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Reestablishment of spiny hopsage (Grayia spinosa [Hook.] Moq.) where depleted or lost on shrub steppe sites can improve forage, plant cover, and soil stabilization. The objectives of this study were to: 1) determine direct-seeding requirements; 2) develop optimum germination pretreatments; and 3) examine dormancy mechanisms in spiny hopsage fruits and seeds.

The effects of seed source, planting date, and site preparation method on seed germination and seedling establishment (SE) were examined at Birds of Prey and Reynolds Creek in southwestern Idaho. Three seed sources were planted on rough or compact seedbeds on 4 dates in 1986-87 and 3 dates in 1987-88. Exposure to cool-moist environments improved spring SE from early fall (EF) and late fall (LF) plantings. Few seedlings emerged from early (ESp) or late spring (LSp) plantings. SE was low at 1 site in 1986-87 and at both sites in 1987-88, probably due to lack of precipitation. For the successful 1986-87 planting, seedling density was greater on rough compared to compact seedbeds in April and May, possibly due to improved microclimate conditions. Growth rate varied among seed sources, but seedlings developed a deep taproot (mean length 266 mm) with few lateral roots the first season.

Seeds were planted on 3 dates in 1986-87 and 1987-88, and nylon bags containing seeds were planted on 4 dates each year to study microenvironment effects on germination (G), germination rate (GR), and SE. Bags were recovered on subsequent planting dates, and seeds were tested for moisture content, viability, G, and GR. In 1987-88 with low precipitation, seedlings established only from LF plantings ($<1/m^2$). In response to high March 1989 precipitation, establishment was 6 and 26 times greater on LF compared to ESp plantings. Incubating seed in soil from LF to ESp 1987-88 increased G 6-11 times and GR 12 and 13 days. Incubating seeds in soil from W to ESp increased G 1-6 times and GR 4 and 8 days compared to controls. In 1988-89, incubation from LF to W increased G 17 times and GR 10 and 11 days compared to controls, while incubation from W to ESp increased G 4 and 7 times and GR 10 and 11 days.

Utricles and seeds responded to stratification for 60 days at 3-5°C. Mean G at 5/15°C (44%) was similar to maximum constant temperature G obtained over the 20-30°C (37-40%). Embryo excision and mechanical scarification released dormancy imposed by the elastic inner layers of the testa. Moist heat at 35°C reduced dormancy; the effect was greater for seeds than utricles. Dormancy imposed by bracts was not reduced by leaching. Bracts did not inhibit water uptake or provide mechanical restraint to the radicle; they may act by reducing permeability to oxygen or other gases.

Germination and Seedling Establishment of Spiny Hopsage (*Grayia spinosa* [Hook.] Moq.)

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GERMINATION AND SEEDLING
ESTABLISHMENT OF SPINY HOPSAGE
(GRAYIA SPINOSA [HOOK.] MOQ.)

INTRODUCTION

A member of the Chenopodiaceae, one of the most successful plant families in arid and semiarid areas of the western United States, spiny hopsage (*Grayia spinosa* [Hook.] Moq.) is distributed east of the Cascade and Sierra Nevada Mountains from central Washington to southern California and eastward to southwestern Montana and western Colorado at elevations ranging from 160 to 2,900 m (Hitchcock and Cronquist 1973; University of Wyoming Herbarium, specimens on file, Laramie, Wyoming, 1986; Welsh et al. 1987). Spiny hopsage is unusual among woody chenopods in that it occurs in a variety of salt desert shrub communties as well as in drier portions of Wyoming big sagebrush communities (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & A. Young) (Daubenmire 1970, Welsh et al. 1987). It also occurs in pinyon-juniper (*Pinus* L.-*Juniperus* L.) communities and in blackbrush (*Coleogyne ramosissima* Torr.), creosote bush (*Larrea tridentata* [DC.] Cov.) and other warm desert shrub communities of the Mojave Desert (Beatley 1976, Welsh et al. 1987).

Highly palatable in spring, spiny hopsage is often heavily grazed by livestock and in some areas is being replaced by less palatable species (Blaisdell and Holmgren 1984). Areas within its range have been impacted by wildfires and drastic disturbances associated with mining, off-road vehicle use, road and pipeline construction, nuclear testing and research, and military training programs. Several characteristics of the shrub have generated interest in its reestablishment on these sites. Where abundant, spiny hopsage provides palatable and nutritious late-winter and spring forage for big game and livestock, particularly sheep (McCullough 1969; Daubenmire 1970, 1978; Blauer et al. 1976; Blaisdell and Holmgren 1984). McCullough (1969) and Krysl et al. (1984) reported available forage contained 18% crude protein in late winter and 11.8% in summer. The shrub provides food and dense, low-growing cover for birds, rodents, rabbits, and other small animals (Dasmann and Blaisdell 1954, Gullion 1964, USDA-SCS 1968), although its cover value is diminished to some extent following summer leaf fall.

Spiny hopsage is capable of resprouting following burning or mechanical damage (USDA-SCS 1968, Daubenmire 1970, Smith 1974, Wasser 1982) and is least susceptible to burning damage during the period of summer dormancy (Rickard and McShane 1984). Both attributes are of considerable interest in areas with high wildfire frequencies and invading exotic annuals. Spiny hopsage is also a useful shrub for control of wind erosion and an effective soil surface stabilizer on gentle to moderately steep slopes due to its dense, low-growing crown and spreading root system (USDA-SCS 1968, Institute for Land Rehabilitation 1979, Dittberner and Olsen 1983). Growth and nutrient content of vegetation growing near spiny hopsage plants are enhanced by accumulation of litter rich in potassium, magnesium, calcium, and other cations (Rickard and Keough 1968).

Direct seeding or transplanting spiny hopsage would permit reestablishment of the species and improve diversity of shrub plantings in areas where it is adapted. Few woody species occur on many of these sites. Seeding technology is generally lacking and commercial sources of seed or planting stock are rarely available. The USDA Soil Conservation Service has established a field trial near their Aberdeen Plant Materials Center in southeastern Idaho for selection of a spiny hopsage cultivar for the shrub steppe. Efficient planting strategies will be required to maximize use of this cultivar.

The overall objective of this investigation was to determine requirements for establishment of spiny hopsage from seed to maximize returns from rangeland seedings and to obtain rapid and uniform emergence under nursery conditions. Specific objectives were to (1) review literature relevant to seed biology, seedling establishment, and propagation; (2) determine effects of planting date, seed source, seedbed preparation, and seedbed environment on seed germination and seedling establishment; (3) evaluate germination pretreatments to improve speed and uniformity of seedling establishment under greenhouse or nursery conditions; and (4) begin an examination of the nature of seed dormancy in the species.

LITERATURE REVIEW

Common Names

The common name spiny hopsage is derived from the similarity of the shrub's fruits to agricultural hops (Aldous and Shantz 1924, Mozingo 1987). Alternative common names are grayia, Gray's saltbush, saltbrush, spiny-sage, wintersage, and horsebrush (Dayton 1931, Smith 1974, Kay et al. 1977). Ranchers in southwestern Idaho refer to the shrub as greenbrush because of its deep green coloration in early spring (G. Secrist, personal communication, USDI-BLM, Craig, Colo., 1984). In some Utah localities, the species' palatability has earned it the common name applebush (Welsh 1984, Welsh et al. 1987).

Taxonomic History and Status

The first spiny hopsage specimens were collected in 1826 by David Douglas who was commissioned to collect plant materials in the Pacific Northwest by the Royal Horticultural Society of England in cooperation with the Hudson's Bay Company (Hooker and Arnott 1841). He was recommended for this position by Sir William J. Hooker who became Director of the Royal Botanic Gardens at Kew in 1841 (Davis 1980). From his Fort Vancouver base, Douglas traveled approximately 10,000 km in 1825 and 1826, exploring and collecting over a vast area in what is now Oregon, Washington, California, and British Columbia. Douglas' spiny hopsage material is dated "Nov. 1826. D.D." and the collection site recorded as "In the interior of California" (G.L. Lucas, specimens on file, Royal Botanic Gardens, Kew, England, 1988).

Based on the Douglas and "Snake River Mr. Tolmie" collections, Hooker and Arnott (1841) created the genus *Grayia* (H. & A.) in honor of Asa Gray, a distinguished American botanist (1810-1888), describing the first species as *G. polygaloides* Hook. and Arn. (Hooker and Jackson 1895). C.H.B.A. Moquin-Tandon (1849) noted that Hooker had originally named the species *Chenopodium* ? *spinosum* Hook. This identification was based on the Douglas material alone, described by Hooker as "extremely young and imperfect specimens with only a few male flowers" (Hooker 1838). Moquin-Tandon (1849) corrected the nomenclature in de Candolle's *Prodromus Systematis Naturalis Regne Vegetablis*, forming the combination *G. spinosa* (Hook.) Moq. and adding "La Platte, Gordon n. 217" to the specimens cited.

In 1900, E.L. Greene, then a professor at Catholic University, Washington, D.C., created a new genus, *Eremosemium*, and transferred *Grayia spinosa* to *E. spinosa* Greene, thinking *Grayia* to be a previously established genus (Greene 1900). *Eremosemium* was never widely used, but remains a valid synonym.

The Douglas, Tolmie, and Gordon specimens are all preserved at the Royal Botanic Gardens (G.L. Lucas, specimens on file, Royal Botanic Gardens, Kew, England, 1988). The exact collection sites for these specimens are not known. According to Douglas' journal, he spent the month of November 1826 west of the Cascade Mountains on a successful search for sugar pine (*Pinus lambertiana* Dougl.) specimens (Douglas 1959, Davis 1980). It seems unlikely that he could have personally collected spiny hopsage during this period.

The "Snake River Mr. Tolmie" specimens were part of a small collection made by John McLeod, a Hudson's Bay Company trapper, during the summer of 1837, as he traveled from Fort Vancouver to the rendezvous of the American trappers on the Green River in what is now Sublette County, Wyoming (McKelvey 1955). His spiny hopsage material was collected in early summer when the fruits were nearly mature (McKelvey 1955). On his return to the Northwest, McLeod presented his collection to William Fraser Tolmie, a surgeon for the Hudson's Bay Company. A student of botany, Tolmie was patronized by Sir William Hooker to whom he forwarded the specimens.

The "Gordon, La Platte n. 217" material was collected by Alexander Gordon, a Scotsman who collected and sold North American plant specimens and seeds to nurserymen and taxonomists, including Sir William Hooker. McKelvey (1955) suggests Gordon's undated Platte River specimens were collected in 1843 when Gordon and 3 other botanists: Charles Mersh, Fredreich Lüders, and Karl Geyer were invited by Sir William Drummond Stewart, a Scottist adventurer, on a lavishly equipped scientific expedition along the Oregon Trail to the Rocky Mountains. Gordon evidently traveled and collected as far west as the Green River in Wyoming (Cronquist et al. 1972). Some of his plants eventually reached Hooker who described them as "exquisitely dried specimens" (McKelvey 1955).

Type specimens of spineless hopsage (Zuckia brandegei [Gray] Welsh & Stutz var. brandegei, originally Grayia brandegei Gray), a subshrub confined to fine-textured saline and seleniferous substrates of the Colorado River Basin from southern Wyoming to northern Arizona (Welsh et al. 1987), were collected in 1875 by Thomas Brandegee on the San

Juan River near the boundary between Colorado and Utah. Brandegee was employed as a plant collector for F.V. Hayden's geological and topographical survey expedition to the Four Corners region of southwestern Colorado on the recommendation of Asa Gray (Collotzi 1966, Crosswhite and Crosswhite 1985). Gray described the spineless hopsage specimens, naming the new species G. brandegei in Brandegee's honor (Gray 1876).

Asa Gray evidently had several opportunities to personally field inspect his namesake genus after retiring from Harvard University in 1870. During the summer of 1872, he toured the West by train, returning to Dubuque, Iowa, to preside over the annual meeting of the American Association for the Advancement of Science. Dupree (1959) states that

> "As the Union Pacific train with its palace car made its way westward from the plains into the intermountain plateau, Gray made every stop a sortie for flowers. On one such, his hand clutched the genus Grayia, named in his honor by Sir William Hooker when he was but a stripling visitor in Glasgow. These original specimens had been gathered by a Hudson's Bay Company fur trapper only some 40 years before."

In 1877, Gray accompanied Sir Joseph Dalton Hooker, Sir William's son and successor at the Royal Botanic Gardens, on a botanical tour of the West, stopping in Colorado to collect with Thomas Brandegee.

The taxonomic status of both spiny and spineless hopsage remain uncertain. Grayia, Zuckia, and the closely related genus Atriplex are included in Subfamily Chenopodioideae of Family Chenopodiaceae. The Chenopodioideae are characterized by the presence of a cyclical embryo and a small amount of endosperm (Williams and Ford-Lloyd 1974, Blackwell 1977). Gray (1876) wrote that the 2 hopsage species should be separated from Atriplex L. on the basis of their inferior radicle and conduplicate fruiting bracts that form an obcompressed rather than a laterally compressed sac united to the tip. Later taxonomists separated the 2 hopsages from *Atriplex* using slightly different combinations of vegetative and reproductive characteristics (see, for example, Harrington 1964 or Hitchcock et al. 1964).

Confusion arose in 1960 when Arthur H. Holmgren, Utah State University, and A.P. Plummer, USDA Forest Service, collected several Utah specimens thought to be a new species of *Atriplex*, but which were eventually identified as spineless hopsage. In examining this problem, A.W. Collotzi, one of Holmgren's students, completed an embryological, morphological, and chromatographic study of spiny hopsage, spineless hopsage and members of *Atriplex* and several other related genera. He proposed that both hopsages be transferred to *Atriplex* with spiny hopsage being renamed *A. grayia* Collotzi (Collotzi 1966). Hitchcock and Cronquist (1973) accepted this classification, but corrected the nomenclature to *A. spinosa* Collotzi.

More recently, Goodrich and Neese (1986) suggested the genus *Zuckia* Standley could be included in *Grayia*. S.L. Welsh, Brigham Young University, in preparing a key to the chenopods of Utah, retained *G. spinosa*, but reclassified *G. brandegei* as *Zuckia brandegei* (Gray) Welsh & Stutz var. *brandegei* and *Z. arizonica* Standley, previously the only species in its genus, as *Z. b.* var. *arizonica* (Standl.) Welsh (Welsh 1984, Welsh et al. 1987). He used the combination of pubescence of simple or branched hairs, axillary rounded buds, and bracts lacking appendages and either laterally compressed or 6 to 8 ribbed to separate

Grayia and Zuckia from Atriplex. Grayia was separated from Zuckia on the basis of its thorny, divaricate branches; pubescence of branched hairs; and fruiting bracts with thickened, spongy margins.

Description

The following description of spiny hopsage is derived from Moquin-Tandon (1849), Watson (1880), Standley (1916), Bidwell and Wooton (1925), Tidestrom (1925), Munz (1935), Tidestrom and Kittell (1941), Abrams (1944), McMinn (1951), Davis (1952), Munz and Keck (1959), Kearney and Peebles (1960), Peck (1961), Jepson (1963), Sampson and Jesperson (1963), Harrington (1964), Hitchcock et al. (1964), USDA-SCS (1968), Rydberg (1969), N.L. Shaw, file data (1991), Welsh and Moore (1973), Blauer et al. (1976), Dorn (1977), Young and Evans (1980), Benson and Darrow (1981), Wasser (1982), Welsh (1984), Goodrich and Neese (1986), and Welsh et al. (1987).

Shrubs are erect to rounded with divergent, rigid branches and whitish-gray to brownish bark that exfoliates in long strips. Plants range from 0.3-1.2 (1.5) m in height. New twigs and both surfaces of younger herbage are scurfy or sparingly to densely pubescent with small stellate hairs. New twigs become glabrate and indurate in age and spinose-persistent following leaf fall. Alternate, entire, gray-green exstipulate leaves develop from prominent, globose axillary buds. Leaves are fleshy and somewhat flattened, narrowing to sessile or short petiolate bases. They range from 5-30 (40) mm or more in length and 2-13 mm in width. Blades are linear-oblanceolate, spatulate, or obovate with obtuse to subacute apices. Leaves often turn bright red-orange prior to abscission.

Staminate flowers are small and yellowish, produced in short, leafy-bracted axillary glomerate spikes of 2-5 flowers. Lower bracts are foliaceous, becoming progressively reduced upward. Individual flowers are pedicillate and ebracteolate. Perianths are membranous and usually 4-lobed. Individual lobes are 1.5-2.0 mm long and equal or exceed and enclose the 4 (5) stamens. Filaments are subulate and shorter than the anthers.

Pistillate flowers develop in dense terminal spicate inflorescences of 1 to several flowers that exceed the staminate spikes in length, but with subtending bracts more reduced. Some flowers are commonly vestigial. Each flower is enclosed in 2 connate orbicular to elliptic or somewhat chordate bracteoles that are stipelike to sessile at the base, obcompressed, and united along their margins except for a minute, retuse, apical opening. The perianth is absent. The style is 2 or rarely 3 lobed, protruding through the opening in the covering. The accrescent bracteoles form a thin-walled dorsally wing-margined reticulate sac free of the ovary, but closely investing it (Fig. 1). Bracteoles of the mature fruit are 6-15 mm in diameter; white, green, or straw-colored; and may become suffused with pink or red when nearly mature. Wings of the bracteoles contain a thick, highly hygroscopic layer of spongy mesophyll with an extensive network of vascular tissue. The fruit is included within the bracteoles and consists of a compressed, membranous utricle with a thin pericarp (Fig. 2). The orbiculate seed is free, vertical, cellular-reticulate, and about 2 mm in diameter. The outer dark brown layer of the testa sometimes ruptures during imbibition, but the light brown middle layer and

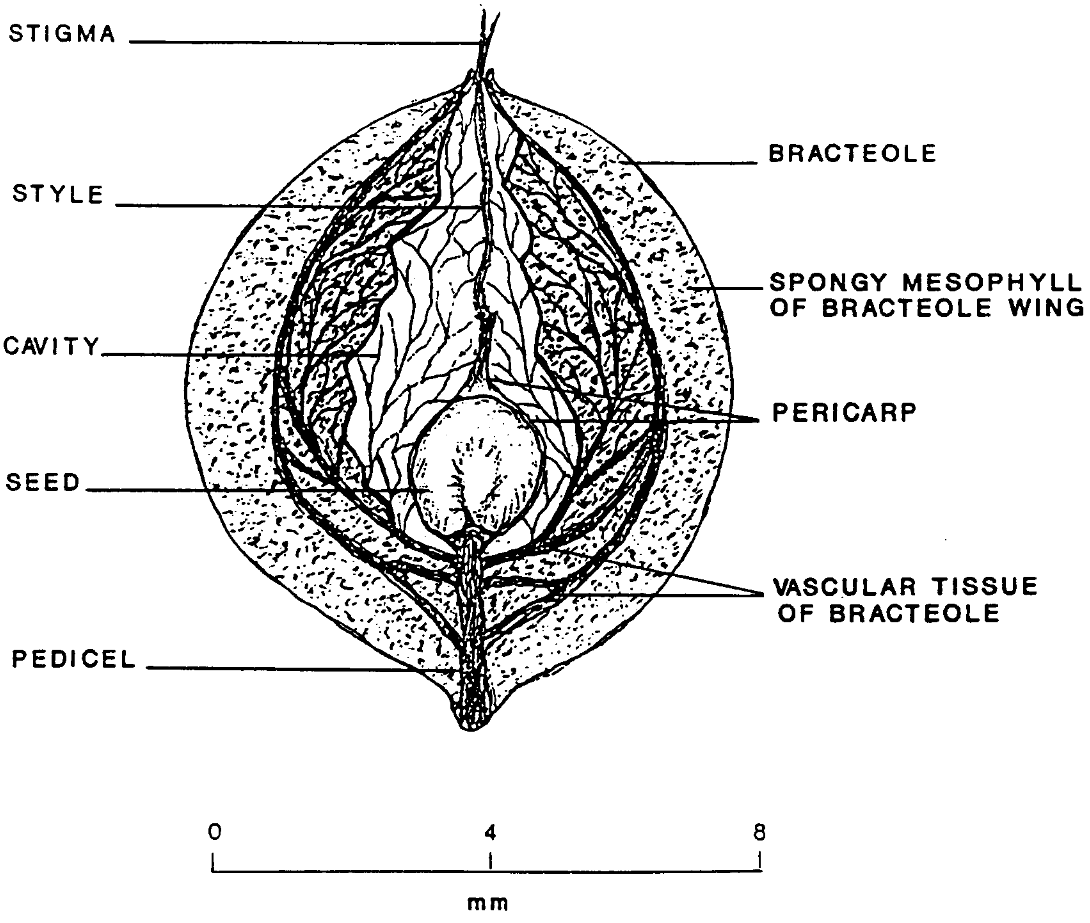

Figure 1. Spiny hopsage utricle and bracteole.

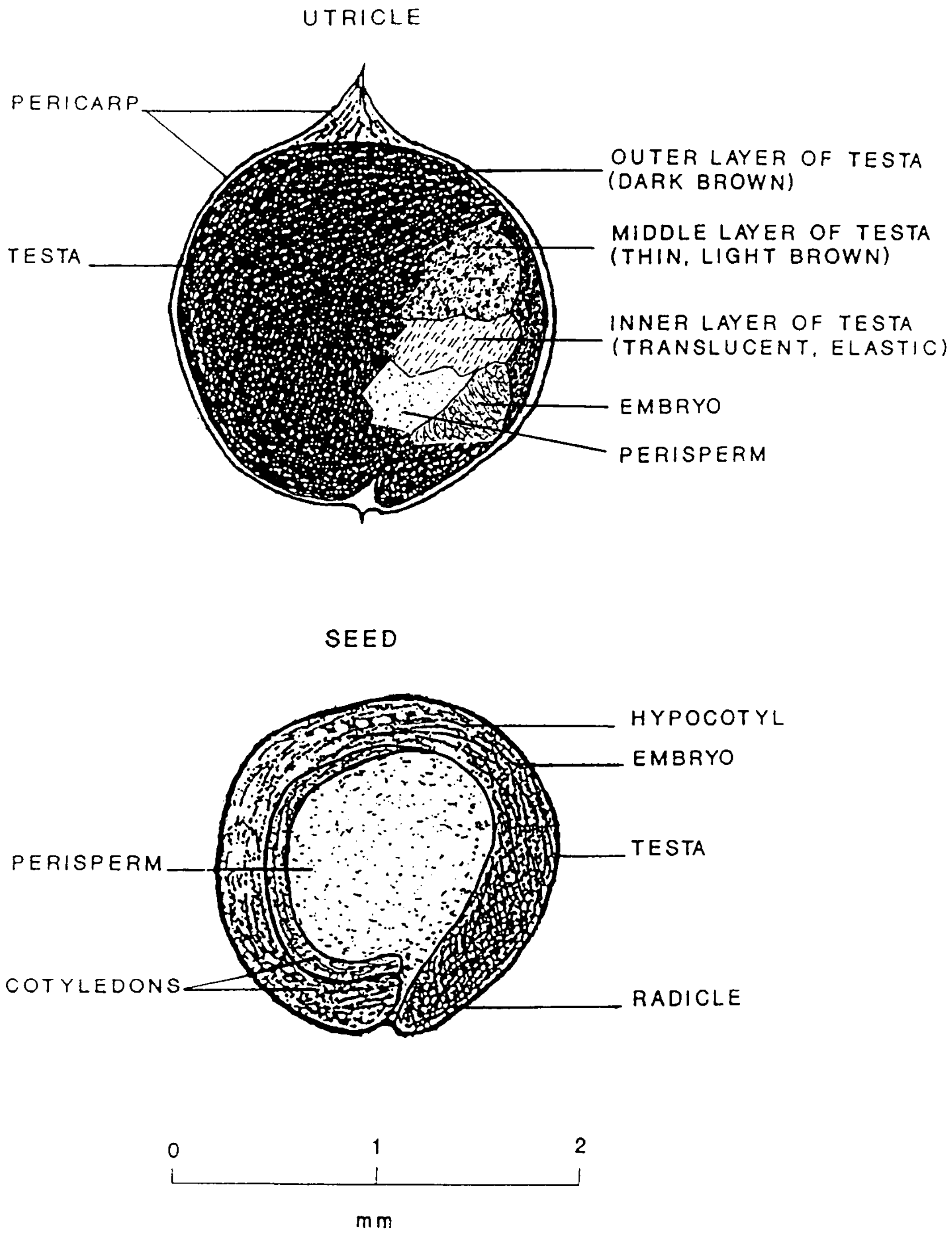

Figure 2. Spiny hopsage utricle and seed anatomy.

translucent inner layer are tough and elastic. The annular embryo is white with an inferior radicle and yellowish achlorophyllous cotyledons that green rapidly on imbibition and exposure to light. The embryo encircles a disk of starchy, mealy, nonliving white perisperm. A small amount of endosperm is present (Blackwell 1977). Germination is epigeal (Hitchcock et al. 1964, Smith 1974).

