	4	6.36	.0
Transect & Distance	15	5.19	.0
Study area & Date	8	2.73	.006
Distance & Date	12	5.45	.0
Transect, Distance & Date	60	1.44	.018

APPENDIX C

GERMINATION FACTORIAL ANALYSIS OF VARIANCE TABLE

Summarization of analysis of variance in germination factorial experiment. Five factors were examined individually and interactions among factors were also examined. Note that interactions that included stratification are not included in this table.

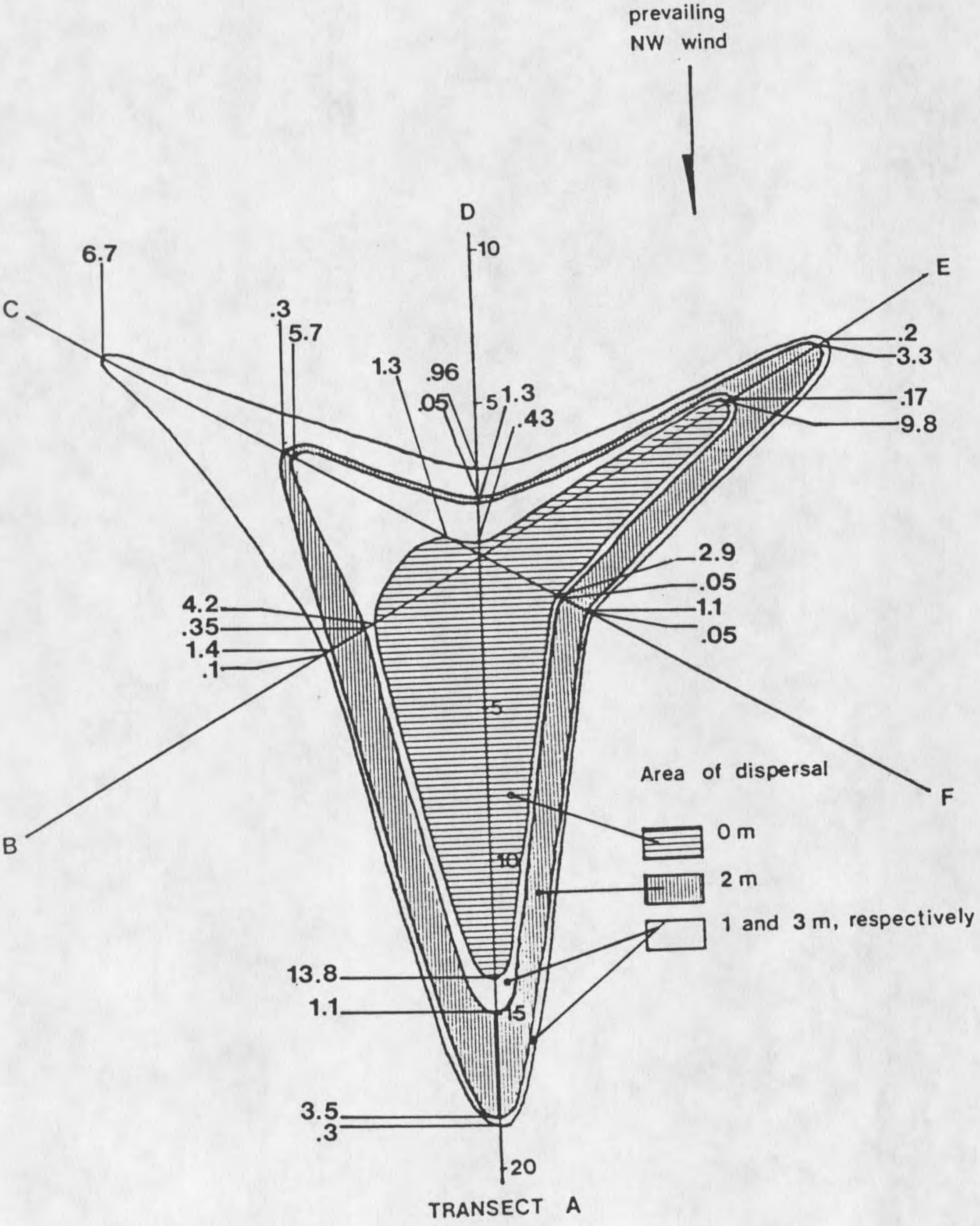
Table 11. Summarization of germination analysis of variance.

Source of variation	Degrees of freedom	F-ratio	Significance level
Date of seed collection	2	72.3	.0007
Stratification	1	.0015	.97
Light/Dark	1	58.4	.0
Temperature	2	90.0	.0
Osmotic Potential	3	890.7	.0
Light/dark & Date	2	16.2	.0004
Temperature & Date	4	16.9	.0
Light/dark & Osmotic potential	3	79.1	.0
Light/dark & Temperature	2	93.5	.0
Light/dark, Date & Temperature	4	5.6	.0009
Temperature & Osmotic potential	6	4.6	.0002
Temperature, Date & Osmotic potential	12	4.9	.0
Light/dark, Temperature & Osmotic potential	6	12.5	.0
Light/dark, Temperature, Osmotic potential & Date	12	2.6	.003

APPENDIX D

CONSTRUCTION OF DISPERSAL FIGURES

Example of construction of dispersal graphs. Scale on axes are numbers of seeds dispersed in each of six directions. At each distance from the parent plant (0, 1, 2, and 3 m), the number of seeds that fell at that distance were graphed and connected to approximate the degree of dispersal in each direction.



Walton, T. P.
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