Breeding System

The breeding system of spiny hopsage is poorly defined. Like those of other chenopods, the shrub's small, inconspicuous, usually unisexual flowers are wind pollinated, a system considered to be more reliable than insect pollination in arid lands (McArthur 1984). The species has been described as dioecious, but sometimes monoecious (Hitchcock et al. 1964, Goodrich and Neese 1986) or monoecious (Welsh et al. 1987). Blauer et al. (1976) described spiny hopsage as usually dioecious, but up to 5% monoecious in some populations. R.L. Pendleton (file data, USDA Forest Serv., Provo, Utah, 1987) determined a population in Rush Valley, Utah was more than 90% dioecious during 1 year. Ninety percent of the dioecious plants were male. McArthur and Sanderson (1984) described the species as monoecious but varying in particular investment in male and female function from dry to mesic sites. McArthur and Blauer followed floral phenotypes of a population in Sanpete County, Utah for 3 years (E.D. McArthur, file data, USDA Forest Serv., Provo, Utah, 1987). Each year all shrubs were scored as staminate, pistillate, or monoecious. Many plants were non-flowering.

With the exception of 1 individual, the phenotype of all shrubs that flowered did not vary over time. The exception was staminate one year and monoecious the following year.

Zuckia brandegei var. *brandegei* is heterodichogamous (Pendleton et al. 1988). Plants are either protogynous or protoandrous with the 2 types occurring in a 1:1 ratio. Heterodichogamy also exists in *Z. b.* var. *arizonica*, but not in spiny hopsage (R.L. Pendleton, file data, USDA Forest Serv., Provo, Utah, 1987).

McArthur and Sanderson (1984) noted that as monoecy is considered the ancestral condition of chenopods, both hopsage species exhibit transitional forms to more specialized systems that insure outcrossing. They conjectured that these derived breeding strategies developed in response to stressful, heterogenous habitats.

Phenology and Plant Growth

Wallace and Romney (1972), Ackerman and Bamberg (1974), and Ackerman et al. (1980) recorded meteorological data and phenological stages of major shrubs at several northern Mojave Desert and Transition Zone (Great Basin/Mojave Desert interface) locations within the USAEC Nevada Test Site. Spiny hopsage was one of the earliest shrubs to initiate spring growth (Wallace and Romney 1972). At elevations ranging from 1,006-1,037 m in Rock Valley, a northern Mojave Desert site, new leaf and twig growth began when minimum and maximum daily temperatures alternated between 3 and 20°C (Ackerman and Bamberg 1974). The cycle of vegetative and reproductive phenology was rapidly completed as plants utilized moisture accumulated in the first 1 m of soil from winter and early spring precipitation. Spiny hopsage entered summer dormancy as air and soil temperatures increased and soil moisture was depleted (Wallace and Romney 1972).

Spiny hopsage's mode of growth produces a compact, densely branched shrub. Overwintering buds consist of conspicuous grey-green rosettes that give the bare shoots a warty appearance (Wallace and Romney 1972). The buds produce new twigs and leaves that begin growth nearly simultaneously in spring. At the end of the season's activity, the tip of each shoot loses all meristematic activity and develops into a sharp thorn. Consequently, increase in plant size is dependent upon elongation of new lateral shoots. At Rock Valley in the northern Mojave Desert, numerous shoots, usually less than 50 mm in length, form the active margin of the shrub (Wallace and Romney 1972). These and the older, inactive shoots give the shrub its compact, spiny appearance.

Flowers form on new floral shoots that are sometimes longer than vegetative shoots (Wallace and Romney 1972). These die back after utricle dispersal in early to mid-summer. Flowering in spiny hopsage may be determined by photoperiod as flowers appear only in spring (Ackerman and Bamberg 1974, Ackerman et al. 1980). Flowering is not triggered by summer or fall precipitation.

Number and size of new shoots, leaf size, and numbers of flowers and fruits produced by spiny hopsage are highly dependent upon available soil moisture (Wallace and Romney 1972, Rickard and Warren 1981). Plants respond readily to irrigation following dry winters if soil temperatures are favorable for growth. During years with unusually high soil moisture during the growing season, vigorous long shoots may develop from the root crown or lower portions of major branches and sometimes grow to lengths of 0.6 m or more in 1 season (Wallace and Romney 1972; N.L. Shaw, file data, 1988). In 1966, an exceptionally high precipitation year in the Mojave Desert, some shrub volumes increased 20% due to long shoot development (Wallace and Romney 1972).

Growth of spiny hopsage plants from the northern Mojave Desert decreased in response to increasing soil temperatures in a greenhouse experiment (Wallace et al. 1970, Wallace and Romney 1972). Plants grown at a 16°C root temperature were productive throughout the 60-day study while plants grown at soil temperatures of 21 and 28°C remained nearly dormant, exhibiting only limited growth. An 18°C soil temperature was considered optimal for growth. This pattern held for other shrubs classified as typical Great Basin species. Transition Zone or Mojave Desert species were equally or more productive at the higher root temperatures. Wallace et al. (1970) speculated that root temperature response of these 2 groups might be correlated with mode of photosynthesis.

Bud formation, leaf fall, and onset of summer dormancy normally occur shortly after seed dispersal, but there is wide variation in this characteristic. A high elevation population in Daggett County, Utah, retains some leaves throughout the summer (Blauer et al. 1976). Some populations in the southern portion of the species' range are reportedly evergreen (McMinn 1951, Wasser 1982).

Spiny hopsage is one of the earliest species to enter summer dormancy at the USAEC Nevada Test Site (Wallace and Romney 1972). At Rock Valley in the northern Mojave Desert this process begins for spiny hopsage, Anderson wolfberry (Lycium andersonii Gray), and pale wolfberry (L. pallidum Miers), all summer deciduous species, when soil moisture falls below 4% and air temperature rises above 30°C (Ackerman and Bamberg 1974). Spiny hospage was consistently dormant when temperatures reached 35-40°C (Ackerman and Bamberg 1974) or exceeded 40°C (Ackerman et al. 1980).

Branson et al. (1976) reported that of 12 woody species studied near the Book Cliffs in western Colorado, spiny hopsage had one of the longest dormant periods. During the year of study, spiny hopsage broke dormancy later than 7 other species and was the first to enter summer dormancy. Because of the high water holding capacity of sandy soils in the Grayia community, they hypothesized summer dormancy might be related to day length as well as to water availability.

Spiny hopsage does not break dormancy following summer rains or when irrigated. In the Mojave Desert, it will break dormancy after fall rains if nighttime temperatures are below 0°C (Wallace et al. 1970, Wallace and Romney 1972, Beatley 1974, Ackerman et al. 1980). Wallace et al. (1970) and Wallace and Romney (1972) found that spiny hopsage broke dormancy after 8 days at 4°C or 2 weeks at 5°C. Lathhouse plants exposed to nighttime temperatures of 13°C also broke dormancy, indicating that a chilling requirement existed, but was not great. The cold temperature requirement may determine the southern boundary of the species' distribution. Wallace et al. (1970), however, noted the occurrence of soil temperatures conducive to growth might be more critical than the chilling requirement in regulating growth.

Wallace and Romney (1972) reported the chilling requirement for release of dormancy may be circumvented by the action of gibberellin. Applications of 2, 7, or 35 mg of gibberellin to pots containing 3.5 kg of soil caused dormant plants to resume growth in a greenhouse study. Greatest response occurred following the 35 mg treatment. They hypothesized dormancy was triggered physiologically by heat or a photoperiod and released by soil temperature-regulated production of a growth substance in the roots.

Dates of phenological events for spiny hopsage vary considerably with location and deviations in local weather patterns. At an elevation of 1,700 m in Hot Creek Valley, Nevada, a Great Basin site, average date of leaf bud break was 19 March with a range of 31 days over a 4-year period (Everett et al. 1980). The active cycle averaged 103 days with a range of 39 days. Leaf abscission and seed dispersal occurred in early to mid-August. Over a 3-year period in Rock Valley, Nevada, a northern Mojave Desert site, initial growth occurred between early January and early March (Wallace and Romney 1972). The period of active growth ranged from 3-7 months.

Beatley (1974) found a heavy rainfall event of at least 25 mm between September and early December was the most important factor in triggering growth of plants during the ensuing spring at Rock Valley in the northern Mojave Desert of Nevada. Rainfall of this magnitude occurred during 10 years between 1960 and 1972. Turner and Randall (1987) used data from several studies (Wallace and Romney 1972, Ackerman and Bamberg 1974, Ackerman et al. 1980) to develop multiple regression models relating meteorological data to phenological observations made from 1968 through 1976 at Rock Valley. Models based on precipitation and air temperature were used to predict dates of first leafing and flowering for spiny hopsage and other common shrubs. The models accounted for a greater percent of annual variability in flowering than in leafing. The models were not sensitive to short periods of unusually low temperatures and did not predict failure to flower. Additional years of data and better understanding of process-limiting effects were considered essential for model improvement.

Natural Seedling Establishment

The USDA-SCS (1968) reported spiny hopsage establishes readily in eastern Washington when bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Smith) or needle-and-thread (*Stipa comata* Trin. & Rupr.) communities are depleted by overgrazing or impacted by other disturbances. In contrast, Daubenmire (1970) found no spiny hopsage plants with fewer than 16 xylem rings after extensive searches in eastern Washington. Several vegetation studies conducted at the USAEC Nevada Test Site documented the occurrence of spiny hopsage seedlings in the northern Mojave Desert. Seedling establishment was restricted to microenvironments within and under shrub clumps, particularly in heavily grazed areas (Beatley 1979/80, Manning and Groeneveld 1990).

Season of seedling emergence varies geographically. Glazebrook (1941) noted that seedlings emerge in fall immediately after seeds reach maturity. Although he collected seed in eastern Washington, he did not specify the site of this observation. In southeastern Oregon and southwestern Idaho, emerging seedlings were observed only in years with good spring moisture (N.L. Shaw, file data, 1989 and 1990; Shaw and Haferkamp 1990). Seedlings emerged in early spring from litter accumulations beneath the mother plant canopy or from open soil surfaces slightly downwind. Greasewood (Sarcobatus vermiculatus [Hook.] Torr.), Wyoming big sagebrush, and male spiny hopsage plants growing near seed sources also acted as nurse plants (N.L. Shaw, file data, 1989 and 1990; Shaw and Haferkamp 1990). Rickard et al. (1988) reported areas shaded by spiny hopsage canopies averaged 10°C cooler than adjacent open areas.

Ackerman (1979) found seeds of 11 common Mojave Desert shrubs germinated following fall or winter rains (October to March) of at least 160 mm. Establishment of these species was assumed to be highly episodic as only 1 of 201 seedlings emerging on study plots between 1971 and 1975 survived until spring 1977. Of 63 spiny hopsage seedlings emerging, 62 succumbed the first year and 1 the second year.

El-Ghonemy et al. (1980) documented the episodic nature of spiny hopsage seedling establishment at the USAEC Nevada Test Site. Biomass of spiny hopsage and 9 other major perennial species was sampled in undisturbed areas of Rock Valley in the northern Mojave Desert. Frequency histograms for size-class distribution on a natural log basis showed a somewhat negatively skewed distribution for spiny hopsage, resulting from segregation of the numerous smaller (younger) individuals into many size classes. The mean dry weight of spiny hopsage plants was 74.3 ± 85.8 g. Approximately 66.5% weighed less than the modal size class (24.39-64.65 g) and 17.1% weighed more, again indicating an abundance of small (young) plants. This distribution possibly reflected emergence and survival of many seedlings in response to good rainfall 2 years prior to sampling.

Impact of supplemental moisture on seedling emergence and establishment was examined near Mercury in the northern Mojave Desert of Nevada (Hunter et al. 1980a). Plots of native vegetation were sprinkler irrigated to maintain soil moisture content above 5%, increasing annual moisture input from an average of 100-150 mm to 350-450 mm (Wallace and Romney 1972). After 3 years of irrigation followed by 4 years of natural rainfall, spiny hopsage density increased by 53.8% and biomass by 494%. Corresponding increases on nonirrigated plots after 7 years were 27.8% for density and 118% for biomass.

Recovery of spiny hopsage on disturbed sites was studied at the USAEC Nevada Test Site. Wallace and Romney (1972) found few spiny hopsage seedlings normally emerged in disturbed creosote bush communities of the Mojave Desert unless artificial irrigation was applied. In the southern Great Basin, shrub recovery was monitored at Pahute Mesa following nuclear testing in 1965. Elevation of the site is 1,800-1,890 m and mean annual precipitation 119-279 mm. Following testing, no spiny hopsage seedlings remained in the totally killed area (Wallace et al. 1977, 1980). Shrub recovery began rather quickly, even though the totally killed area was dominated by Russian thistle and the partially killed area by grasses during the first 5 years. By 1976, spiny hopsage and total shrub seedling density had increased in both the partially and totally killed areas to the point that shrub recruitment appeared adequate for replenishing the site. In an unusually good moisture year, a large number of spiny hopsage seedlings emerged on disturbances within this site and grew to heights of 0.3-0.4 m (Wallace and Romney 1972).

Seed Technology

Terminology

The spiny hopsage utricle and the bracteoles that enclose it will be referred to as "bracted utricles" or "utricles" throughout the remainder of this review.

Utricle Production, Maturation and Dispersal

Spiny hospage utricle crops vary immensely among years, sites, and shrubs. Few utricles develop during dry years. Good production is often observed along drainageways or roadsides receiving extra runoff. In monotypic stands, shrubs scattered beyond the stand's periphery often produce heavy crops compared to plants within the stand. Shrubs regenerating by sprouting in years following wildfires may produce considerable new growth if adequate moisture is available. As a result, new twig growth and utricle production in succeeding years are often greater than on shrubs growing in adjacent undisturbed sites.

Flowers and fruits develop only on current year's growth. Mature utricles readily detach from the shrub and are dispersed by wind, gravity, and insects. The period suitable for harvesting bulk quantities of utricles is usually less than 1 week, depending upon wind and temperature conditions. Small quantities of later-developing utricles may be harvested over a period of 2 or 3 weeks. Summer storms occurring when the crop is mature can remove most utricles within a few hours. During years of good production, drifts of utricles accumulate around the bases and downwind from the shrubs, in cracks or depressions in the soil, and around other obstacles.

Many utricles are consumed by insects. Grasshoppers (species not determined) remove utricles prior to dispersal, leaving the perforated bracts on the shrub. Following dispersal, many utricles are carried away by ants. The seed harvester ant (*Pogonomyrmex salinus* Olsen), is a common predator of spiny hopsage utricles in southeastern Oregon and southwestern Idaho (W.H. Clark, specimens on file, Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, Idaho, 1989). Large quantities of bract fragments may be found around the periphery of their hills during and following utricle dispersal.

Harvesting

Utricles are harvested by hand stripping or by beating shrubs with wooden paddles or tennis rackets. Detached utricles are caught in canvas hoppers, aluminum collection trays, or other containers (Plummer et al. 1968, Vories 1981, Shaw and Haferkamp 1990). Utricles are easily collected during good production years. Kay et al. (1977) reported drifts of recently fallen utricles could be gathered with a backpack or vehicle-mounted vacuum seed harvester. Degree of insect predation, however, must be checked carefully prior to collecting dispersed utricles.

Freshly-harvested utricles should be spread in a thin layer over drying racks or screens in an enclosed area with good ventilation. The hygroscopic bracts absorb moisture at night if dried outside and exposed to temperature and humidity fluctuations. It is sometimes necessary to place netting or wire screens over collections during drying as bracted utricles are scattered by very light breezes.

Conditioning

Utricles may be planted with bracts intact (Young and Young 1987). Conditioning then requires only removal of twigs, large leaves, and other coarse material with an M2B Clipper cleaner (Seedburo Equipment Co., Chicago, Ill.) or larger air-screen cleaner equipped with a no. 36 top screen and a no. 8 bottom screen (Kay et al. 1977). It may be necessary to change screens for each seed lot as bract diameter varies considerably with population and year of collection.

Bracts are threshed, if necessary, using a hammermill fitted with a 3/16th inch (5 mm) screen operating at 720 rpm (King 1947). A Forsberg scarifier (Forsbergs, Inc., Thief River Falls, Minn.), Missoula dewinger (USDA-Forest Serv., Missoula, Mont.), or modified Dybvig seed cleaner (Melvin R. Dybvig, Oregon City, Oreg.) lined with corrugated rubber and fitted with corrugated rubber paddles attached to a rotating central axle may be used to thresh bracts of small seed lots (Shaw and Haferkamp 1990). Some embryos are usually damaged during threshing.

Seeds are separated from chaff using an air-screen cleaner with a 1/12 top screen and a 1/21 bottom screen. Other screen sizes may be required for seed lots with unusually large or small seeds. Removal of chaff is necessary only if it is desirable to reduce bulk for storage or shipping as the bract powder can serve as a diluent for the small seeds or for a mix of shrub seeds and can be fed through most seeding mechanisms, if dry. A seed blower is used to remove chaff and obtain high purities required for precision seeding in nurseries or experimental work.

Based on a 1982-83 survey of seed companies and suppliers, Plummer (1984) estimated that approximately 45.4 kg of spiny hopsage seeds were being marketed annually with demand increasing. Recommended quality standards for purchasing spiny hopsage seeds are 90% purity and 25-88% viability (Plummer et al. 1968, Wasser 1982, Stein et al. 1986). Depending upon the seeding technique used, lower purities may be acceptable if seed purchases are made on a pure live seed (PLS) basis. Number of filled bracted utricles ranges from 337,900-369,000/kg and seeds from 869,000-932,000/kg (Swingle 1939, Glazebrook 1941, Smith 1974). Smith (1974) reported 45.4 kg of bracted utricles (18% fill) yielded 1.2 kg of pure seed.

Storage

King (1947) and Plummer et al. (1968) reported spiny hospage seeds stored under warehouse conditions remain viable for 2-6 years. Kay (1976) and Kay et al. (1977, 1984, 1988) found germination of air-dried seeds stored in cloth bags in a warehouse declined from 42 to 20% after 18 months and to 0% after 84 months. Germination of seeds dried to a 5.1% moisture content and stored in sealed glass jars containing silica gel desiccant at room temperature, $4^{\circ}C$, or $-15^{\circ}C$ exceeded initial germination after 14 years of storage (Kay et al. 1988).

Testing

Standardized laboratory testing procedures for spiny hopsage seeds have not been accepted by the Association of Official Seed Analysts (1988). Techniques for laboratory analyses recommended by Belcher

(1985), and C.C. Duelhemeier (file data, Idaho State Seed Laboratory, Boise, Idaho, 1987), and N.L. Shaw (file data, 1986-87) are as follows:

Purity

Routine analysis requires 5 g sample. Noxious weed count requires 50 g.

Germination

Incubate seeds at 5/15 (16 hours/8 hours) or 15°C, first count at 7 days, last count at 14 days. Prechill of 30-60 days at 3-5°C required for dormant seeds.

Normal Seedling

Hypocotyl thin, 10-15 mm long; cotyledons small, narrow; epicotyl short; root as long as hypocotyl; root hairs well developed.

Excised Embryo

Soak seeds in water at 28°C for 24 hours. Drain. Excise embryos with sharp needles. Excised embryos germinate rapidly at 5/15 or 15°C. Evaluate as described for germination.

Tetrazolium Chloride

Soak seeds in water at 28°C for 24 hours. Drain. Pierce seeds through perisperm with a sharp probe or needle. Soak in 1% 2,3,5-triphenyl tetrazolium chloride (TZ) solution for 1-4 hours at 28°C. Excise embryo with sharp needles. Evaluate as described by Grabe (1970) for dicotyledonous species other than legumes.

X-ray

Twelve KV, 30 seconds for Kodak AA film and Industrex paper; 12 KV, 60 seconds for Polaroid film. Filled, empty, and abnormal development visible.

Germination

Glazebrook (1941) demonstrated light had no influence on germination when 1-year old seeds were incubated at 22-26°C. Maximum germination (92%) occurred after 35 days at 20/30°C. Seeds incubated at 20°C for 101 days before being transferred to 30°C required a total of 254 days to complete germination with final germination approaching that obtained at 20/30°C. Based on the positive response of his seed lot to alternating temperatures, Glazebrook (1941) recommended early spring or late fall sowing for nursery production of seedlings. Preliminary work indicating seedlings could be frozen solid "while still very young" and yet survive supported this recommendation.

King (1947) compared germination of 4 and 6-year old seed lots from Soap Lake, Washington. Maximum germination of the 6-year old seed lot obtained following a 2-week stratification at 5°C while a 12-week stratification was required to maximize germination percentage and rate of the 4-year old seed lot. Neither the 4 or 6-year old seed lots responded to 2, 8, or 12-week stratification treatments at 1°C, but 4-week stratifications at 1 and 5°C were equally effective in improving total germination of each seed lot. Based on these observations, King (1947) suggested that older seed lots might require shorter stratification periods to relieve dormancy.

Smith (1974) reported higher total germination of seeds stratified for 60 or 90 days at 4°C and incubated at 22°C than controls. Only the 60-day stratification improved germination relative to controls when seeds were incubated at 20/30°C. Regardless of incubation temperature, germination of stratified seeds was completed in 8 or less days compared to 30 days for unstratified seeds.

Wood et al. (1976) tested germination of 1 California (Mojave Desert) and 4 Nevada seed lots at constant temperatures ranging from 2 to 40°C. The highest germination percentages were obtained at 10 and 15°C after a 1-week incubation. Germination percentage of seeds from Nevada populations was similar at all constant temperatures tested. Germination of the California seed lot exceeded the others at 30 and 40°C. Cold stratification or other pretreatments were not required for these seed lots as seeds were nondormant and germinated rapidly when imbibed. Lack of dormancy in Mojave Desert seed lots has been reported by Wallace et al. (1970) and Wallace and Romney (1972).

Wood et al. (1976) also evaluated the response of their seed lots to 55 alternating temperature regimes. A 5°C low temperature alternating with high temperatures between 10 and 30°C, inclusive, provided the greatest germination percentages for all 5 seed lots after 14 days of incubation. Greatest elongation of seedlings developing from a Dayton, Nevada seed lot after 1 week occurred at incubation temperatures of 5, 15/20, 20, and 5/25°C. The authors considered the positive response to low temperatures an indication of the ecological requirement for seeds produced by species in cold-arid environments to germinate in late fall or early spring when soil moisture levels are high.

Bracts of spiny hopsage play an important role in their dispersal by wind. Wood et al. (1976) and Young et al. (1984) speculated that drifts of utricles accumulating under and around shrubs might also modify the microenvironment of the seedbed surface. Air-dried bracted utricles were highly hygroscopic, increasing 41% by weight when placed over water in a desiccator. Bracted utricles of the Mojave Desert seed lot were highly tolerant of osmotic stress. Germination percentage of utricles incubated in polyethylene glycol solutions of -0.8 to -1.2 MPa was not reduced compared to a water control. They suggested the bracts might function to regulate the osmotic potential of the utricles, thus enabling them to attain the osmotic potential required for germination.

Germination of bracted utricles was reduced to a greater extent by ion concentration than by water potential. In NaCl solutions, germination of bracted Mojave Desert utricles occurred only at water potentials greater than -1.3 MPa, suggesting ion toxicity. Analysis of surface soils at the Nevada seed collection sites did not reveal salinity levels capable of producing water potentials this low, although the authors suggested they might occur at the California site.

Meyer and Pendleton (1990) and Pendleton and Meyer (1990) examined germination of spineless hopsage, a fall-fruiting species. Dormancy of fresh utricles varied with collection site and decreased with afterripening (Meyer and Pendleton 1990). Debracting improved germination of fresh, but not afterripened utricles. Of the constant temperatures tested (15, 20, 25, 30°C), incubation at 15°C provided the highest mean germination percentage for the 4 utricle lots examined. Germination was enhanced by 2, 4, and 8-week stratification treatments at 1°C with the 8-week stratification being most effective.

Pendleton and Meyer (1990) reported bract leachate solutions with conductivities of 8 and 16 mmhos/cm depressed germination of debracted spineless hopsage utricles. Utricles stored 19 months at room temperature exhibited less sensitivity to leachate than fresh utricles. Inhibition by the 16 mmhos/cm leachate exceeded NaCl or mannitol at similar osmolalities or conductivities, suggesting the activity of another inhibitory substance in leachate. Further tests indicated this inhibition could not be attributed to saponin activity.

Revegetation

Direct Seeding

Dayton (1931), Billings (1949), Plummer (1966), and Monsen and Christensen (1975) encouraged development of spiny hopsage as a revegetation species because of its palatability and occurrence in both salt desert shrublands and Wyoming big sagebrush communities. Revegetation attributes of spiny hopsage were evaluated by Plummer et al. (1961, 1968). They assigned high ratings for germination, persistence, and resistance to insects and disease and low ratings for initial establishment and natural spread.

Plummer et al. (1968) and Plummer (1977) recommended spiny hopsage for pinyon-juniper, basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata), Wyoming big sagebrush, shadscale (Atriplex confertifolia [Torr. & Frem.] Wats.) and blackbrush vegetation types. Use of local seed sources was encouraged by Stark (1966) and Plummer et al. (1968). The problems encountered and low probability for returns for plantings in salt desert shrub areas were discussed by Bleak et al. (1965), Plummer (1966), Wallace et al. (1980), Kay and Graves (1983), and Blaisdell and Holmgren (1984).

Planting requirements for spiny hopsage have not been well defined. Failures of early spiny hopsage plantings in Utah were attributed to planting the small seeds at excessive depths (A.P. Plummer, personal communication, Provo, Utah, 1984). Suggested planting depths are surface broadcasting (Glazebrook 1941), 5 mm (sandy loam soil) (Wood et al. 1976), and 10 mm (washed plaster) (Kay et al. 1977). Wood et al. (1976) found few or no seedlings established when seeds were broadcast on smooth, packed, or rough soil surfaces or when bracted utricles were broadcast on smooth or packed surfaces in a greenhouse experiment. Broadcasting bracted utricles on a rough soil surface resulted in 18% seedling establishment. Establishment of 51% from bracted utricles and 48% from seeds resulted from planting at a depth of 5 mm.

Appropriate season for planting has not been determined. Glazebrook (1941) recommended late fall or early spring planting while Wasser (1982) recommended planting in early fall or early to late spring. Spiny hopsage seeds have been planted at rates of 1.1 to 2.2 kg/ha in Utah (Plummer et al. 1968, Wasser 1982). Seeds were mixed with other shrub seeds, but planted separately from grasses. Rosentreter and Jorgensen (1986) recommended a planting rate of 0.6 kg pure live seeds/ha for southern Idaho. Anderson and Shumar (1989) recommended cultipacker planting in mixtures at rates of 2.2 to 4.4 kg of spiny hopsage seeds/ha in winterfat (*Ceratoides lanata* [Pursh] J.T. Howell) and saltbush (shadscale and Nuttall saltbush [*Atriplex nuttallii* S. Wats]) communities on Idaho's Upper Snake River Plains.

Successful establishment of spiny hopsage seedlings requires reduction of vegetative competition and control of seed and seedling predation (Kay and Graves 1983). Competition with annuals for available moisture reduces seedling establishment. Seedling predation by mice and rabbits was noted by Everett (1957) and Kay and Graves

(1983). Shaw and Haferkamp (1990) reported seedling predation by seed harvester ants and nymphs of an unidentified plant bug (Melanotrichus spp.) in southwestern Idaho.

Transplanting

Vegetative propagation

Wallace and Romney (1972) reported spiny hopsage cuttings from the northern Mojave Desert rooted when cut tips were dipped in Hormodin No. 2 powder (0.3% indole-3 butyric acid [IBA] in talc) and stuck in vermiculite under conditions of relatively low humidity and cool day and night temperatures in a lathhouse. Rooting occurred over a 2-6 month period. Once rooted, cuttings grew very poorly in a glasshouse at 18/27°C (night/day). Their dormancy was broken by a 14-day chill at 5°C in a refrigerator, exposure to nighttime temperatures of 13°C in a lathhouse, or soil application of gibberellin at a rate of 0.5 g/l. Growth was stimulated by additional gibberellin applications of 1.8 or 9.2 mg/l or by exposure to a 16°C root temperature.

Wieland et al. (1971) obtained greater rooting success with spiny hopsage cuttings taken from plants grown in a greenhouse or lathhouse and chilled to 4°C before harvesting compared to cuttings from field grown plants. Stem pieces dipped in a talc preparation of 0.3% IBA rooted more readily than those treated with 0.8% IBA or untreated cuttings. Rooting success was greater in a lathhouse than in an unheated glass house, bottom-heated closed glass house, or a bottom-heated open glass house. Mist house results were satisfactory. Rooting temperature varied with season and ambient conditions, ranging from 20-30°C during the day and 10-20°C at night.

Richardson et al. (1979) harvested cuttings of previous years' growth from a native population on a salt desert shrub site near Bonanza, Uintah County, Utah, in March. Moistened stem sections 80 mm long were treated in talc preparations of 0.0, 0.3, 0.8, or 2.0% IBA, stuck in moistened peat pellets, and rooted at 21°C. After 30 days, all IBA treatments were equally effective in inducing 25-30% rooting compared to less than 10% for controls.

Everett et al. (1978) harvested softwood, semihardwood, and hardwood cuttings from 16 Nevada populations of spiny hopsage at 6 phenological stages: dormant, leaf growth, twig growth, flowering, seed, and predormancy quiescence. Basal ends of cuttings were wounded, dipped in a commercial talc preparation of 0.8% IBA and placed in coarse perlite on a greenhouse bench with an intermittent mist system. Rooting by phenological stage and population varied from 0.0 to 99.5% with a mean of 33%. Semihardwood cuttings collected during the flowering stage rooted most readily. Rooting required from 3-12 weeks with a mean of about 4 weeks. Rooted cuttings were transplanted into containers. Within 3-12 weeks they attained sizes comparable to 6-month old greenhouse-grown seedlings. The authors recognized vegetative propagation as a rapid and inexpensive means of producing planting stock, but emphasized the need for further refining propagation procedures.

Bareroot Stock

Bareroot chenopod shrub seedlings are produced by seeding for a target density of 215 seedlings/m^2 at the USDA Forest Service, Lucky Peak Nursery near Boise, Idaho (Shaw and Monsen 1984). A seedbed mortality rate of 40% and culling rate of 20% are used in computing seeding rates. Spiny hopsage is fall seeded to permit overwinter stratification and early spring emergence as soil temperatures rise above freezing. This practice maximizes the period of active seedling growth prior to leaf abscission and onset of summer dormancy. Seedlings developing from fall plantings grow rapidly, producing branched shoots and extensive root systems during the first season. Seeding stratified seeds in May has not been a successful means of producing usable stock after 1 growing season as plants fail to reach adequate size for outplanting prior to summer leaf fall (N.L. Shaw, file data, 1983 and 1984).

Bareroot seedlings must be lifted, packed, and handled with care as stems and branches are brittle and break easily. Seedlings should be planted soon after the soil thaws and before native spiny hopsage shrubs in the vicinity of the planting site break dormancy. Removal of competing vegetation is critical to seedling survival (Wallace et al. 1980, Frischknecht and Ferguson 1984). Vegetation should be removed from strips 1 m in width for mechanical transplanting or from 1 m^2 scalps for hand transplanting.

Luke and Monsen (1984) outplanted bareroot spiny hopsage seedlings and pads of mature spiny hopsage plants at the Black Butte Mine, Sweetwater County, Wyoming. Annual precipitation at this site averages 190 mm. Bareroot seedlings were planted in mid-April 1981 on 0.3 m of replaced sandy loam topsoil with a pH of 7.5-8.0. First-year survival was 40%. Nearly all transplant losses occurred soon after planting. Cost per established seedling was $0.50 (U.S.). Pads of mature shrubs were planted in mid-May 1982 on an overburden dump with a pH of 7.5-8.0. First-year survival averaged 71% at a cost of $6.32 per surviving plant. Use of bareroot stock was recommended as a supplement to direct seeding to increase shrub diversity and density as required by mine reclamation regulations. Planting pads of mature vegetation was recommended to quickly create islands of seed sources for future seedling establishment, thereby reducing cost per total number of plants established. Vegetation pads provided immediate forage availability for wildlife, improved aesthetics and diversity, and acted as sources of active microorganisms, insects, native forbs, and grasses. The authors estimated cost of transplanting vegetation pads could be reduced 50% with increased experience, but the procedure would remain costly.

Container Stock

Soil mixes and greenhouse propagation techniques have not been developed specifically for spiny hopsage. Technology for greenhouse production of related chenopods and other western shrubs has been described by Everett (1957), Ferguson and Monsen (1974), Landis and Simonich (1974), Augustine et al. (1979), Ferguson (1980) and Nelson (1984).

Based on results of test plantings, Ferguson and Frischknecht (1981) recommended use of spiny hopsage container stock for reclamation of reconstructed soils following mining in semiarid areas. Seedlings of 2 spiny hopsage (Uintah County, Utah and Kern County, Calif.) and a number of other chenopod shrub seed lots grown in Spencer-Lamaire "Rootrainers" were planted on 5 soil types including 4 topsoils and a shaley subsoil derived from oil shale at the Emery Coal Mine in central Utah (Ferguson and Frischknecht 1985). Mean average precipitation at the site is 192 mm. Each seedling was watered with 1 liter of water at the time of outplanting. Supplemental water was provided periodically during the first growing season. After 5 years, survival of spiny hopsage averaged 73% on the 4 topsoil sites and 44% on the shaley subsoil. Plant height averaged 0.25 m and diameter 0.33 m on the 4 topsoil sites. Mean height was 0.10 m and diameter 0.13 m on the shaley subsoil site.

A similar study was conducted at Sand Wash in the salt-desert zone of eastern Utah's Uintah Basin. Twenty-four chenopod shrub seed lots were fall seeded (1977) and spring transplanted (1988) on 0.3 m of native soil placed over approximately 0.8 m of processed oil shale (Frischknecht and Ferguson 1984). Due to drought and low germination, direct-seeded seed lots were replanted in fall 1988. Excellent germination of 1988, and in some cases, 1987 seedings occurred in 1989. After 5 years, plants established from seedings and transplanting were comparable in size. Spiny hopsage (Uintah Basin seed lot) survival averaged 56% and plant height 0.3 m.

Smith et al. (1978) recommended use of spiny hopsage container stock for eastern Sierra Nevada roadside plantings on rocky slopes in the upper sagebrush portion of the Upland Trans-Sierra vegetation in California. Acceptable success resulted from April planting when seedlings grown in plastic pots were placed in planting holes in barren rhyolite.

Tueller et al. (1974) recommended furrow-seeding grasses and spring planting containerized shrubs for revegetation projects in Hot Creek Valley, Nevada, a southern Great Basin location with annual precipitation of about 150 mm. Transplanted shrubs were provided with supplemental water during the first growing season. First-year survival of spring-transplanted spiny hopsage container stock on a big sagebrush site (*Artemisia* *tridentata* Nutt.) was 47%. Restricting revegetation projects to big sagebrush communities and years following exceptionally wet winters was recommended as trials planted on shadscale sites or initiated following unusually dry winters were largely unsuccessful.

Container stock of spiny hopsage and other native shrub species was planted in a series of studies to evaluate transplanting as a means of reestablishing vegetation following nuclear testing and related disturbances in the northern Mojave Desert portion of the Nevada Test site (Romney et al. 1971, Wallace and Romney 1974, Hunter et al. 1980b, Wallace et al. 1980). Seedlings were irrigated during the first season after planting to aid establishment. Greatest survival of spiny hopsage seedlings after 5 years was 60% (Wallace et al. 1977, 1980). At most planting sites, some shrubs were individually protected with chicken wire sleeves (25 mm mesh). Mean survival and growth were generally greater for fenced compared to non-fenced shrubs. Differences in establishment were attributed to reduced predation by rodents and rabbits, primarily valley pocket gophers (*Thomomys* *bottae* Edeux & Gervais), Merriam's kangaroo rats (*Dipodomys* *merriami* Mearns), grasshopper mice (*Onychomys* *torridus* Coues), deer mice (*Peromyscus* spp. Golger) blacktailed jack rabbits (*Lepus* *californicus* Gray), and desert cottontails (*Sylvilagus* *audubonii* Baird). Palatable shrubs were grazed most heavily during seasons when annual species were absent. Some fenced plants of palatable species were killed when burrowing rodents, particularly pocket gophers, were present in high densities. Plantings on a gravel excavation site with sandy to rocky soil not conducive to rodent burrowing received relatively light use, primarily by rabbits (Hunter et al. 1980b). Fencing was recommended as an inexpensive means of reestablishing seed sources of desired species in the absence of high densities of burrowing rodents (Hunter et al. 1980b). The animal repellant Z.I.P. was found to be as effective as fencing during the first 15 months following planting (Wallace and Romney 1974).

In discussing principles for revegetation of disturbed arid lands, Wallace et al. (1977, 1980) stated that in more arid portions of the Mojave Desert where conditions for germination and seedling survival are rarely met, revegetation requires preparation of moisture catchment basins, use of pioneering species, preservation of shrub clump fertile islands, fertilization, irrigation, organic amendments, and vigorous planting stock. They recommended use of rooted cuttings or container stock and late-fall or early-spring planting when seasonal moisture is most favorable (Romney et al. 1971, Wallace et al. 1980). Spring irrigation was most critical during years with low winter recharge. The importance of matching phenological stage of planting stock with that of native plants of the same species at or near the planting site was emphasized, particularly for spiny hopsage and other summer-dormant species.

MANUSCRIPT I

FIELD ESTABLISHMENT OF SPINY HOPSAGE

Abstract

Development of appropriate seeding technology is requisite to inclusion of spiny hopsage (Grayia spinosa [Hook.] Moq.) in revegetation projects on sites where the species has been depleted or lost due to livestock grazing practices or other human activities. This study examined the effect of seed source, planting date, and site preparation method on spiny hopsage emergence and seedling establishment. Seeds harvested from 3 collection sites were planted on rough or compact seedbeds in early fall, late fall, early spring, and late spring 1986-87 at the Birds of Prey and Reynolds Creek planting sites in southwestern Idaho. In 1987-88 plots were planted in late fall, early spring, and late spring at Reynolds Creek and in late fall, winter, and early spring at Birds of Prey. Plots 3 X 1.5 m replicated 4 times were drilled at a rate of 66 pure live seeds/m of row. Seedlings emerged from early fall, late fall, and winter plantings in early spring. Few seedlings emerged from spring plantings. Germination and seedling establishment were severely limited at Birds of Prey in 1986-87 and at both sites in 1987-88, probably due to low precipitation. March 1987 seedling density was greater on early fall (137.3 seedlings/m^2) compared to late fall (103.5 seedlings/m^2) plantings of 1 seed source. Density of the other 2 sources did not vary by fall planting date. Seedling density was greater on rough compared to compact seedbeds in April (51.3 seedlings/m^2 for rough and 41.4 seedlings/m^2 for compact) and May (32.6 seedlings/m^2 for rough and 25.7 seedlings/m^2 for compact), possibly due to improved microclimates on these plots. Many seedlings were lost due to dry soil conditions and predation by *Melanotrichus* ssp. nymphs. Seedling density and growth rate varied among the 3 seed sources. Seedlings developed a single shoot and a taproot system with few lateral roots during the first season. The globose, densely branched growth habit typical of mature plants developed during the second and third growing seasons. Results indicate overwinter stratification is required to relieve dormancy of these populations with seeding success highly dependent upon availability of moisture in early spring.

Key Words: germination, *Grayia spinosa*, revegetation, sagebrush steppe, salt desert shrubs, seedling establishment, utricles

Introduction

Several characteristics of spiny hopsage (Grayia spinosa [Hook.] Moq.) have generated interest in its use as a revegetation species. Where abundant, it furnishes palatable and nutritious late-winter and spring forage for wildlife and livestock (Dasmann and Blaisdell 1954, Gullion 1964, McCullough 1969, Krysl et al. 1984). The species' dense low-growing crown provides cover for small animals, reduces wind erosion, and stabilizes soil surfaces (USDA-SCS 1968, Institute for Land Rehabilitation 1979, Dittberner and Olsen 1983). Spiny hopsage is capable of resprouting following burning or mechanical damage (Daubenmire 1970, Smith 1974, Wasser 1982) and is least susceptible to burning damage during the period of summer dormancy (Rickard and McShane 1984).

To date, spiny hopsage has received limited use in reseeding projects. Early planting failures in Utah were attributed to placing seeds at excessive depths. Although Glazebrook (1941) recommended surface broadcasting, Kay et al. (1977) and Wood et al. (1976) found the small seeds (869,000-932,000/kg) (Smith 1974) emerged best when planted at depths of 10 mm or less. The appropriate season for planting in the northern portions of the species' range has not been determined. Eastern Washington collections examined by Glazebrook (1941) were nondormant, but King (1947) reported seeds from the same area required a 2-6-week stratification to germinate. Natural seedling emergence has been reported to occur in fall in eastern Washington (Glazebrook 1941) and in early spring in southwestern Idaho (N.L. Shaw, file data, 1989-90).

In the northern shrub steppe, spiny hopsage is commonly associated with a variety of salt desert shrub communities and drier portions of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle and A. Young] Welsh) communities. Technology is needed for establishing spiny hopsage from seed or planting stock on sites where populations have been depleted by livestock management practices or other human activities. Few woody species occur in these communities and most are not used in revegetation efforts. The objective of this study was to examine the effects of planting date and seedbed preparation on emergence and seedling establishment of 3 spiny hopsage populations at 2 southern Idaho sites.

Materials and Methods

Seed Collections

Mature utricles (fruits enclosed within the papery bracteoles) were harvested in June 1986 at Sponge Springs (SS86 seed collection), Malheur Co., Oreg. (43°47'42"N;117°25'59"W), Reynolds Creek (RC86A seed collection), Owyhee Co., Idaho (43°15'31"N;116°12'37"W), and at the Birds of Prey National Conservation Area (BOP seed collection), Ada Co., Idaho (43°14'31"N;116°21'43"W) (Table I.1). Seeds were air-dried for 2-4 weeks. Bracts were removed using a modified Dybvig seed cleaner (Shaw and Haferkamp 1990). Chaff was removed using an M2B air-screen cleaner and a seed blower. Conditioned seed was stored in plastic containers at approximately 3-5°C. Moisture content was 9.6% for the RC86A collection and 8.0% for the SS86 collection.

Planting Sites

Field plantings were made at the Birds of Prey and Reynolds Creek. The Birds of Prey site (43°17'59"N;116°22'0"W) is located approximately 36 km southwest of Boise, Idaho. Site characteristics and vegetation are as described for the seed collection site (Table I.1) located approximately 6 km to the southeast. Mean annual temperature is 11°C (Collett 1980). Temperature at the Kuna 2 weather station, approximately 20 km northwest of the site averages -2°C in January and 21°C in July (NOAA 1986). The frost-free season averages 150 days (Collett 1980). Approximately 56% of the mean annual precipitation is received between October and March (NOAA 1986). Soils are formed over loess on a basalt plain (Collett 1980). Depth to the hardpan is 0.5 to

1.0 m. Russian thistle (*Salsola iberica* Sennen & Pau), and clasping pepperweed (*Lepidium perfoliatum* L.) are common annuals on disturbances. A wildfire removed most woody cover from the site in July 1985 (M. Pellant, file data, USDI-BLM, Boise, Idaho, 1990). The burn was drill seeded in March 1986 to a mix of Fairway crested wheatgrass (*Agropyron cristatum* L. Gaertner), Siberian wheatgrass (*Agropyron sibiricum* [Willd.] Beauv.), Russian wildrye (*Elymus junceus* Fisch.), fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), and winterfat (*Ceratoides lanata* [Pursh] J.T. Howell). Seeding success was variable, possibly due to drought conditions.

The Reynolds Creek site (43°42'37"N;116°44'2"W) is located approximately 66 km southwest of Boise, Idaho and 2.5 km south of the Reynolds Creek seed collection site. Elevation is 1,200 m. Mean annual temperature is 8°C (C.L. Hanson, file data, USDA-ARS, Boise, Idaho, 1991). Temperature averages -2°C in January and 20°C in July. The frost free season averages 90-110 days (Stephenson 1977). Approximately 54% of the precipitation falls between October and March (C.L. Hanson, file data, USDA-ARS, Boise, Idaho, 1991). Snowfall accounts for about 20% of the precipitation (Stephenson 1977). Soils are fine loamy mixed mesic Typic Haplargids derived from granitic, basaltic, and rhyolitic alluvium (Stephenson 1977). Vegetation is as described for the seed collection site (Table I.1) with shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats) as an additional woody species. Russian thistle and clasping pepperweed are common annuals on disturbances. The site was control burned in August 1984 and fall seeded to Siberian wheatgrass, 'Nomad' alfalfa (*Medicago sativa* L.), and fourwing saltbush (J. Mowbray, file data, USDA-ARS, Boise, Idaho, 1990).

Precipitation, soil temperature (0-20-mm depth), and soil moisture content (0-30-mm depth), were measured on site at Birds of Prey and Reynolds Creek during the study. Soil moisture content was determined gravimetrically. Air temperature was measured on site at Birds of Prey and at the Reynolds weather station approximately 3 km south of the Reynolds Creek study site (NOAA 1986-88).

Seedling Establishment Study

A grid of ninety-six 3.0 X 1.5 m plots was established and planted at each location in 1986-87 and in 1987-88. Seedbeds were prepared by twice-over rototilling to a depth of 150 mm in fall. Residual rootcrowns of shrubs and perennial grasses were removed manually. Treatments were seed source (Table I.1), planting date (Table I.2), and site preparation (rough or compact seedbed surface) arranged in a randomized complete block design with 4 replications. Plot surfaces were prepared just prior to planting. Rough surfaces were created by hand raking. Compact surfaces were prepared by hand raking followed by twice over compaction with a roller 0.7 m wide and 0.5 m in diameter, weighing 109 kg.

Five rows, 3 m long and 0.3 m apart were planted in each plot using a single-row, small-plot, cone-type seeder. Viable seeds were planted approximately 5 mm deep at a rate of 66 seeds/linear meter of row, equivalent to $217/m^2$. Calculations of viability were based on results of tetrazolium staining tests (AOSA 1970, Belcher 1985). Both sites were fenced to exclude livestock. Weeds were removed manually from each site during the first growing season.

Seedling emergence and establishment from each planting were monitored on selected dates during the first growing season. The Reynolds Creek 1986-87 plantings were also monitored during the second growing season. Seedling density was measured on three 2-m transects and frequency of distribution on twelve 0.5-m transects in each plot. Seedling counts for the Birds of Prey 1986-87 planting were made on 22 April and 25 March 1987; counts for the 1987-88 planting were made on 19 April, 20 May, and 27 June 1988. Counts for the Reynolds Creek 1986-87 planting were made on 27 March, 23 April, 24 May, and 13 July 1987 and on 28 April and 26 July 1988. New seedlings emerging from this planting were also counted on 11 April and 13 July 1989. Counts for the 1987-88 planting were made on 19 April, 26 May, and 24 June 1988.

Three seedlings (1 small, 1 average, 1 large) were excavated from each Reynolds Creek 1986-87 early fall and late fall plantings between 11 and 17 July 1987. Dry weights of roots, shoots, and leaves; root-shoot ratios, and root and shoot lengths were measured. Total leaf area for each seedling was measured using a Li-Cor 3100 leaf area meter (LI-COR, Inc., Lincoln, Neb.). Five seedlings were harvested at random from each plot on 28 June 1988 for shoot height and dry weight determinations.

Statistical Analysis

Effect of seed source, planting date, and seedbed preparation on seedling emergence, establishment, and seedling growth parameters were evaluated by analyses of variance. Counting dates were analyzed separately. Means were separated by Fisher's least significant difference. The square root transformation was used to normalize seedling emergence and establishment data. Frequency data were transformed for analysis with arcsin $\sqrt{p}$. Means and standard errors were calculated by seed source to describe development of seedlings harvested at Reynolds Creek in July 1987.

Results

1986-87 Birds of Prey Plantings

Site Conditions

December 1986 and January 1987 were dry at the Birds of Prey site; precipitation totaled only 12 mm (Fig. I.1). Heavy rains fell in late May. Surface soils were dry on all 4 planting dates (Fig. I.2). Seedbeds were open during most of the fall and winter due to low snowfall. Minimum air temperatures and maximum and minimum soil temperatures were below freezing through January (Figs. I.3 and I.4). Nightly frosts occurred through February. With few exceptions, maximum and minimum air and soil temperatures in March and April were in the 0-15°C range considered effective for stratification of many species (Bewley and Black 1982).

Fall Plantings

Most seedling emergence occurred between 1 and 10 March. During this period, air temperature maximums averaged 15°C and minimums averaged 3°C (Fig. I.3). Soil temperature maximums during emergence averaged 12°C and minimums averaged 2°C (Fig. I.4). Twenty-three days with minimum air temperatures at or below freezing occurred after earliest emergence (Fig. I.3).

Seedling density on 25 March averaged $2.8/m^2$ for the Reynolds Creek and Sponge Springs seed lots and $1.6/m^2$ for the Birds of Prey seed lot. Some dead or withering seedlings were observed. All but 8 seedlings succumbed by 22 April, apparently as a result of dry soil conditions. A few seedlings were damaged or destroyed by seed harvester ants (*Pogonomyrmex salinus* Olsen). All seedlings succumbed by 23 May.

Poor seedling emergence resulted in uneven seedling distribution. Sponge Springs seedlings (34.2% frequency) were most evenly distributed on 25 March and Birds of Prey seedlings least evenly distributed (20.2% frequency). Distribution of Reynolds Creek seedlings was similar to the other 2 seed lots, with frequency averaging 27.1%.

Spring Plantings

No seedlings emerged from early or late spring plantings, even following heavy May rainfall. Undetected seedlings may have emerged and died between observation dates.

1986-87 Reynolds Creek Plantings

Site Conditions

December 1986 and January 1987 precipitation was 27% of normal (Fig. I.5). With the exceptions of above average rainfall in February and early March and record rainfall in late May, dry conditions prevailed through the spring and summer months (Figs. I.5 and I.6). Early fall and late fall plantings were exposed to below freezing minimum air temperatures almost nightly through March. The last frost occurred in mid-April. Minimum air temperatures were in the 0-15^{o}C range through May and intermittently through summer leaf fall in late July (Fig. I.7).

Early Fall and Late Fall Plantings

Most seedlings emerged from early fall and late fall plantings between 4 and 15 March. During this period growth conditions were good with precipitation totaling 13 mm (Fig. I.5). Air temperature maximums averaged 13°C and minimums averaged 2°C (Fig. I.7). Air temperature minimums were at or below freezing on 32 days after earliest seedling emergence. The last frost occurred on 22 May.

By 22 March greater densities of SS86 seedlings were present on early fall compared to late fall plantings, but density of BOP86 and RC86A seedlings did not vary with planting date (Table I.3). SS86 seedlings were more numerous than either RC86A or BOP86 seedlings on both early fall and late fall plantings. Densities of RC86A and BOP86 seedlings on early fall plantings did not differ, but density of RC86A seedlings exceeded BOP86 seedlings on late fall plantings.

Seedling density of each of the 3 seed sources did not differ between rough and compact seedbeds (Table I.3). Density was greater for the SS86 compared to RC86A or BOP86 seed source on both seedbeds, while density was greater for RC86A compared to BOP86 seedlings on rough, but not compact seedbeds.

By 24 April, many seedlings had died or were withering, presumably in response to low soil moisture conditions (Table I.4). A small percentage of seedlings were damaged or killed by nymphs of a plant bug (Melanotrichus spp.). Density of surviving seedlings was greater on rough compared to compact seedbeds. Seedling density was greatest for the SS86 and lowest for the BOP86 seed source with density of the RC86A source intermediate.

Additional seedlings were lost between 23 April and 24 May in response to continued dry soil conditions and predation by Melanotrichus spp. nymphs (Table I.4). A small number of seedlings were also damaged or broken by a hail storm. Seedling density remained greater on rough compared to compact seedbeds. SS86 seedlings were more numerous than BOP86 seedlings. Density of RC86A seedlings was similar to density of the other 2 sources.

The final seedling count for 1987 was completed on 13 July as leaves were beginning to dry prior to abscission and onset of summer dormancy (Table I.4). New seedlings emerged in response to unusually heavy rains in late May (Fig. I.5). Difficulty in distinguishing all recently emerged seedlings from earlier emergents prevented determination of seedling losses and gains since the previous sampling date. Few *Melanotrichus* spp. nymphs were noted, but drought effects continued to impact seedling survival and vigor. Seedling density no longer differed between seedbed types, averaging $28.9/m^2$. Relative seedling densities for the 3 seed sources were as noted for the April count.

Low precipitation and dry soil conditions prevailed during spring 1988 (Figs. I.5 and I.6), but few withering or dead seedlings were noted on the 1986-87 plots. No new seedlings were noted to emerge from early fall or late fall 1986-87 plantings. On 28 April 1988 relative densities by seed source had not changed from the previous year: density was greater for SS86 ($33.0/m^2$) compared to BOP ($20.4/m^2$) seedlings. Density of RC86A seedlings was similar to the other 2 sources, averaging $26.2/m^2$. Seedling density averaged $22.2/m^2$ on 26 July.

Good seedling distribution, resulting from high emergence in March 1987, persisted through the first 2 growing seasons. Frequencies ranged from a mean of 98.4% on 27 March 1987 to 86.3% on 13 July 1988.

Spring Plantings

Although minimum daily air and soil temperatures were within the stratification range during much of March and April 1987, the process may have been limited by high daytime temperatures and insufficient soil moisture. Density on spring 1986-87 plantings in 1987 and 1988 ranged from 0.0 seedlings/m^2 during the 1987 growing season to 0.2 seedlings/m^2 in April 1988. Additional seedlings emerged from spring 1987 plantings following March 1989 rainfall totaling 39 mm (C.L. Hanson, file data, USDA-ARS, Boise, Idaho, 1989). On 11 April 1989 seedling density was greater on SS86 plots (1.3 seedlings/m^2) than on BOP86 or RC86A plots (0.1 seedlings/m^2). Mean density was 0.4 seedlings/m^2 on 13 July 1989.

Seedling Development

Seedling size on all early fall and late fall plantings varied considerably following 1 growing season (Table I.5). Most seedlings developed a single main shoot with or without short lateral branches and a strong taproot system with few lateral branches (Fig. I.8 and Table I.5). In contrast, mature plants produce a moderately deep, diffusely branched root system lacking a strong taproot/lateral root structure (Wallace and Romney 1972, Manning and Groeneveld 1990).

By June 1988, seedling height averaged 110 mm (Table I.6). Many seedlings had begun to assume the globose, densely branched habit of mature plants. Weight of RC86A and SS86 seedlings was greater on compact compared to rough seedbeds, while weight of BOP86 seedlings was similar on both seedbeds. Seedling weight of SS86 and RC86A seedlings was greater than BOP86 seedlings on compact seedbeds, while weight was greater for SS86 compared to BOP86 seedlings on rough seedbeds.

1987-88 Plantings

Birds of Prey Site Conditions

Due to lack of snowfall, seedbeds at Birds of Prey were open and exposed to the effects of wind throughout most of the winter. Surface soil was frozen intermittently following precipitation events which totaled 30 mm from December through February (Figs. I.1 and I.2). Surface soils were dry on all 3 planting dates (Fig. I.2). Seeds planted in late fall and winter were subjected to below freezing surface soil temperatures almost continuously from early December through early February (Fig. I.4). Minimum daily soil and air temperatures were below $0^{\circ}C$ almost nightly through February and within the $1\text{-}15^{\circ}C$ range with occasional frosts through mid-May (Figs. I.3 and I.4).

Reynolds Creek Site Conditions

December 1987 through July 1988 precipitation at Reynolds Creek was 63% of the long-term average (Fig. I.5). Late fall plantings were under snow cover almost continuously through mid-January. Surface soils were dry on the early and late spring planting dates (Fig. I.6). Minimum daily soil and air temperatures were below $0^{\circ}C$ almost nightly through March and within the $1\text{-}15^{\circ}C$ range with occasional frosts through early May (Figs. I.7 and I.9)

Seedling Emergence

Very few seedlings emerged at either study site in 1988 due to dry seedbed conditions (Figs. I.5 and I.6). Emerging seedlings were first noted on 13 March at Birds of Prey and 1 March at Reynolds Creek. Seedling density did not vary with planting date, seed lot, or site preparation technique on any counting date at either site. Nearly all seedlings surviving until June 1988 emerged from late fall plantings. Establishment from late fall plantings averaged 0.6 seedlings/m^2 at Birds of Prey and 0.8 seedlings/m^2 at Reynolds Creek.

Discussion and Conclusions

Spiny hopsage can be established by direct seeding on southern Idaho rangelands. However, results at 2 study sites during 2 years of low precipitation indicate a need for further work to more closely define requirements for emergence and seedling establishment, develop technology to enhance planting success, and determine the economic feasibility of adding the species to revegetation projects.

Planting to provide overwinter stratification may be essential for release of dormancy. Laboratory work indicated all 3 seed lots required 45-60-day stratification treatments at 2-5°C for germination (N.L. Shaw, file data, 1987). A requirement for overwinter stratification and low temperatures for germination is common among perennial Great Basin species adapted to terminate dormancy in early spring when soil moisture conditions are most likely to support germination and seedling emergence (Vallentine 1980). Decreased dormancy persisting into early summer in at least some ungerminated seed was indicated by scattered emergence at Reynolds Creek following heavy rainfall in May 1987.

Emergence of seedlings from early and late fall plantings at Reynolds Creek in 1987 occurred rapidly and uniformly at both sites as the soil surface rose above freezing in spring. Haferkamp et al. (1990) reported late fall and winter planting favored germination of prostrate kochia (Kochia prostrata [L.] Schrader) at similar low temperatures in southeastern Oregon. Young spiny hopsage seedlings were capable of surviving periods of below-freezing temperatures. Glazebrook (1941) commented that spiny hopsage seedlings could be frozen solid "while still very young" and yet survive. Early emergence maximizes the ability of seedlings to compete with cheatgrass and other winter and summer annuals (Vallentine 1980) and also permits maximal seedling growth prior to soil moisture depletion and onset of summer dormancy. Emerging seedlings develop a deep taproot system during the first growing season. Large seedlings were noted to retain leaves and continue growth longer than small ones (N.L. Shaw, file data, 1987-88).

The surface compaction treatment was designed to increase uniformity of seeding depth. On both the compact and rough seedbeds, soil was compacted directly over the seeds by the press wheel of the drill. Greater survival on rough surfaces through the May evaluation at Reynolds Creek in 1987 suggests average planting depth in these plots was not excessive. The rough surface may have provided more favorable microclimates for initial emergence. After 2 growing seasons, however, seedling weight of 2 of the 3 seed sources was greater on compact compared to rough seedbeds.

The apparently greater germinability and vigor of the SS86 seed lot was not examined further. Differences could be genetic or environmental in nature with the later relating to factors impacting seed maturation, harvest date, and seed handling and storage. Long term adaptability of the Sponge Springs seed source to the planting sites is not known.

Poor emergence at Birds of Prey and high attrition of seedlings at both sites was not unexpected given the generally dry conditions both years. Native spiny hopsage seedlings are rarely observed in southern Idaho or eastern Oregon, but are most common in high moisture years. They generally emerge beneath the densest portions of nurse plant canopies (Beatley 1979/80; N.L. Shaw, file data, 1989; Manning and Groeneveld 1990) where competition with other species is reduced and temperature and moisture conditions ameliorated by shading and litter. Rickard et al. (1988) reported areas shaded by spiny hopsage canopies averaged 10°C cooler than adjacent open areas. These conditions contrast strongly with seedbed conditions provided on the seeded plots, but may have been more closely approximated by rough compared to compacted seedbed surfaces.

Seeds failing to germinate during dry years may accumulate in the soil seed bank and could contribute to episodic seedling establishment in good moisture years as has been reported by Wallace and Romney (1972) and El-Ghonemy et al. (1980) for spiny hopsage in the Mojave Desert. Kay et al. (1988) reported spiny hopsage seeds remained viable in sealed storage at room temperature for 14 years. Frischknecht and Ferguson (1984) reported excellent second-year germination of several chenopod shrub seed collection planted in Utah's Uinta Basin during a drought year.

This work indicates successful inclusion of spiny hopsage in rangeland seedings requires overwinter stratification. Early spring emergence may be high if adequate soil moisture is present, but may be low if soils are dry and germination fails to occur. Site preparation measures to provide water catchment and shading may be beneficial to achieve high establishment percentages.

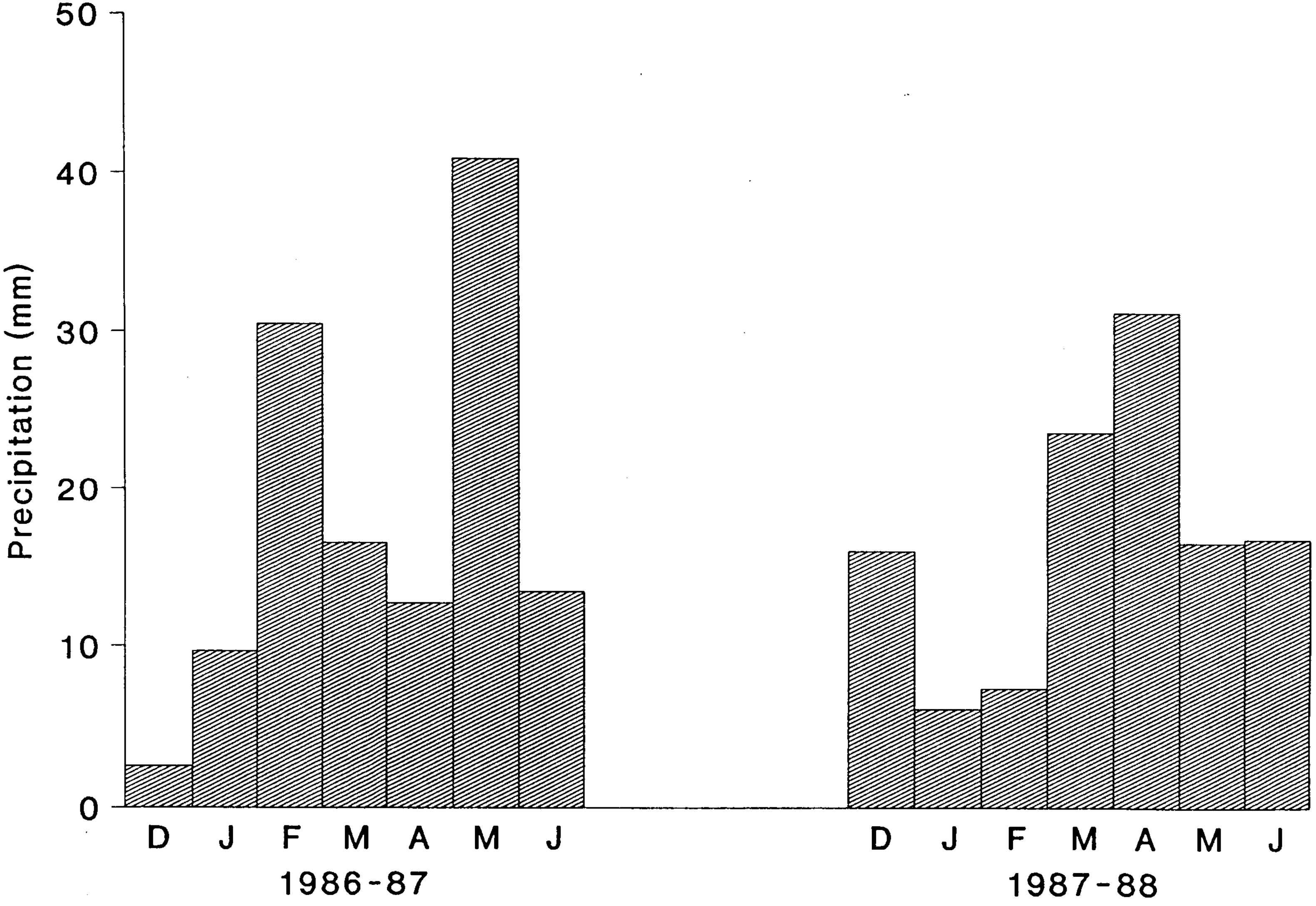

Fig. I.1. December to July precipitation for the Birds of Prey planting site, southwestern Idaho, 1986-87 and 1987-88.

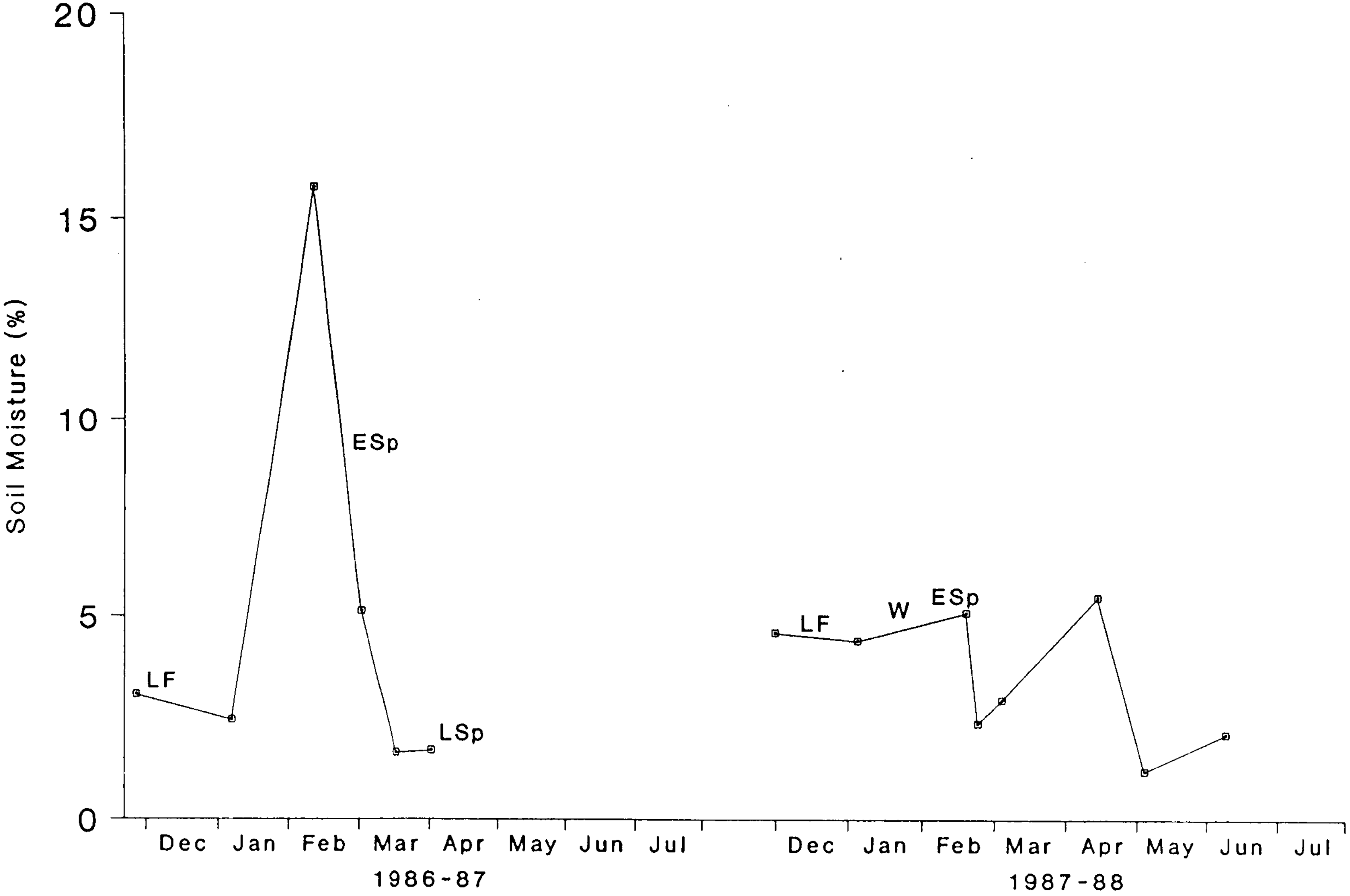

Fig. 1.2. December to July soil moisture profile (0-30-mm depth) for the Birds of Prey planting site, southwestern, Idaho, 1986-87 and 1987-88. Planting dates: LF=late fall, W=winter, ESp=early spring, LSp=late spring.

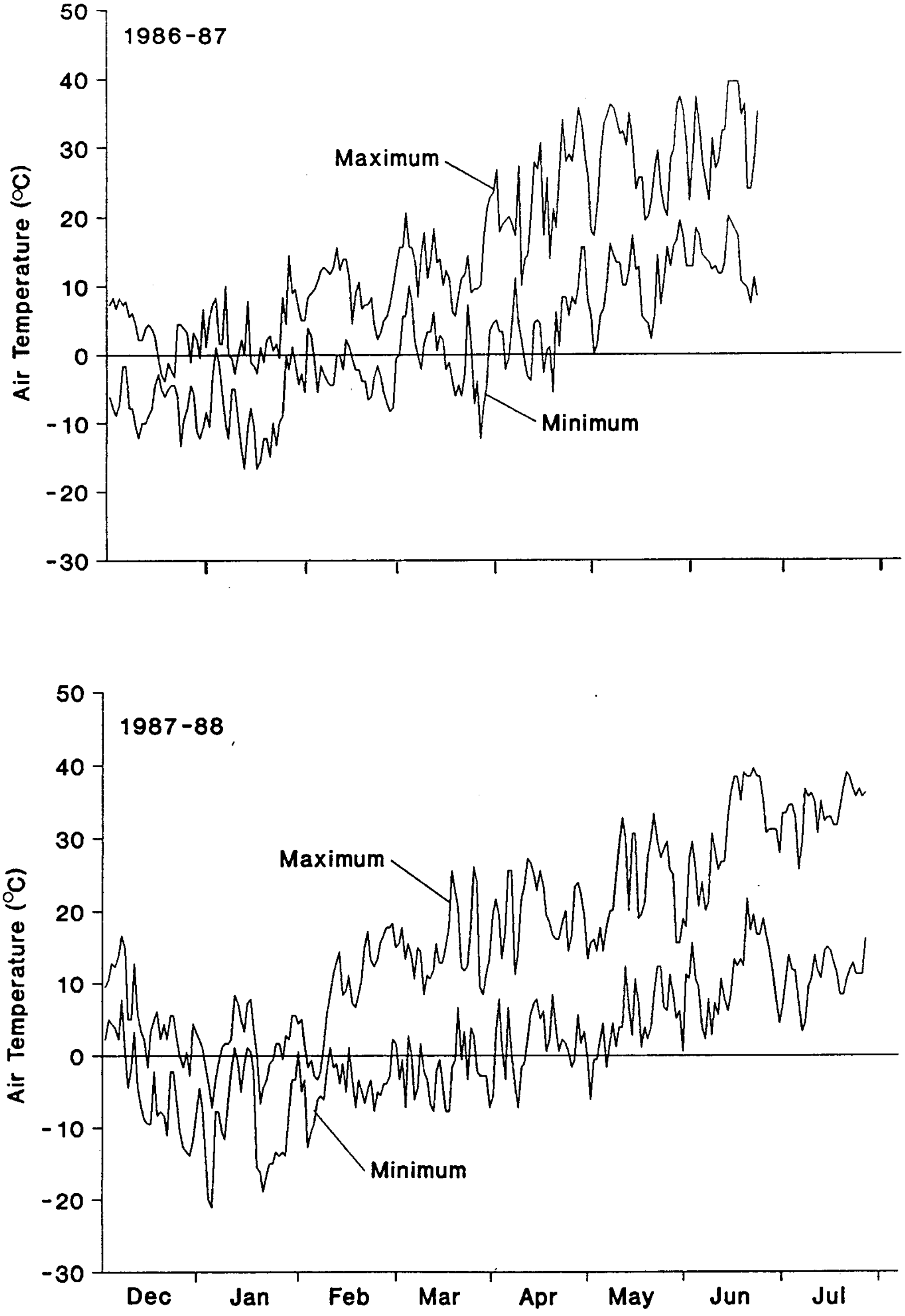

Fig. I.3. December to July air temperature profile for the Birds of Prey planting site, southwestern Idaho, 1986-87 and 1987-88.

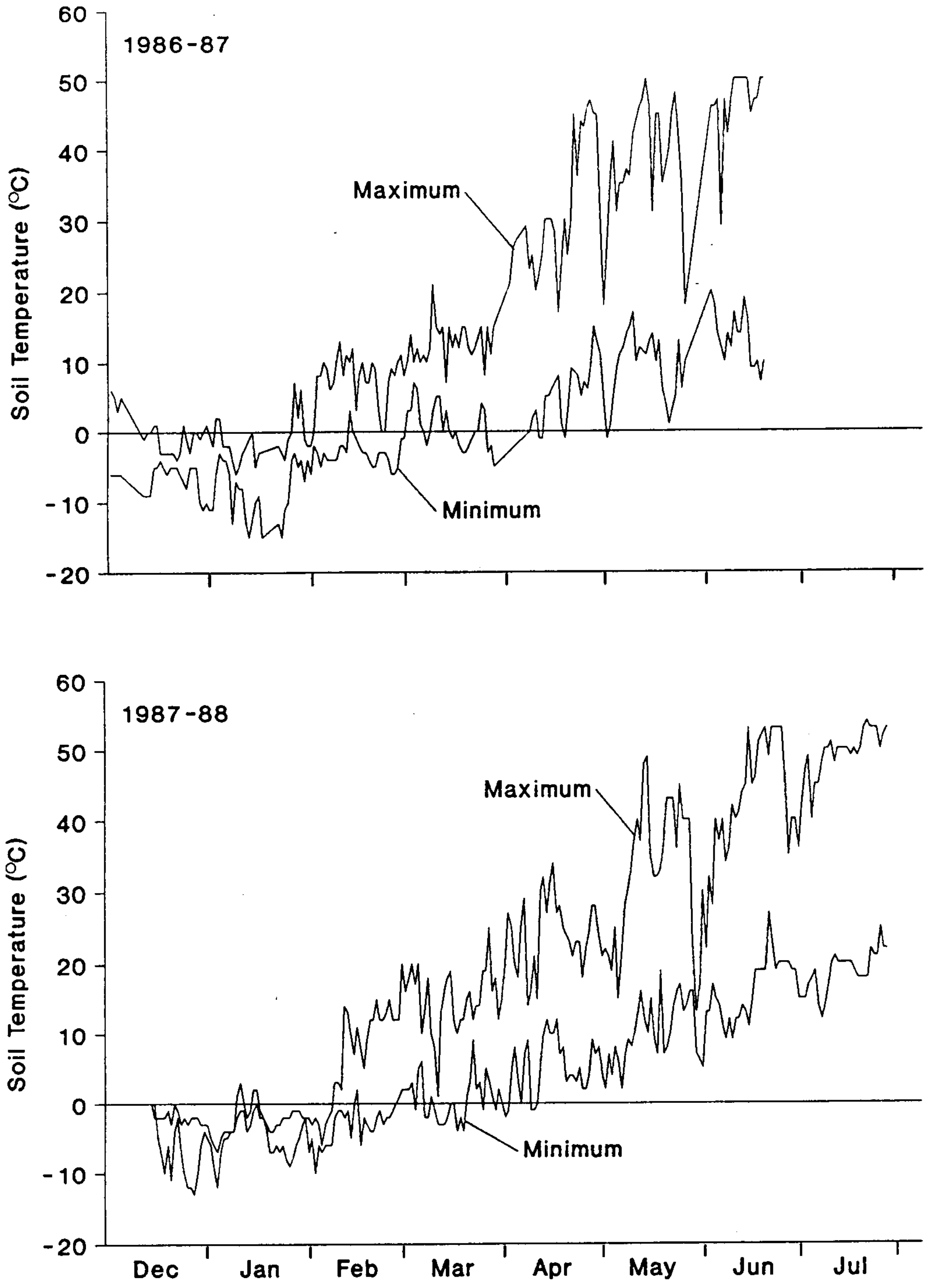

Fig. I.4. December to July soil temperature profile (0-20-mm depth) for the Birds of Prey planting site, southwestern Idaho, 1986-87 and 1987-88.

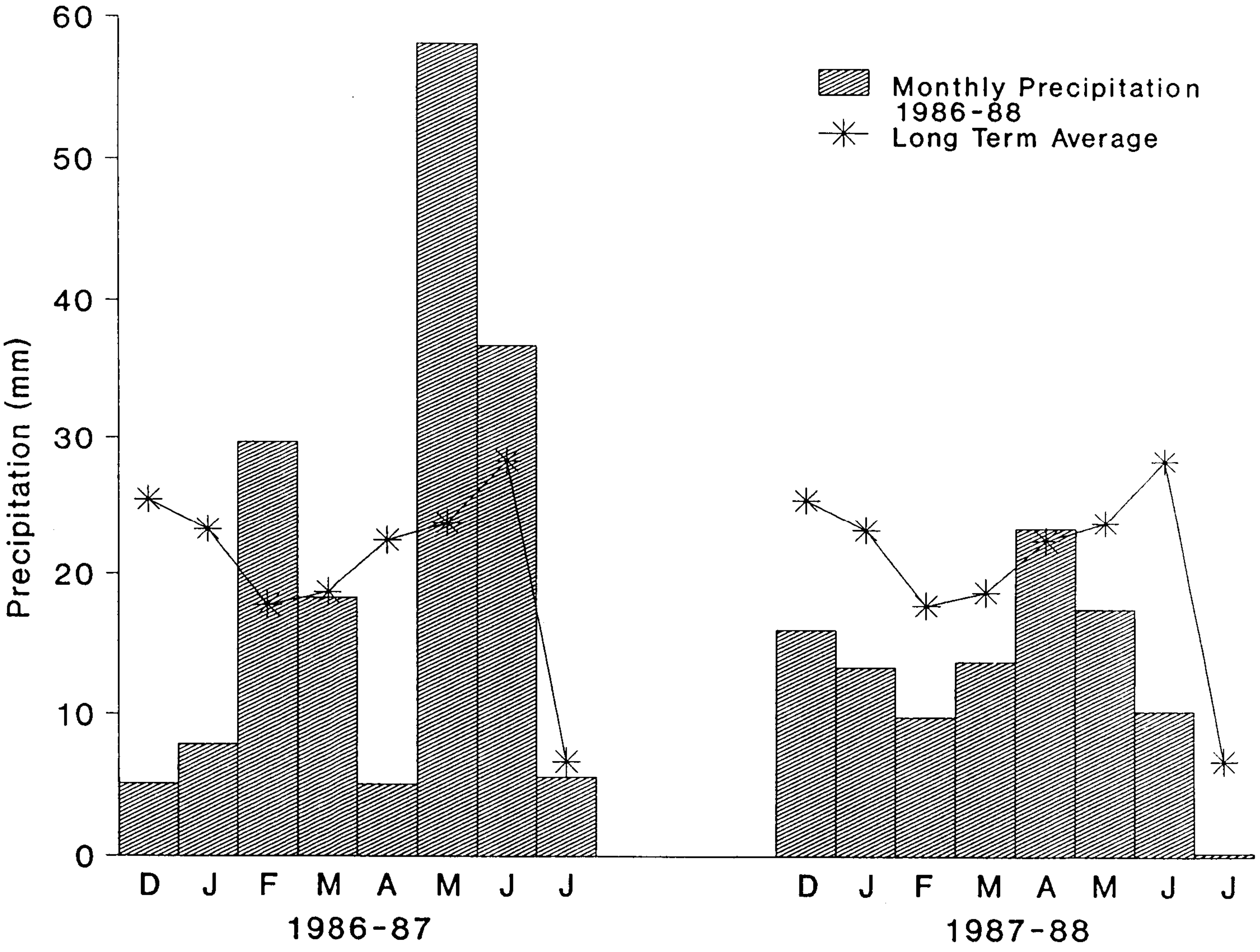

Fig. I.5. December to July precipitation for the Reynolds Creek planting site, southwestern Idaho, 1986-87 and 1987-88 and 21-year average.

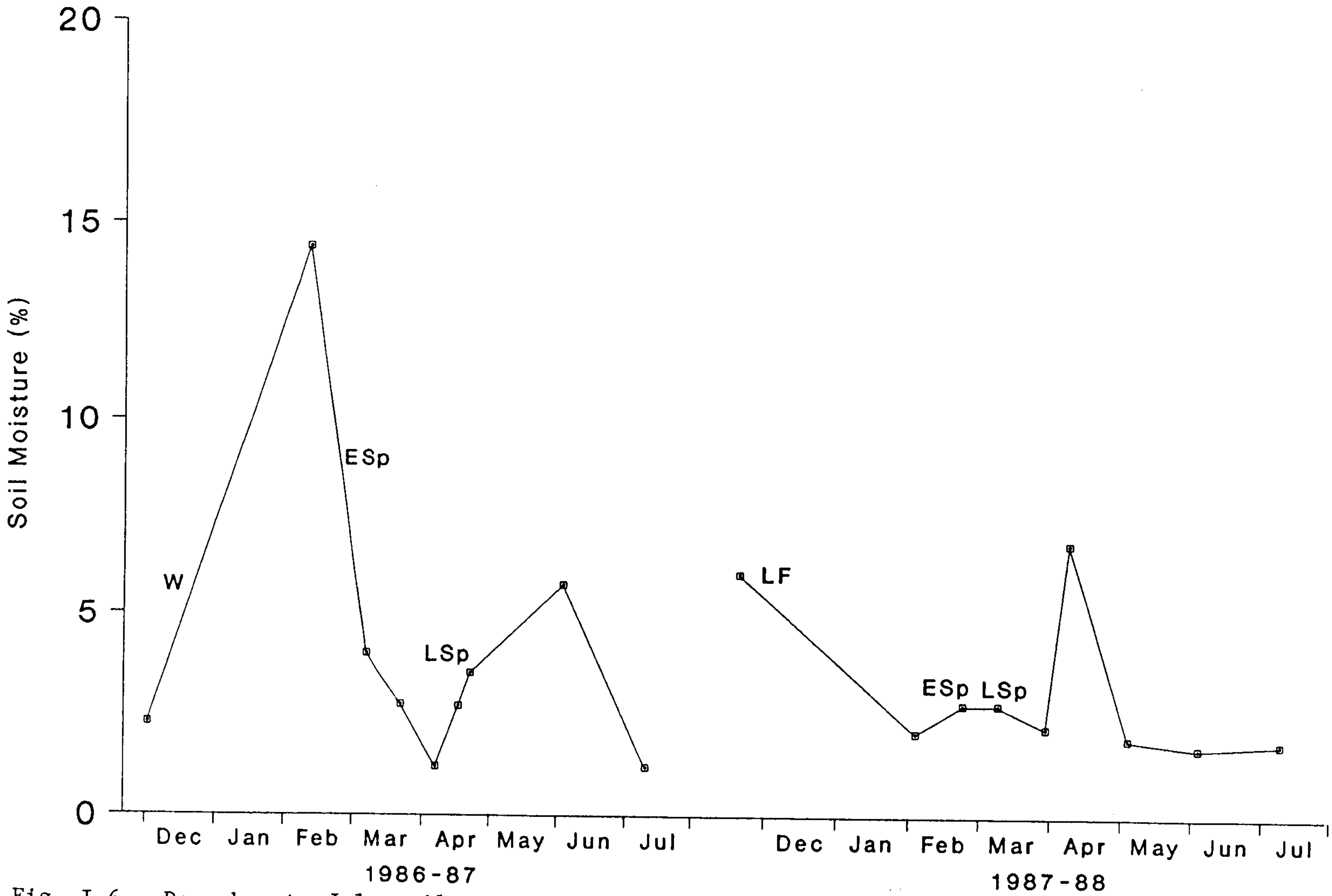

Fig. I.6. December to July soil moisture profile (0-30-mm depth) for the Reynolds Creek planting site, 1986-87 and 1987-88. Planting dates: LF=late fall, W=winter, ESp=early spring, LSp= late spring.

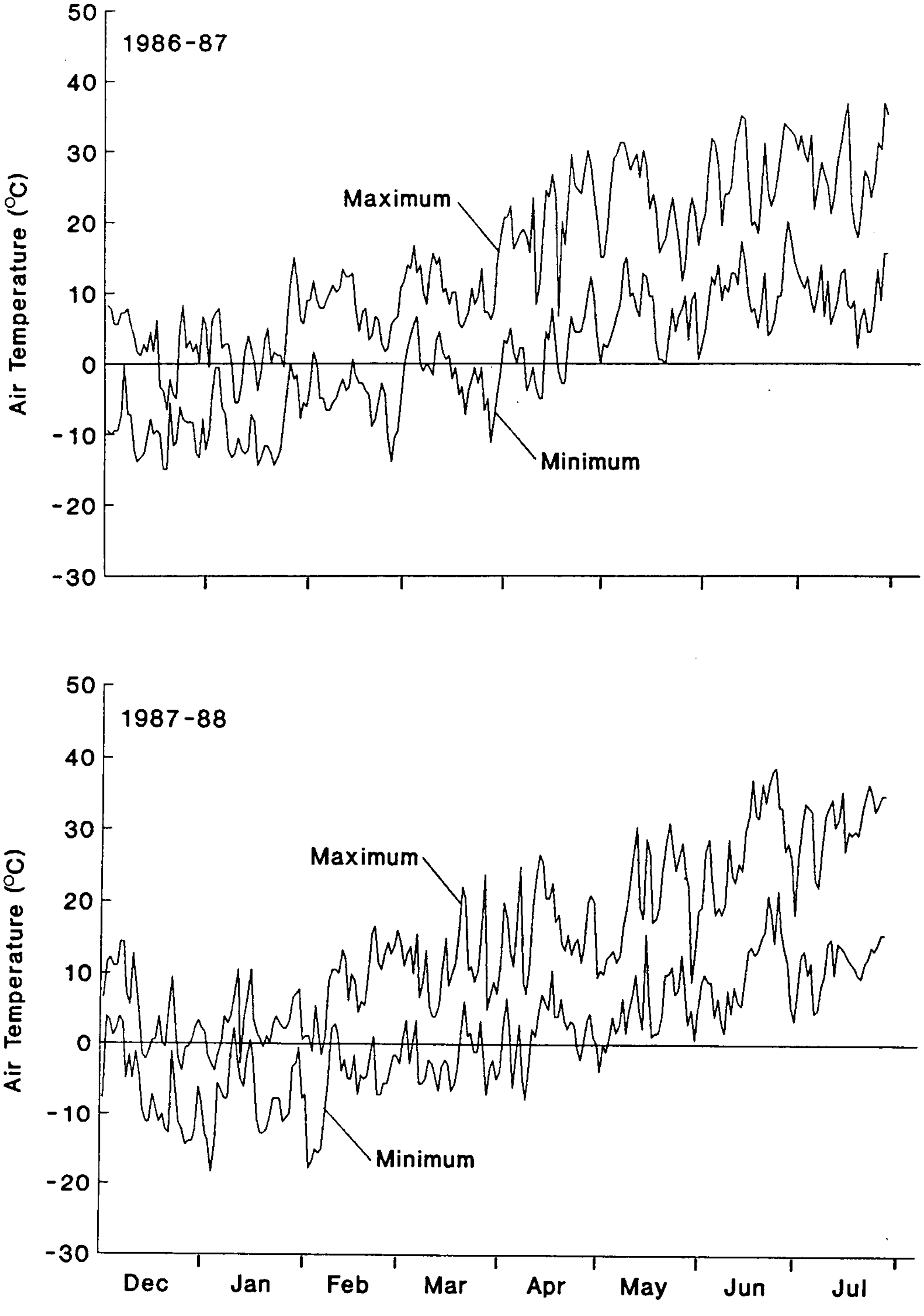

Fig. I.7. December to July air temperature profile for Reynolds, southwestern Idaho, 1986-87 and 1987-88.

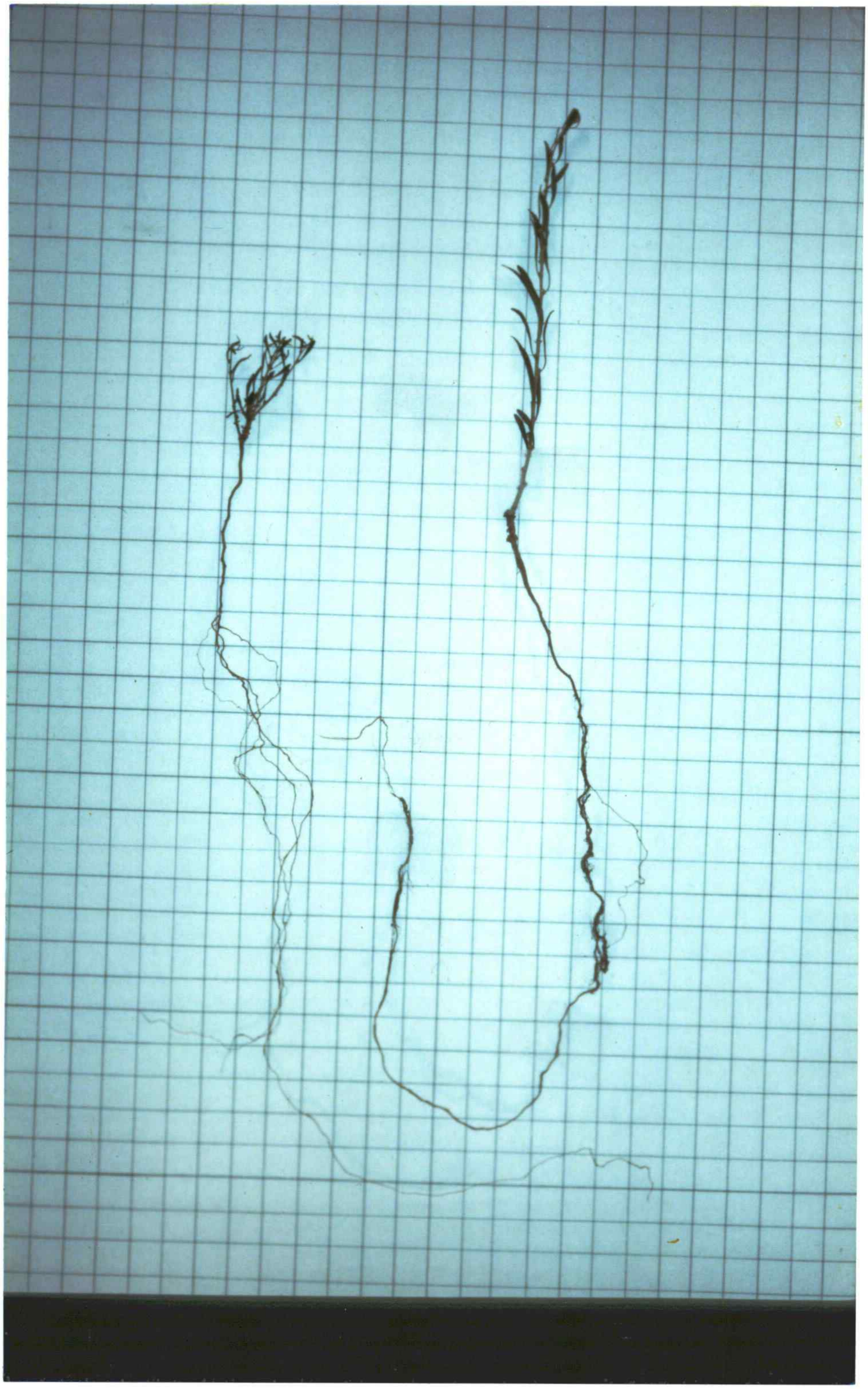

Fig. I.8. Spiny hopsage seedlings (Sponge Springs 1986 seed lot, early fall planting, rough seedbed), Reynolds Creek 1986-87 plots, July 16, 1987.

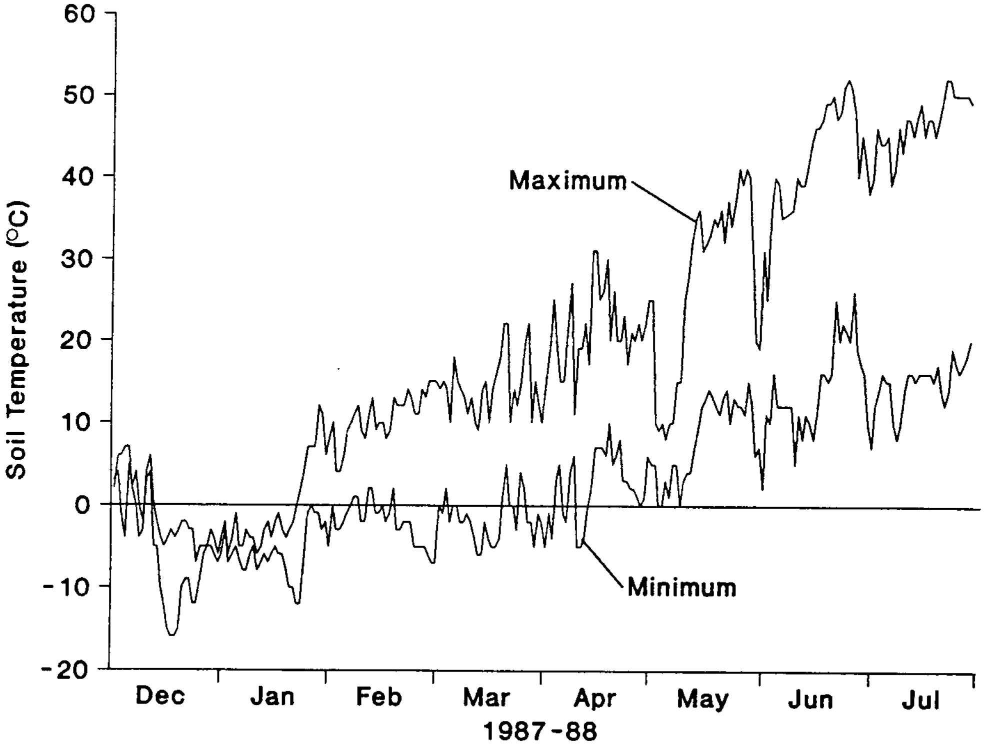

Fig. I.9. December to July soil temperature profile (0-20-mm depth) for the Reynolds Creek planting site, southwestern Idaho, 1987-88.

Table I.1. Characteristics of spiny hopsage utricle collection sites.

	Collection Site		
	Reynolds Creek	Sponge Springs	Birds of Prey
Location	Northern foothills of Owyhee Mountains, southwestern Idaho	Malheur Basin, southeastern Oregon	Snake River Plains, southwestern Idaho
Vegetation	*Artemisia tridentata* ssp. *wyomingensis* *Grayia spinosa*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis* *Ceratoides lanata*, *Grayia spinosa*, *Poa sandbergii*
Elevation (m)	1,260	991	850
Precipitation (mm)	249[1]	228[3]	248[5]
Soil	Coarse-loamy, mixed, non-acid, mesic Xeric Torriorthents[2]	Fine-loamy, mixed, mesic Xerollic Durargids[4]	Coarse, silty, mixed, mesic Haplo Xerolic Durorthids[6]

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[1] C.L. Hanson (file data, USDA-ARS, Boise, Idaho, 1992).
[2] Stephenson (1977).
[3] J.M. Findley (file data, USDI-BLM, Vale, Oregon, 1990).
[4] Oregon Water Resources Board (1969).
[5] Mean annual precipitation at the Kuna 2 weather station, approximately 20 km northeast of the collection site (NOAA 1986).
[6] Collett (1980).

Table I.2. Planting dates for Birds of Prey and Reynolds Creek plots, southwestern Idaho, 1986-87 and 1987-88.

		Date	
		Location	
Planting	Year	Birds of Prey	Reynolds Creek
Late Fall	1986-87	Nov. 12	Nov. 5
	1987-88	Dec. 17	Dec. 7
Winter	1986-87	Dec. 2	Dec. 11
	1987-88	Jan. 26	________[1]
Early Spring	1986-87	Mar. 11	Mar. 14
	1987-88	Feb. 19	Feb. 21
Late Spring	1986-87	Apr. 8	Apr. 12
	1987-88	________[1]	Mar. 13

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[1] Plots not planted due to adverse weather conditions.

Table I.3. Spiny hopsage seedling density on Reynolds Creek 1986-87 plots, March 22, 1987.

Planting Date	Site Preparation	Seed Lot RC86A	Seed Lot SS86	Seed Lot BOP86
		seedlings/m^2	seedlings/m^2	seedlings/m^2
Late Fall		86.0Ab[1]	137.3Aa	71.0Ab
Winter		69.0Ab	103.5Ba	50.7Ac
		seedlings/m^2	seedlings/m^2	seedlings/m^2
	Rough	89.1Ab	133.0Aa	62.8Ac
	Compact	66.0Ab	107.7Aa	58.9Ab

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[1] Site preparation means within seed lots followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within seed lots followed by similar lower case letters do not differ significantly at $p \leq 0.05$. Seed lot means within site preparation methods or planting dates followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

Table I.4. Spiny hopsage seedling density on Reynolds Creek 1986-87 plots on selected 1987 dates.

	Site Preparation		Seed Lot		
Counting Date	Rough	Compact	RC86A	SS86	BOP86
	seedlings/m^2				
April 23	51.3a	41.4b	42.5b	61.1a	35.5c
May 24	32.6a	25.7b	29.2ab	34.7a	23.6b
July 13	31.9a	25.9a	29.4ab	35.5a	21.7b

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[1] Site preparation means within counting dates followed by similar lower case letters do not differ significantly at $p \leq 0.05$. Seed lot means within counting dates followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

Table I.5. Means and standard errors for spiny hopsage seedling measurements, Reynolds Creek 1986-87 planting.

Seedling Measurement	Seed Lot								
	RC86A			SS86			BOP86		
	Large	Medium	Small	Large	Medium	Small	Large	Medium	Small
Shoot Length (mm)	98	50	22	109	62	24	84	54	22
	(10)	(5)	(2)	(11)	(4)	(3)	(10)	(5)	(2)
Root Length (mm)	380	287	215	369	237	205	294	242	169
	(43)	(40)	(44)	(52)	(44)	(35)	(35)	(39)	(39)
Leaf Area (mm^2)	749	292	97	904	279	84	491	224	56
	(86)	(37)	(16)	(136)	(36)	(12)	(60)	(31)	(8)
Leaf Weight (g)	0.16	0.05	0.01	0.19	0.05	0.01	0.10	0.04	0.01
	(0.03)	(0.01)	(0.00)	(0.03)	(0.01)	(0.00)	(0.01)	(0.01)	(0.00)
Stem Weight (g)	0.25	0.10	0.02	0.34	0.10	0.03	0.16	0.05	0.01
	(0.04)	(0.03)	(0.00)	(0.10)	(0.03)	(0.01)	(0.01)	(0.00)	(0.00)
Root Weight (g)	0.19	0.06	0.02	0.20	0.07	0.03	0.14	0.04	0.02
	(0.03)	(0.01)	(0.01)	(0.03)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)
Root/Shoot	0.58	0.75	0.56	0.48	0.50	0.61	0.83	0.80	0.91
	(0.16)	(0.13)	(0.10)	(0.10)	(0.04)	(0.10)	(0.33)	(0.47)	(0.30)

Table I.6. Dry weight of spiny hopsage seedlings by seed lot and seedbed preparation method, Reynolds Creek 1986-87 plots, June 26, 1988.

Seedbed Preparation	Seed Lot Birds of Prey	 Reynolds Creek	 Sponge Springs
	---------------dry weight (g)-------------		
Rough	1.2 Ab	1.3 Bab	1.6 Ba
Compact	1.0 Ab	2.0 Aa	2.2 Aa

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[1] Seedbed preparation means within seed lots followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Seed collection means within site preparation methods followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

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MANUSCRIPT II

GERMINATION AND SEEDLING ESTABLISHMENT OF SPINY HOPSAGE IN RESPONSE TO PLANTING DATE AND SEEDBED ENVIRONMENT

Abstract

Reestablishment of spiny hopsage (Grayia spinosa [Hook.] Moq.) in the shrub steppe is hindered by a lack of seeding technology. This study examined the effect of planting date and seedbed environment on seed germination and seedling establishment. Seeds harvested from 2 collection sites were planted in tilled seedbeds at 2 southwestern Idaho locations in 1987-88. Plantings were conducted at 1 location in late fall, winter, and early spring and at the second location in late fall, early spring and late spring. Plots 3 X 1.5 m replicated 4 times were drilled at a rate of 66 pure live seeds/m of row. Seeds collected from the 2 sites in 1986 and 1988 were planted in tilled seedbeds at the 2 locations in late fall, early spring, and late spring 1988-89. Seeds were broadcast at a rate of 400 pure live seeds/m^2 in 0.25 m^2 plots replicated 10 times. Seeds enclosed in nylon bags were planted in the field in late fall, winter, early spring, and late spring of each year. On each succeeding planting date and in early summer, 5 bags of each seed lot placed in soil on each of the earlier planting dates were recovered and their moisture content, viability, and germination compared to air-dry controls stored in the laboratory. Germination and seedling emergence were severely limited in 1987-88, probably because of low precipitation. At both locations, seedlings established only from late fall plantings at densities of 0.3 and 0.7/m^2. Greater March precipitation in 1989 may have favored seedling emergence at both locations. Establishment from late fall plantings was 6.0 and 25.6 times greater than from early spring plantings. Incubation in soil from late fall to early spring 1987-88 increased laboratory germination

6.0-11.4 times and germination rate by 12.4 and 13.1 days. Germination of seeds incubated in soil from winter to early spring was 1.4-6.3 times greater than controls and germination 3.6 and 8.5 days faster. In 1988-89 germination of seeds incubated in soil from late fall to winter was 17 times greater than controls and germination rate 10.2 and 11.3 days faster. Germination of seeds incubated in soil from winter to early spring was 4.5 and 7.1 times greater than controls and 10.5 and 10.6 days faster. Results indicate late fall or early winter planting are essential to release dormancy and permit early spring germination when surface soils are moist.

Key Words: chenopod shrubs, *Grayia spinosa*, salt desert shrubs, seedling establishment, shrub steppe, revegetation

Introduction

Spiny hopsage (Grayia spinosa [Hook.] Moq.) is a summer deciduous chenopod shrub endemic to the interior western United States. In the shrub steppe it commonly occurs in drier portions of Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis [Beetle and A. Young] Welsh) communities and in a variety of salt desert shrub communities (Daubenmire 1970, 1978; Blaisdell and Holmgren 1984). Highly palatable in spring, spiny hopsage is often heavily grazed by livestock and in some areas is being replaced by less palatable species (Blaisdell and Holmgren 1984). Local populations have been destroyed or damaged by wildfires and drastic disturbances associated with human activities (Wallace and Romney 1972, Rickard and McShane 1984). Reestablishment of the species is desirable due to its forage, cover, and soil stabilization values (Dasmann and Blaisdell 1954, Gullion 1964, USDA-SCS 1968, McCullough 1969, Krysl et al. 1984).

Establishment of any species on these sites is often difficult because of unpredictable environmental conditions. Requirements for germination and seedling establishment of Nevada and California spiny hopsage populations producing nondormant seeds were examined by Wood et al. (1976), Ackerman (1979), Beatley (1979/80), and Manning and Groeneveld (1990). Requirements for northern populations, however, are poorly understood. Glazebrook (1941) found seeds of an eastern Washington population were nondormant, while King (1947) reported seeds from the same area required stratification to germinate.

Guidelines for field planting are also limited. Recommended planting dates are early spring or late fall for eastern Washington

(Glazebrook 1941) and late fall or early winter for southwestern Idaho (Shaw and Haferkamp 1990). The small seeds (869,000-932,000/kg) require shallow planting (Smith 1974, Wood et al. 1976).

Fall or winter planting provides natural stratification, but seeds planted near the soil surface are also subjected to extremes of moisture and temperature conditions that may lead to decreased vigor. More information on the effects of environmental conditions on seedling establishment is needed to develop planting strategies, possibly including seed pretreatments, to maximize returns from field or nursery seedings. The objective of this study was to examine effects of planting date and seedbed environment on seed germination and seedling establishment of spiny hopsage on 2 southwestern Idaho sites.

Materials and Methods

Seed Collections

Mature utricles (fruits enclosed within the papery bracteoles) were harvested in June 1986 and 1988 at Sponge Springs (SS86 and SS88 seed lots), Malheur Co., Oregon (43°47'42"N;117°25'59"W) and at Reynolds Creek, Owyhee Co., Idaho (43°15'31"N;116°12'37"W) (Table II.1). Utricles were collected from 2 Reynolds Creek sites approximately 1 km apart in 1986 (RC86A and RC86B seed lots). Adequate quantities of utricles for harvest were available at only the RC88B site in 1988. Collections were air-dried for 2-4 weeks. Seeds were removed from the utricles using a modified Dybvig seed cleaner (Melvin R. Dybvig, Oregon City, Oregon) (Shaw and Haferkamp 1990). Chaff was removed using an air-screen cleaner and a seed blower. Conditioned seeds (8.3% mean moisture content) were stored in plastic containers at approximately 3-5°C. Moisture content of these seed lots ranged from 6.5 to 9.6%.

Planting Sites

Field plantings were made at Birds of Prey and Reynolds Creek. The Birds of Prey site (43°17'59"N;116°22'0"W) is located on the Snake River Plains approximately 36 km southwest of Boise, Idaho, at an elevation of 850 m. Mean annual temperature is 11°C. Temperature averages -2°C in January and 21°C in July. The frost-free season averages 150 days (Collett 1980). Mean annual precipitation at the Kuna 2 Weather Station, approximately 20 km northwest of the site, is 248 mm with 56% falling from October through March (NOAA 1987-89). Soils are well-drained coarse silty mixed mesic Haplo Xerolic Durorthids formed over loess on a basalt plain. Depth to the hardpan is 0.5-1.0 m. Major perennial species are Wyoming big sagebrush, winterfat (Ceratoides lanata [Pursh] J.T. Howell), spiny hopsage, Sandberg bluegrass (Poa secunda Presl), and bottlebrush squirreltail (Sitanion hystrix [Nutt.] Smith). Cheatgrass (Bromus tectorum L.), Russian thistle (Salsola iberica Sennen & Pau), and clasping pepperweed (Lepidium perfoliatum L.) are common introduced annuals. A wildfire removed most woody cover from the site in July 1985 (M. Pellant, file data, USDI-BLM, Boise, Idaho, 1990). The burn was drilled in March 1986 to a mix of Fairway crested wheatgrass (Agropyron cristatum L. Gaertner), Siberian wheatgrass (Agropyron sibiricum [Willd.] Beauv.), Russian wildrye (Elymus junceus Fisch.), fourwing saltbush (Atriplex canescens [Pursh] Nutt.), and winterfat. Seeding success was highly variable due to low precipitation.

The Reynolds Creek site (43°42'37"N;116°44'2"W) is located in the northern foothills of the Owyhee Mountains approximately 66 km southwest of Boise, Idaho and 2.5 km south of the Reynolds Creek seed collection sites. Elevation is 1,200 m. Mean annual temperature is 8°C (C.L. Hanson, file data, USDA-ARS, Boise, Idaho, 1991). Temperature averages -2°C in January and 20°C in July. The frost free season averages 90-110 days (Stephenson 1977). Approximately 54% of the annual precipitation falls between October and March (C.L. Hanson, file data, USDA-ARS, Boise, Idaho, 1991). Snowfall accounts for about 20% of the precipitation (Stephenson 1977). Soils are fine loamy mixed mesic Typic Haplargids derived from granitic, basaltic, and rhyolitic alluvium (Stephenson 1977). Vegetation is as described for the seed collection site (Table II.1), with shadscale (Atriplex *confertifolia* [Torr.& Frem.] Wats) as an additional woody species. Russian thistle and clasping pepperweed are common annuals on disturbances. The site was burned in August 1984, and fall seeded to Siberian wheatgrass, 'Nomad' alfalfa (*Medicago sativa* L.), and fourwing saltbush (J. Mowbray, file data, USDA-ARS, Boise, Idaho, 1990).

Precipitation, soil temperature (0-20-mm depth), and soil moisture (0-30-mm depth) were measured at both sites during the study. Soil moisture content for the 0-30-mm depth was determined gravimetrically. Air temperature was measured on site at Birds of Prey and at the Reynolds weather station approximately 3 km south of the Reynolds Creek planting site (NOAA 1987-89).

Seeding Study

Seedbeds for 1987-88 plantings at both study sites were prepared by twice-over rototilling to a depth of approximately 150 mm in fall (Manuscript I). Residual rootcrowns of shrubs and perennial grasses were removed manually. Surfaces of the 3.0 X 1.5 m plots were hand raked just prior to seeding.

Five rows each 3 m long and 0.3 m apart were planted in each plot using a single-row cone-type small-plot seeder. Viable seeds were planted 5 mm deep at a rate of 66/m of row equivalent to $217/m^2$. Viability of each seed lot was evaluated by tetrazolium staining (AOSA 1970, Belcher 1985). Treatments were seed lot (RC86A and SS86) and planting date (Table II.2) arranged in a randomized complete block design with 4 replications (Manuscript I). Seedling density was measured by counting all seedlings on a 2-m row segment in each of the 3 inside rows in each plot. Seedling counts were made at Birds of Prey on 19 April, 20 May, and 27 June 1988 and at Reynolds Creek on 19 April, 26 May, and 24 June 1988 (Manuscript I).

Seedbeds for the 1988-89 plantings were prepared by rototilling. Soil surfaces of 0.25 m^2 plots were hand raked just prior to planting. Seeds were broadcast over the soil surface at a rate of 400 viable seeds/m^2, covered with approximately 5 mm of soil, and compacted lightly. Treatments were seed lot (RC86B, RC88B, SS86, and SS88) and planting date (Table II.2) arranged in a randomized complete block design with 10 replications. Seedling density was determined by counting all seedlings in each plot. Counts were made at Birds of Prey on 12 March, 23 March, 18 April, and 6 July 1989, and at Reynolds Creek on 11 March, 20 March, 11 April, and 3 July 1989.

Recovery Study

On each 1987-88 and 1988-89 planting date (Table II.2) seeds enclosed in nylon mesh bags were placed along the edge of plots planted with the same seed lot. Bags were carefully covered with approximately 5 mm of soil. On the second, third, and fourth planting dates and in early May, 5 bags of each seed lot placed in the field on each of the previous planting dates for that year were recovered (Table II.2). This procedure was followed at each study site.

Seed samples recovered from the field were returned to the laboratory for immediate processing. Samples were sieved, if necessary, to remove soil or seedlings. Only nongerminated seeds were selected for testing, thus viability of some field incubated seed samples may have been reduced by germination and removal of viable seeds as well as by deterioration of low vigor seeds. Control seeds were stored in the laboratory and samples were tested with seeds collected on each recovery date to measure the impact of field environments on seed condition.

Moisture content of one subsample from each bag and air-dry controls were determined gravimetrically by drying for 24 hours at 100°C (Justice and Bass 1978). Moisture content of fully imbibed controls at room temperature was also determined by this method.

One randomly selected subsample of 50 seeds from each bag and controls were tested for viability (AOSA 1970). Another randomly selected subsample of 50 seeds and controls were tested for germination. Germination trials were conducted by placing seeds on 2 blotters moistened with distilled water in 110 X 110 mm square germination dishes. Seeds were incubated for 30 days at 15°C with 8 hours of light alternating with 16 hours of darkness. Germination counts were made at 2-day intervals. Germination dishes were randomly arranged in the germinator and rerandomized after each count. Seedlings were considered normal if all structures essential for development were present, the hypocotyl arch raised and the radicle 10 mm long. Total germination was calculated as the percent of viable seeds producing normal seedlings after 30 days. Germination rate was calculated as days to 50% of 30-day germination.

Statistical Analyses

Effect of planting date and associated seedbed environment on seed moisture content, viability, total percent germination, days to 50% germination, and seedling survival were evaluated by analyses of variance. Means were separated by Fisher's least significant difference. Percentage data for germination and viability were transformed for analysis using arcsin $\sqrt{p}$ (Snedecor and Cochran 1980). The square root transformation was used to normalize seedling establishment data. Data were analyzed separately by year, planting site, and seed recovery or seedling count date due to differences in planting dates between years and sites. Only SS86 seeds were planted in nylon bags in late spring 1988. Consequently, one analysis of early summer 1988 data was conducted for SS86 and RC86A seeds from the first 3 plantings and controls. A second analysis was conducted for SS86 seeds from all 4 plantings and SS86 controls. All differences reported are significant at $p \leq 0.05$.

Results and Discussion

1987-88 Birds of Prey Plantings

Site Conditions

Due to low snowfall, seedbeds at Birds of Prey were open and exposed to effects of wind throughout most of the winter. Surface soil was frozen intermittently following precipitation events which totaled only 30 mm from December 1987 through February 1988 (Figs. II.1 and II.2). Surface soils were dry on all 4 planting dates (Fig. II.3). Seeds planted in late fall 1987 and winter 1988 were subjected to below-freezing surface soil temperatures almost continuously from early December 1987 through early February 1988 (Figs. II.1). Minimum daily soil and air temperatures were below $0^{o}C$ almost nightly through February 1988 and within the $1\text{-}15^{o}C$ range considered effective for stratification of many species (Bewley and Black 1982) with occasional frosts through mid-May 1988 (Figs. II.1 and II.4).

Moisture Content

Moisture content of field-incubated seeds exceeded 25% on both the winter and early spring recovery dates (Table II.3). Seeds were not fully imbibed on either date; trials showed control seeds stored in the laboratory contained 50.2% moisture when fully imbibed at room temperature. In late spring, moisture content of field incubated seeds was somewhat variable and either similar to or drier than controls. This slight variability may have reflected differential rates of drying within seedbed microsites following 6 mm of precipitation received 1 day preceding recovery. By early summer, all field planted seeds had dried below control levels in response to ambient temperature and soil moisture conditions.

Viability

Seed viability was not decreased relative to controls by incubation in soil from late fall to winter (Table II.3). By early spring, approximately 5% of SS86 seeds planted in late fall had begun germinating in the nylon bags. Few germinants were noted in other bags collected on this date. Viability of nongerminated seeds remaining in the bags reflected this field germination pattern: viability of late fall planted SS86 seeds was lower than SS86 controls, while viability of late fall planted RC86A seeds and winter planted seeds of both lots had not declined. Little or no additional field germination was observed on later recovery dates. Incubation in soil from late spring to early summer did not alter viability of SS86 seeds, but viability of seeds of both lots incubated in soil for longer periods had declined by this date.

Germination Total and Rate

On the winter, early spring, and late spring recovery dates, total germination and germination rate differed among all planting dates, increasing with longer field incubation periods (Table II.4). Exceptions were incubation from winter or early spring to late spring as these treatments were equally effective in improving the germination rate. Enhanced total germination and germination rate of seeds incubated in soil from late fall, winter, and early spring persisted with further incubation from late spring to early summer. RC86A seeds planted in early spring were an exception to this pattern; their total germination decreased to control levels. The greater enhancement of total germination and germination rate obtained by planting in late fall compared to winter, observed on earlier recovery dates, was lost by early summer. Total germination and germination rate of SS86 seeds planted in late spring were not improved by incubation in soil to early summer.

Seed Lots

Response of RC86A and SS86 seeds to field environments was generally similar (Tables II.3 and II.4). Within planting dates, viability and total germination tended to be greater for SS86 compared to RC86A seeds. Speed of germination differed only in early and late spring when the mean germination rate was greater for RC86A compared to SS86 seeds. The possibility that dormancy is relieved by a shorter stratification of SS86 compared to RC86A seeds is suggested by germination of some late fall planted SS86 seeds in nylon bags and greater laboratory germination of remaining viable SS86 seeds after incubation in soil from late fall to early spring. Germination of the 2 lots was similar following further incubation in soil until late spring or early summer.

1987-88 Reynolds Creek Plantings

Site Conditions

December 1987 through July 1988 precipitation at Reynolds Creek was 63% of the long term average (Fig. II.5). Plots planted in late fall 1987 were under snow cover almost continuously through mid-January 1988. Seeds were planted in winter 1988 as the snow melted and surface soil thawed during the day (Fig. II.6). Surface soils were dry on the early and late spring 1988 planting dates (Fig. II.7). Minimum daily soil and air temperatures were below 0°C almost nightly through March 1988 and within the 1-15°C range with occasional frosts through early May 1988 (Figs. II.6 and II.8).

Moisture Content

Moisture content of field incubated seeds exceeded 20% on each of the first 3 recovery dates (Table II.5). RC86A and SS86 seeds incubated in soil from winter to early spring were an exception as little precipitation fell during this period. By early spring these seeds had imbibed only slightly more moisture than controls. Late spring variability in seed moisture content may have resulted from microsite differences and high humidity with light rain on the recovery date. By early summer all field planted seeds were drier than controls.

Viability

Field incubation from late fall or winter to early spring did not alter seed viability (Table II.5). Due to low precipitation and dry soil conditions, few seeds germinated in nylon bags by the early spring or later recovery dates. Viability of seeds planted in late fall began declining relative to controls by late spring, but decreases in viability of winter and early spring planted seeds were not observed until early summer. Viability of SS86 seeds was not altered by incubation in soil from late spring to early summer.

Germination Total and Rate

Total germination and germination rate, initially similar for both seed lots, were substantially improved by field incubation from late fall to early spring (Table II.6). Seeds incubated from winter to early spring imbibed little moisture; total germination was not enhanced and speed of germination improved only slightly. By late spring, total germination differed among all planting dates, increasing with longer incubations in soil. Speed of germination also tended to increase with longer incubations in soil, but rates for winter and early spring plantings were similar. In early summer total germination of the first 3 plantings and germination rate of all 4 plantings exceeded controls. As at Birds of Prey, the greater enhancement of total germination resulting from incubation in soil from late fall compared to winter was lost by early summer. Speed of germination for all field planted seeds was similar in early summer and exceeded controls.

Seed Lots

Within planting dates, mean viability and total germination were generally greater for SS86 compared to RC86A seeds (Tables II.5 and II.6). Failure of SS86 seeds to begin germinating in the nylon bags by early spring may have resulted from dry conditions prevailing from winter to early spring. Mean germination rates of the 2 seed lots were similar on all recovery dates.

1988-89 Birds of Prey Plantings

Birds of Prey plots were intermittently snow covered from late December 1988 through mid-January 1989. Seeds were planted when the soil surface was frozen in late fall 1988, but when the surface was thawed and moist in winter 1989 (Figs. II.1 and II.3). Maximum and minimum soil temperatures and minimum daily air temperatures were below freezing almost continuously from mid-December 1988 until early March

1989 (Figs. II.1 and II.4). Minimum daily soil and air temperatures remained in the 1-15^{o}C range with occasional frosts until late May 1989.

Extensive field germination occurred in bags of some plantings at both Birds of Prey and Reynolds Creek in 1988-89. These plantings were excluded from analyses for early spring and later recovery dates.

Moisture content of field planted seeds exceeded 35% on each of the first 3 recovery dates at Birds of Prey (Table II.7). Field incubated seeds were only slightly more moist than controls in early summer. No decreases in viability relative to controls were noted for seeds recovered in winter (late fall planting), early spring (winter planting), or late spring (early spring planting) (Table II.7). Viability of seeds planted in early spring and late spring began declining by early summer.

Total germination and germination rate of all seed lots were enhanced by incubation in the field from late fall to winter, winter to early spring, or from early spring to late spring (Table II.8). In early summer total germination and germination rate were similar for early and late spring-planted seeds and controls.

The 4 seed lots responded somewhat similarly to seedbed environments (Tables II.7 and II.8). Mean viability was greatest for the RC88B seed lot on the first 3 recovery dates. Total germination differed among seed lots in early spring; both germination and germination rate varied among lots in late spring with no clear patterns emerging.

1988-89 Reynolds Creek Plantings

March 1989 precipitation at Reynolds Creek was twice the long-term average, but April through July 1989 were dry (Fig. II.5). Soil was frozen and snow covered during much of late December 1988 and January 1989 (Fig. II.6). Seeds were planted into muddy plots in late fall 1988 and thawed surface soil in winter 1989. Maximum and minimum soil temperatures and minimum daily air temperatures were below freezing until mid-February 1989 (Figs. II.6 and II.8). Minimum daily soil and air temperatures were below $0^{o}C$ almost nightly through March 1989 and in the $1\text{-}15^{o}C$ range with occasional frosts until late May 1989.

Moisture content of field planted seeds exceeded 35% on each of the first 2 recovery dates and 40% on the third recovery date (Table II.9). The high moisture content of winter-planted seeds in early spring may indicate that some seed coats had ruptured.

Viability did not decline relative to controls with field incubation from late fall to winter, winter to early spring, or from early spring to late spring (Table II.9). Embryos of some seeds planted in winter had begun uncoiling in the nylon bags by late spring; viability of remaining nongerminated winter planted RC86B and RC88B seeds was lower than controls on this date. Viability of all seed lots declined with incubation in soil from early or late spring to early summer.

Total germination and germination rate were enhanced by field incubation during late fall, winter, or early spring (Table II.10). In late spring, seeds planted in winter exhibited greater total germination and germinated more rapidly than seeds planted in early spring In early summer, total germination, but not germination rate of RC86B and SS88 seeds planted in early spring and all seeds planted in late spring was slightly enhanced compared to controls.

Viability tended to be greatest for RC88B seeds (Table II.9). Total germination varied among seedlots in early spring, late spring, and early summer, with no definite patterns evident (Table II.10). Germination rate did not differ among seed lots on any recovery date.

1987-88 Seedling Emergence

Total germination and germination rate of late fall, winter and early spring planted seeds were enhanced by incubation in soil at Birds of Prey and Reynolds Creek (Tables II.4 and II.6), but very few seedlings emerged from either planting site in 1988, likely due to dry seedbed conditions (Figs. II.4 and II.5) (Manuscript I). Emerging seedlings were first noted on 13 March at Birds of Prey and 1 March at Reynolds Creek (Manuscript I). Seedling density did not vary with planting date or seed lot on any counting date at either site. Only seedlings emerging from late fall plantings survived until June 1988 (Manuscript I). Establishment from late fall seedings averaged 0.6 seedlings/m^2 at Birds of Prey and 0.9/m^2 at Reynolds Creek.

1988-89 Seedling Emergence

Large numbers of seedlings emerged from late fall 1988 plantings in 1989, possibly due to high March rainfall (Figs. II.2 and II.5 and Table II.11. Seeds in nylon bags planted in late fall began germinating by 1 March at Birds of Prey and 27 February at Reynolds Creek. Emergence was substantially greater from late fall compared to early or late spring plantings at each site on all counting dates (Table II.11). Large numbers of weak or dead seedlings were noted at both sites in early July, possibly due to high temperatures and low soil moisture. Mean density of established seedlings as determined by the July count was 6.0 times greater on late fall compared to early spring plantings at Birds of Prey and 25.6 times greater at Reynolds Creek. Mean seedling density on SS86 and SS88 plots was 57% greater than on RC86B and RC88B plots in July at Birds of Prey. Seedling density did not vary among seed lots at Reynolds Creek.

Seed dormancy in spiny hopsage was relieved by exposure to seedbed environments providing stratification through late fall and winter. This response is common among perennial Great Basin species, permitting early spring emergence when soil moisture conditions are conducive to growth prior to the onset of summer drought (Vallentine 1980). Although incubation of seeds in soil during late fall, winter, or early spring reduced dormancy at both sites in 1988, germination was severely limited, probably due to low precipitation and inadequate soil moisture. In 1989 late fall planted seeds began germinating in late February and early March when maximum and minimum air temperatures at the 2 sites averaged 8 and $0^{o}C$ and soil temperatures averaged 4 and $-2^{o}C$. Seedling emergence occurred in March and early April when maximum and minimum air temperatures averaged 12 and $0^{o}C$ and maximum and minimum soil temperatures averaged 8 and $0^{o}C$. Haferkamp et al. (1990) reported late fall and winter planting favored germination of prostrate kochia (*Kochia prostrata* [L.] Schrader) at similar low temperatures in southeastern Oregon.

Laboratory germination and germination rate of recovered seeds did not vary consistently with seed collection site. Seedling establishment varied with seed collection site only for the 1988-89 Birds of Prey planting. Variation in germination characteristics has been reported for populations of spiny hopsage (Wood et al. 1976), spineless hopsage (Meyer and Pendleton 1990), and shadscale (Sanderson et al. 1990) from diverse environments.

There were no consistent differences in germination of 1986 and 1988 Reynolds Creek and Sponge Springs seeds planted at the 2 locations in 1988-89. King (1947) found 6-year old spiny hopsage seeds from eastern Washington required a shorter stratification treatment than 4-year old seeds. Improved germination with dry afterripening has been reported for several other shrubby chenopods (Springfield 1968, 1970; Baylan 1972). Haferkamp et al. (1990) reported field incubation accelerated afterripening of prostrate kochia.

Some stratified seeds that were nondormant in winter or early spring, but failed to germinate due to dry soil conditions or high temperatures, may have entered secondary dormancy. This possibility is indicated by moderate early summer laboratory germination of viable seeds planted in late fall 1987. In addition, enhanced late spring 1989 germination of early spring planted seeds was lost by early summer, perhaps due to lower April and May precipitation and higher temperatures in 1989 compared to 1988 at both sites. An alternative explanation might be that laboratory germination was reduced by loss of vigor with continued soil incubation to early summer. Induction of secondary dormancy in response to high temperatures and water stress has been reported in Chenopodium bonus-henricus, an herbaceous chenopod (Khan and

Karssen 1980). This mechanism permits seeds to remain viable in soil until conditions favorable for release of secondary dormancy and subsequent germination are encountered. Determining whether spiny hopsage seeds are capable of entering secondary dormancy and affecting factors will require further investigation.

Low germination and emergence from some early and late spring plantings may have resulted from incomplete stratification. Germination of seeds planted in winter or on later planting dates in 1989 may have been delayed relative to germination of late fall planted seeds until dormancy was relieved by stratification in soil. Although spring air and soil temperatures were often in the 0-15°C range, seed moisture content may have been too low for chilling to be effecive. In addition, short periods of chilling are not cumulative; secondary dormancy may be induced during intermittant high temperature periods (Bewley and Black 1984). Seedling emergence and establishment from early spring compared to late fall plantings may also have been reduced as moisture conditions were less favorable for germination and the period for seedling development prior to summer dormancy was shorter.

Accumulation of seeds in either primary or secondary dormancy in the soil seed bank could contribute to episodic seedling establishment in good moisture years as has been reported by Wallace and Romney (1972) and El-Ghonemy et al. (1980) for spiny hopsage in the Mojave Desert. Kay et al. (1988) reported spiny hopsage seeds remained viable in sealed storage at room temperature for 14 years. Ability of some spiny hopsage seeds to survive in soil beyond the planting year was indicated by limited second and third year emergence on Reynolds Creek plots planted in 1986-87 (N.L. Shaw, file data, 1988 and 1989). Frischknecht and

Ferguson (1984) reported excellent second year germination of several chenopod shrub seed lots, including spiny hopsage, planted in Utah's Uinta Basin during a drought year.

Results of this study show that late fall or early winter planting is necessary to provide natural stratification and maximize early spring germination and emergence as the soil thaws and temperatures begin rising. Planting utricles within their hygroscopic bracts might provide a natural mulch as was suggested by Wood et al. (1976). Direct seeding artificially stratified seeds in the nursery in late winter might be a viable planting option if soil conditions permit equipment operation. Seed surfaces are smooth and air-dry quickly, thus imbibed seeds could be dispensed through a seeder.

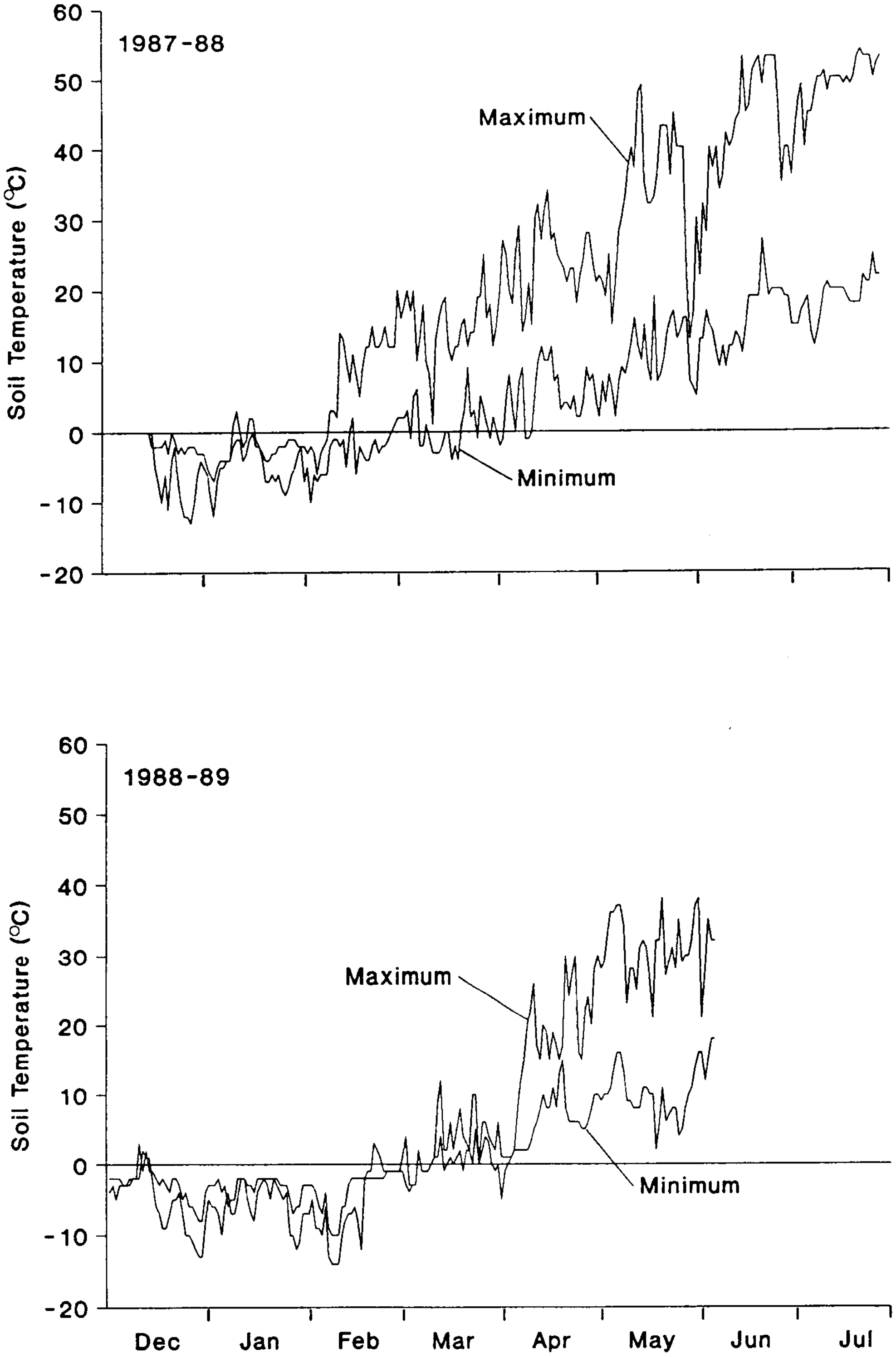

Fig. II.1. December to July soil temperature profile (0-20-mm depth) for the Birds of Prey planting site, southwestern Idaho, 1987-88 and 1988-89.

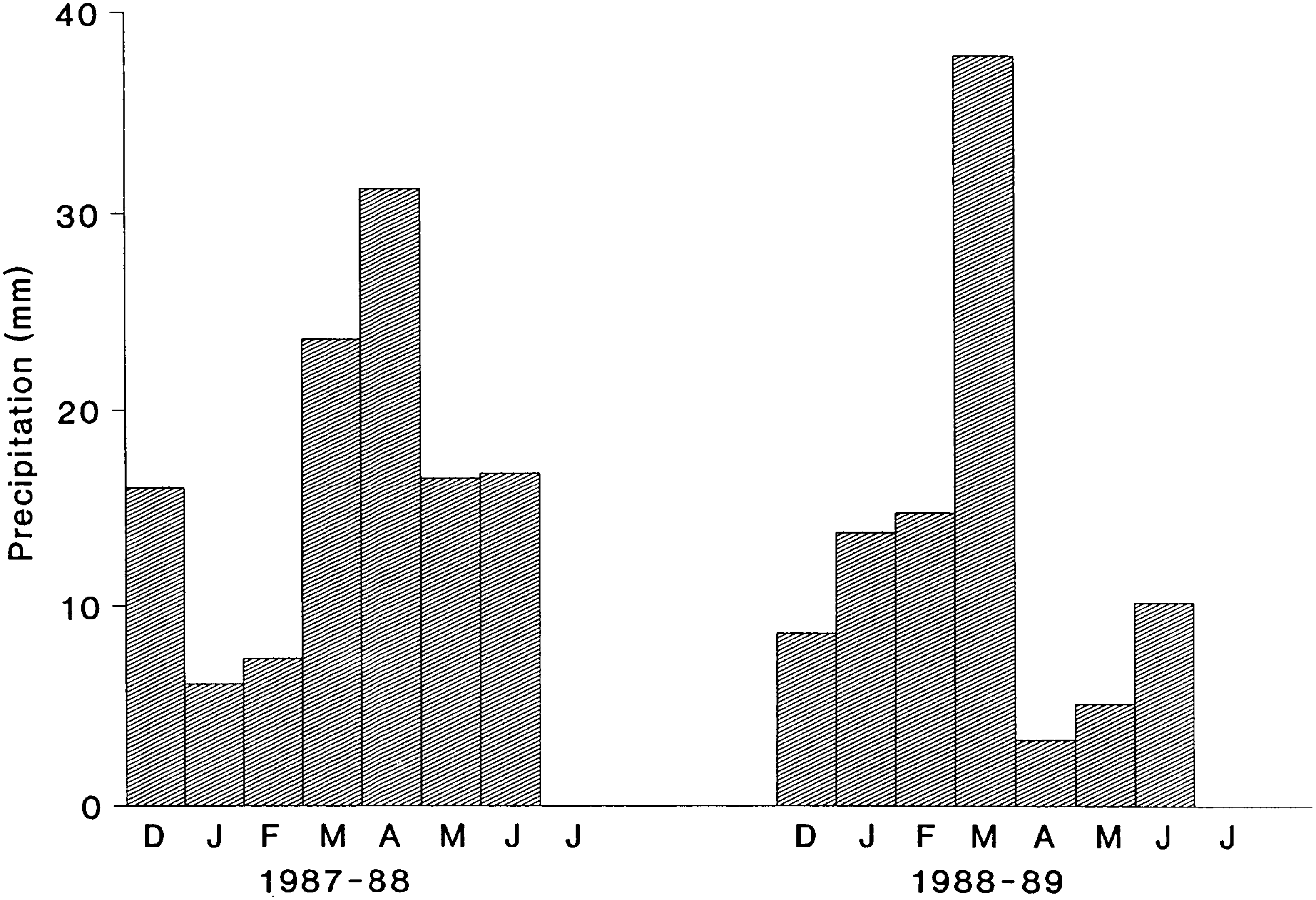

Fig. II.2. December to July precipitation for the Birds of Prey planting site, southwestern Idaho, 1987-88 and 1988-89.

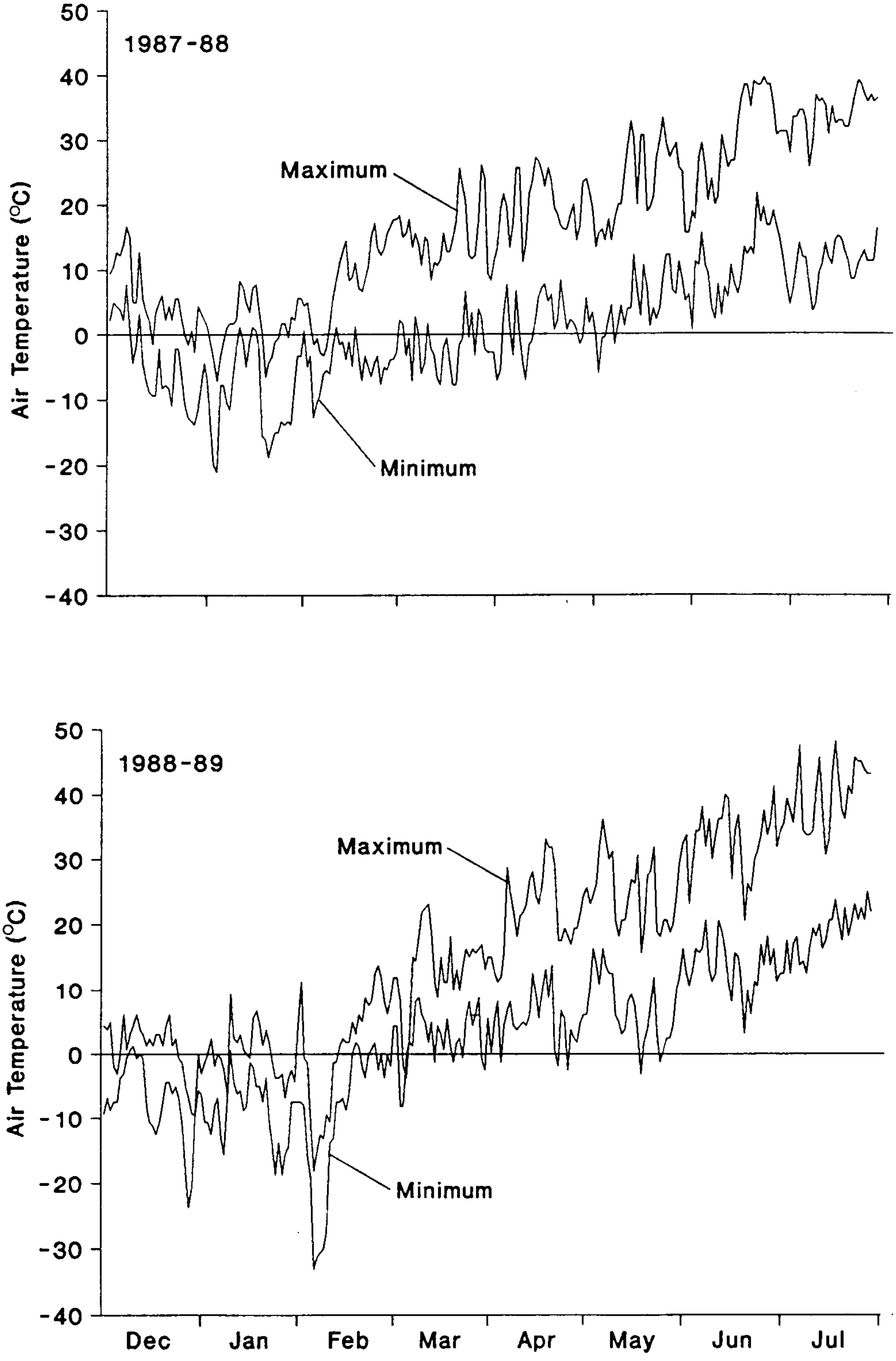

Fig. II.3. December to July air temperature profile for the Birds of Prey planting site, southwestern Idaho, 1987-88 and 1988-89.

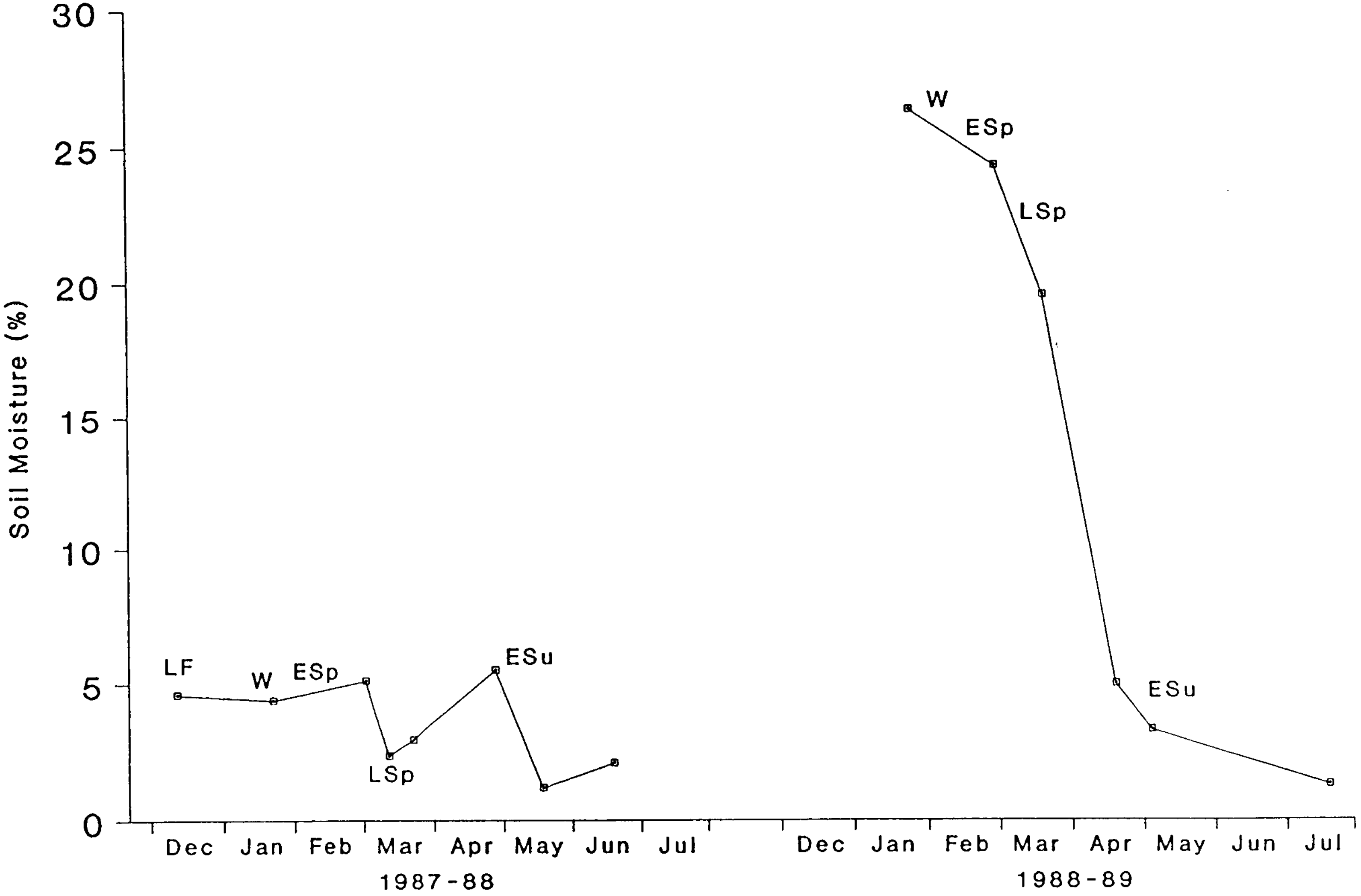

Fig. II.4. December to July soil moisture profile (0-30-mm depth) for the Birds of Prey planting site, southwestern Idaho, 1987-88 and 1988-89. Planting and recovery dates: LF=late fall, W=winter, ESp=early spring, ESu=early summer.

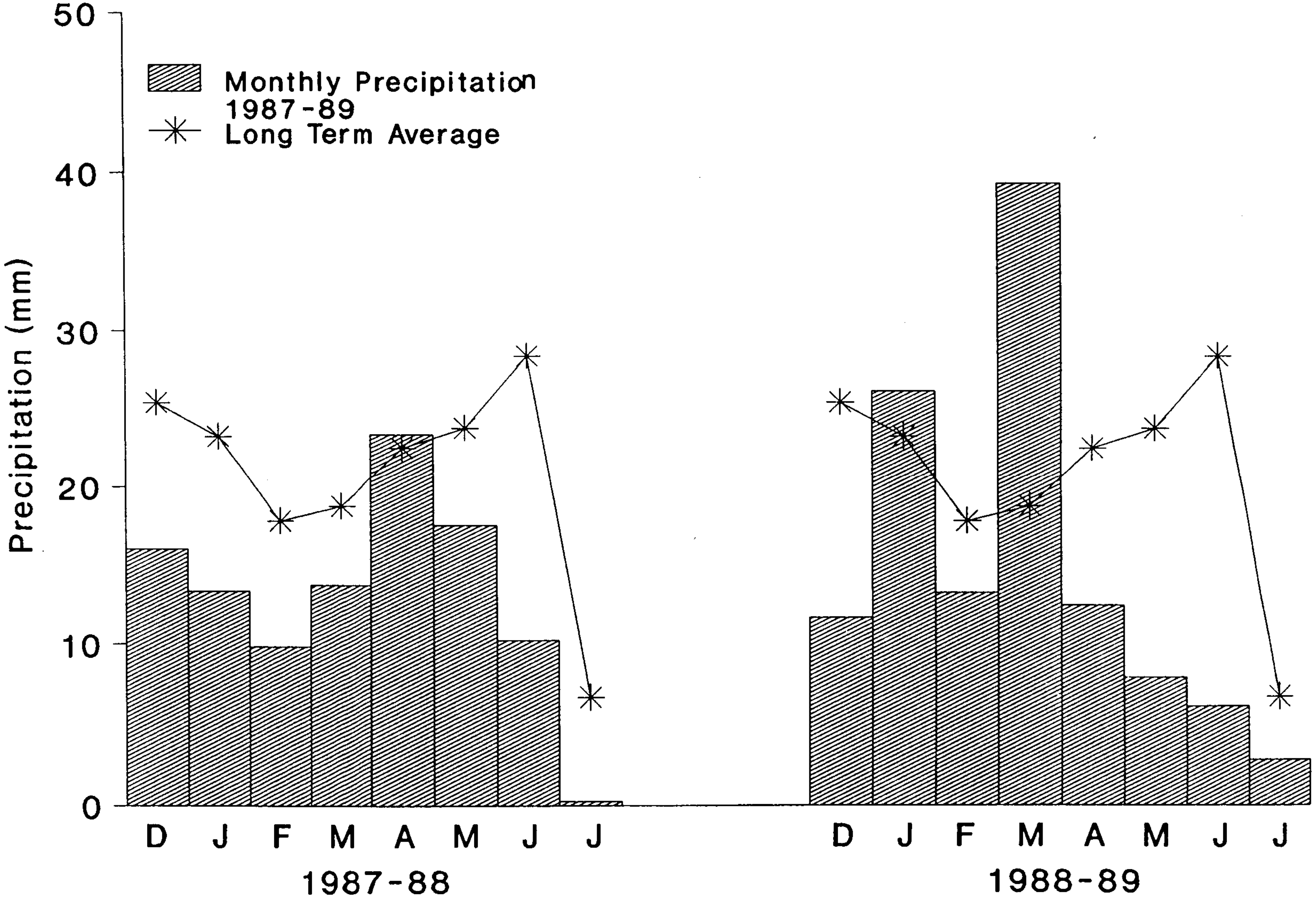

Fig. II.5. December to July precipitation for the Reynolds Creek planting site, southwestern Idaho, 1987-88 and 1988-89 and 21-year average.

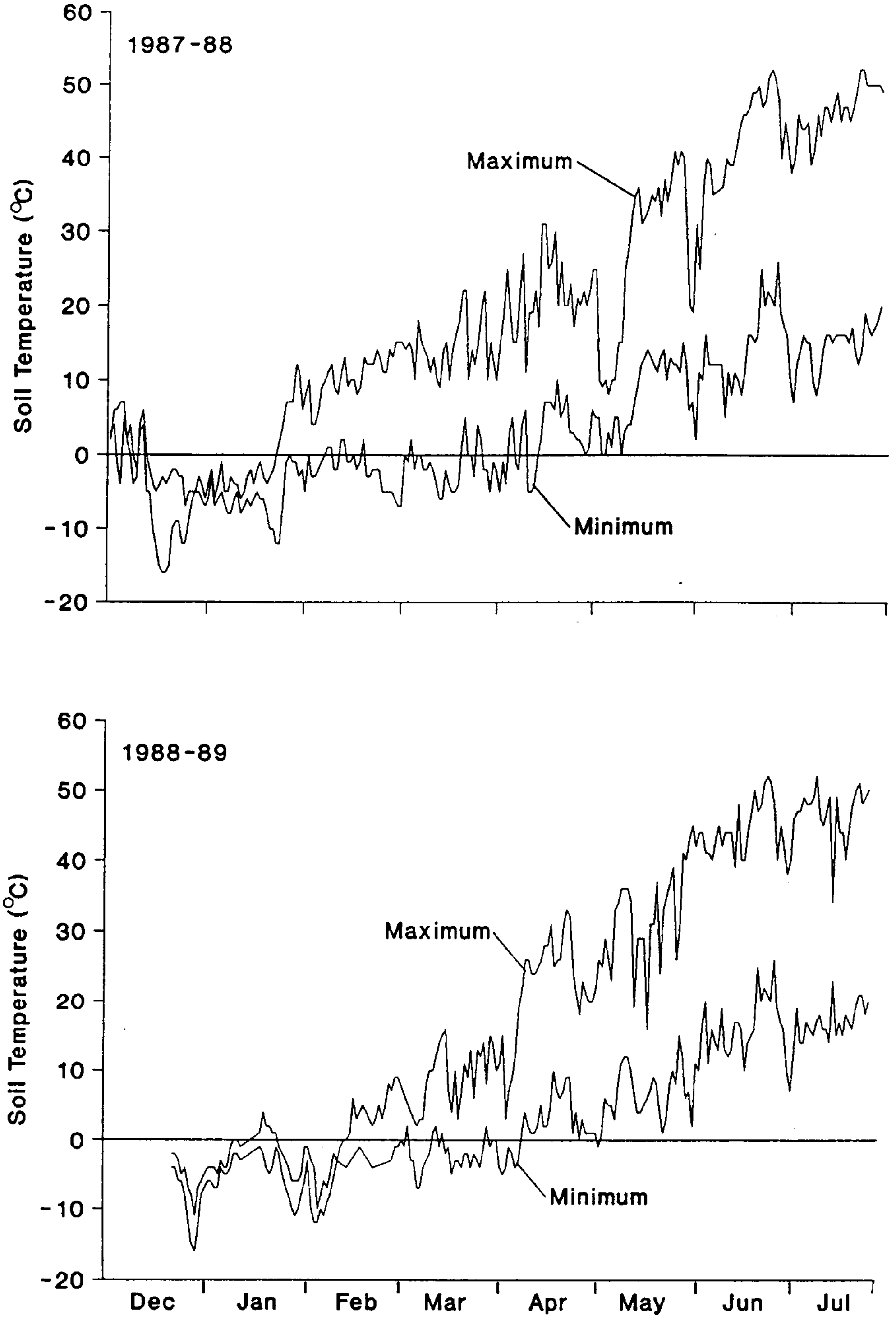

Fig. II.6. December to July soil temperature profile (0-20-mm depth) for the Reynolds Creek planting site, southwestern Idaho, 1987-88 and 1988-89.

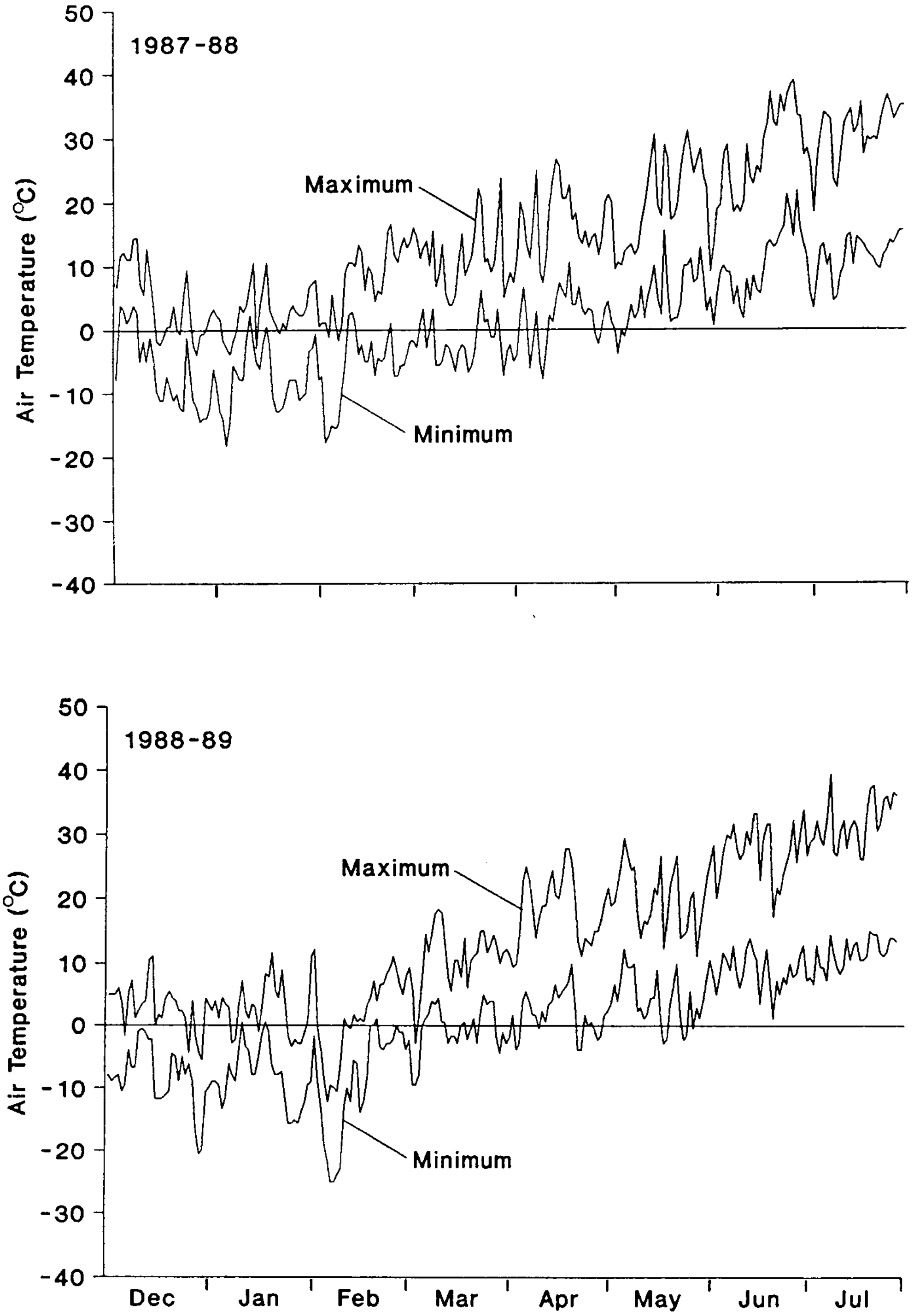

Fig. II.7. December to July air temperature profile for Reynolds, southwestern Idaho, 1987-88 and 1988-89.

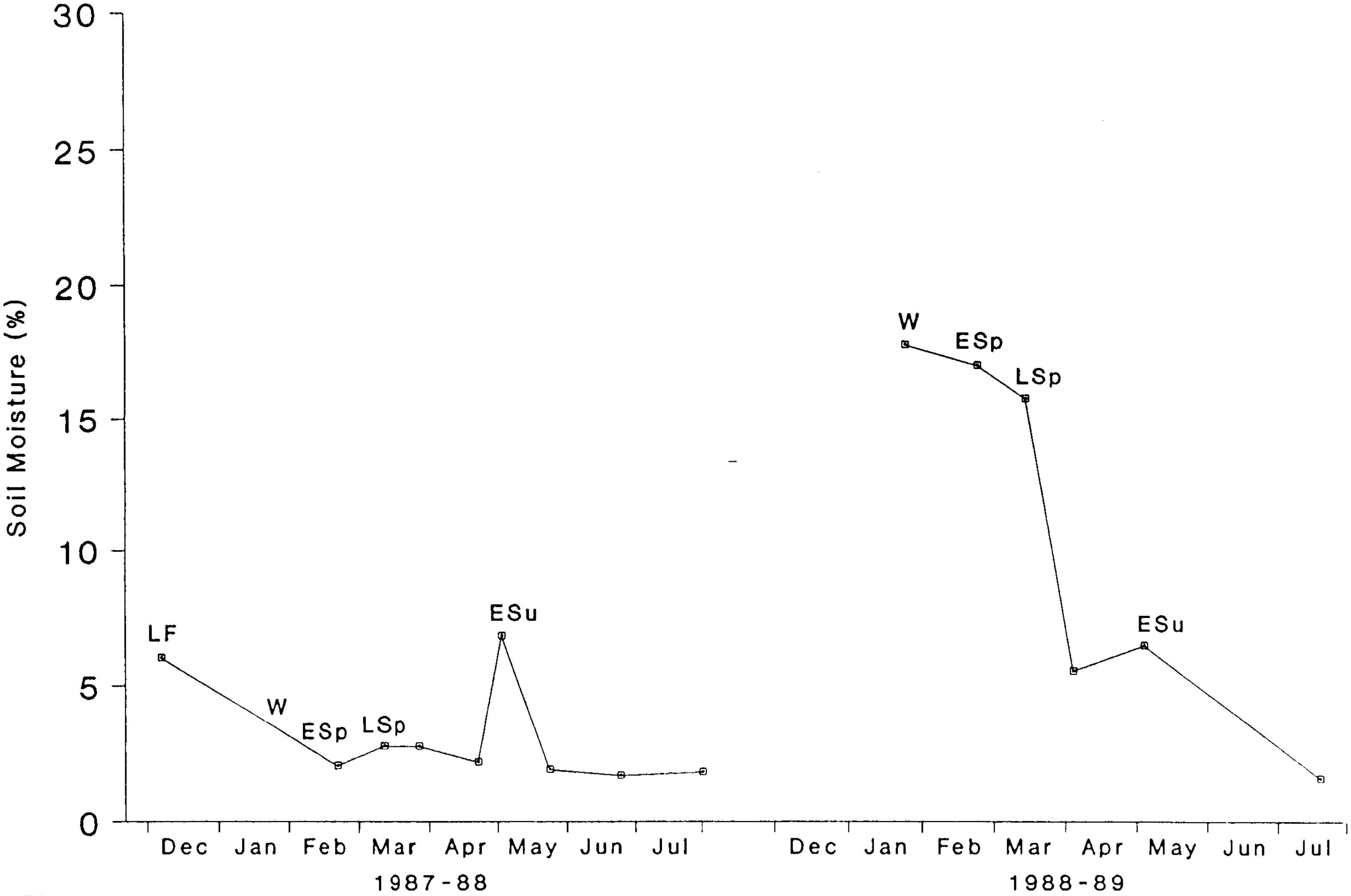

Fig. II.8. December to July soil moisture profile (0-30-mm depth) for the Reynolds Creek planting site 1987-88 and 1988-89. Planting and recovery dates: LF=late fall, W=winter, ESp=early spring, LSp=late spring, ESu=early summer.

Table II.1. Characteristics of spiny hopsage seed collection sites.

	Seed Collection Site	
	Reynolds Creek	Sponge Springs
Location	Northern foothills of Owyhee Mountains, southwestern Idaho	Malheur Basin, southeastern Oregon
Vegetation	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Sitanion hystrix*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Bromus tectorum*
Elevation (m)	1,260	991
Precipitation (mm)	249[1]	228[3]
Soil	Coarse-loamy, mixed nonacid, mesic Xeric Torriorthents[2]	Fine-loamy, mixed mesic Xerollic Durargids[4]

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[1] C.L. Hanson (file data, USDA-ARS, Boise, Idaho 1992).
[2] Stephenson (1977).
[3] J.M. Findley (file data, USDI-BLM, Vale, Oregon, 1990).
[4] Oregon Water Resources Board (1969).

Table II.2. Planting and recovery dates at Birds of Prey and Reynolds Creek plots, southwestern Idaho, 1987-88 and 1988-89.

		Date	
		Location	
Planting/Recovery	Year	Birds of Prey	Reynolds Creek
Late Fall[1]	1987-88	Dec. 17	Dec. 7
	1988-89	Dec. 21	Dec. 9
Winter	1987-88	Jan. 26	Jan. 31[2]
	1988-89	Feb. 1[2]	Jan. 27[2]
Early Spring	1987-88	Feb. 19	Feb. 21
	1988-89	Mar. 1	Feb. 27
Late Spring	1987-88	Mar. 11[2]	Mar. 13
	1988-89	Mar. 23	Mar. 20
Early Summer[3]	1987-88	May 3	May 4
	1988-89	May 8	May 10

[1] Planting only.

[2] Small plots not seeded due to adverse weather conditions. Seeds in nylon mesh bags were field planted on these dates. Only bags containing SS86 seeds were planted in early summer 1988.

[3] Recovery only.

Table II.3. **Percent moisture content and percent viability for 2 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Birds of Prey 1987-88 plots, southwestern Idaho.**

Date		Percent Moisture Content			Percent Viability		
		Seed Lot			Seed Lot		
Planting	Recovery	RC86A	SS86	Mean	RC86A	SS86	Mean
Late Fall 87	Winter 88	29.7	35.3	32.5a[1]	66.0	77.6	
Dry Seed[2]		10.1	9.8	9.9b	66.2	72.4	
Mean					66.1B	75.5A	
Late Fall 87	Early Spring 88	28.3	30.3	28.3a	61.2Aa	61.6Ab	
Winter 88		35.6	28.2	28.9a	64.4Ba	80.0Aa	
Dry Seed		10.1	10.5	10.3b	62.0Ba	76.4Aa	
Mean							
Late Fall 87	Late Spring 88	7.0Aa	6.4Abc		60.4	62.8	
Winter 88		7.9Aa	7.3Aab		64.0	68.4	
Early Spring 88		7.7Aa	5.7Bc		65.6	68.8	
Dry Seed		8.5Aa	8.6Aa		62.0	72.0	
Mean					63.0B	68.0A	
Late Fall 87	Early Summer 88	6.5	6.4y[3]	6.5b	57.2	57.6z	57.4b
Winter 88		6.9	5.8y	6.4b	60.0	61.2yz	60.6b
Early Spring 88		7.8	5.9y	6.8b	60.8	63.2yz	62.0b
Late Spring 88			6.1y			68.0xy	
Dry Seed		9.6	9.4x	9.5a	65.4	75.4x	70.4a
Mean					60.8B	64.1A	

[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

[3] Lower case letters x, y, z apply to analysis of SS86 early summer data only.

Table II.4. Total percent germination and days to 50% germination for 2 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Birds of Prey 1987-88 plots, southwestern Idaho.

Date		Total Percent Germination			Days to 50% Germination		
		Seed Lot			Seed Lot		
Planting	Recovery	RC86A	SS86	Mean	RC86A	SS86	Mean
Late Fall 87	Winter 88	56.8	67.6	62.2a[1]	6.8	8.4	7.6b
Dry Seed[2]		7.2	10.0	8.6b	19.8	22.9	21.4a
Mean		32.0B	38.8A				
Late Fall 87	Early Spring 88	68.2Ba	94.2Aa		7.7	4.3	6.0c
Winter 88		37.6Ab	41.0Ab		10.0	9.8	9.9b
Dry Seed		6.0Bc	15.8Ac		17.5	20.2	18.4a
Mean					10.3B	12.6A	
Late Fall 87	Late Spring 88	75.0	88.4	81.7a	5.8	7.9	6.9c
Winter 88		50.2	44.0	47.1b	10.5	12.5	11.5b
Early Spring 88		19.2	28.4	23.8c	11.1	11.9	11.5b
Dry Seed		8.8	15.4	12.1d	19.0	23.1	21.1a
Mean					11.6B	13.9A	
Late Fall 87	Early Summer 88	32.2Ba	46.0A(x)[3]		13.6	15.4y	14.5b
Winter 88		22.0Ba	41.8Aab(xy)		15.7	13.9y	14.8b
Early Spring 88		10.6Bb	35.0Ab(y)		18.0	16.0y	17.0b
Late Spring 88			12.0c(z)			21.2x	
Dry Seed		7.2Ab	10.7Ac(z)		20.8	22.4x	21.6a

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[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

[3] Lower case letters x, y, z apply to analysis of SS86 early summer data only.

Table II.5. Percent moisture content and percent viability for 2 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Reynolds Creek 1987-88 plots, southwestern Idaho.

Date		Percent Moisture Content			Percent Viability		
		Seed Lot			Seed Lot		
Planting	Recovery	RC86A	SS86	Mean	RC86A	SS86	Mean
Late Fall 87	Winter 88	33.1	34.5	33.8a[1]	64.4	70.0	67.2
Dry Seed[2]		10.1	9.8	9.9b	66.2	72.4	69.3
Mean					65.3	71.2	68.2n.s.
Late Fall 87	Early Spring 88	25.1	21.8	23.5a	58.0	68.4	
Winter 88		15.5	17.7	16.6b	68.8	74.0	
Dry Seed		10.1	10.5	10.2c	62.0	76.4	
Mean					61.5B	72.9A	
Late Fall 87	Late Spring 88	29.8Aa	29.5Aa		56.4	64.0	60.2b
Winter 88		22.3Bb	30.0Aa		62.4	69.2	65.8ab
Early Spring 88		21.1Bb	29.4Aa		65.6	75.2	70.4a
Dry Seed		8.5Ac	8.6Ab		62.0	72.0	67.0a
Mean					61.6B	70.1A	
Late Fall 87	Early Summer 88	6.2	5.5y[3]	5.8b	55.6	62.0z	58.8c
Winter 88		6.0	6.0y	6.0b	54.4	63.6z	59.0c
Early Spring 88		6.8	5.7y	6.2b	64.4	65.6yz	65.0b
Late Spring 88			6.4y			70.4xy	
Dry Seed		9.6	9.4x	9.5a	65.4	74.4x	69.9a
Mean					60.0B	66.4A	

[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

[3] Lower case letters x, y, z apply to analysis of SS86 early summer data only.

Table II.6. Total percent germination and days to 50% germination for 2 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Reynolds Creek 1987-88 plots, southwestern Idaho.

Date		Total Percent Germination			Days to 50% Germination		
		Seed Lot			Seed Lot		
Planting	Recovery	RC86A	SS86	Mean	RC86A	SS86	Mean
Late Fall 87	Winter 88	69.6	67.4	68.5a[1]	7.1	7.4	7.3b
Dry Seed[2]		7.2	10.0	8.6b	19.8	22.9	21.4a
Late Fall 87	Early Spring 88	77.2	88.8	83.0a	5.3	6.2	5.7c
Winter 88		13.4	16.8	15.1b	14.6	15.8	15.2b
Dry Seed		6.0	15.8	10.9b	17.5	20.2	18.8a
Mean		32.2B	40.5A		10.3B	12.6A	
Late Fall 87	Late Spring 88	78.6	87.4	83.0a	6.9	7.7	7.3c
Winter 88		43.8	55.2	49.5b	13.0	11.5	12.2b
Early Spring 88		19.5	29.8	24.6c	13.1	14.1	13.6b
Dry Seed		8.8	15.4	12.1d	19.0	23.1	21.1a
Mean		37.7B	47.0A				
Late Fall 87	Early Summer 88	46.0	66.2x[3]	56.1a	12.6	14.1y	13.4b
Winter 88		36.5	57.8x	47.1a	12.5	14.3y	13.4b
Early Spring 88		24.0	42.2y	33.1b	16.1	14.6y	15.3b
Late Spring 88			18.2z			16.2y	
Dry Seed		7.2	10.7z	9.0c	20.8	22.4x	21.6a
Mean		28.4B	44.2A				

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[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

[3] Lower case letters x, y, z apply to analysis of SS86 early summer data only.

Table II.7. Percent moisture content and percent viability for 2 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Birds of Prey 1988-89 plots, southwestern Idaho.

Date		Percent Moisture Content					Percent Viability				
		Seed Lot					Seed Lot				
Planting	Recovery	RC86B	RC88B	SS86	SS88	Mean	RC86B	RC88B	SS86	SS88	Mean
Late Fall 88	Winter 89	36.6	34.8	36.7	35.7	36.0a[1]	79.2	88.	74.8	80.4	
Dry Seed[2]		6.8	6.8	7.1	6.9	6.9b	79.6	88.4	79.2	80.0	
Mean							79.4B	88.2A	77.0B	80.2B	
Winter 89	Early Spring 89	43.9	45.8	46.0	41.1	44.2a	76.4	87.6	74.0	82.8	
Dry Seed		6.5	6.3	6.9	6.5	6.5b	77.6	86.4	77.6	77.2	
Mean							77.0B	87.0A	75.8B	80.0B	
Early Spring 89	Late Spring 89	43.6	45.6	45.1	42.8	44.3a	82.8	87.6	79.2	77.2	
Dry Seed		5.4	5.9	5.5	5.3	5.5b	82.0	86.8	76.8	77.2	
Mean							82.4B	87.2A	78.0B	77.2B	
Early Spring 89	Early Summer 89	13.1Ba	13.3Ba	12.0Ca	15.0Aa		77.6	67.2	60.8	75.2	70.2b
Late Spring 89		10.3ABb	9.7Bb	10.7Ab	10.0Ab		74.0	76.8	62.4	74.0	71.8b
Dry Seed		6.3Ac	6.7	6.7	7.9		80.4	89.6	78.4	82.0	82.6a
Mean							77.3A	77.9A	67.2B	77.1A	

[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

Table II.8. **Total percent germination and days to 50% germination for 4 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Birds of Prey 1988-89 plots, southwestern Idaho.**

Date		Total Percent Germination					Days to 50% Germination				
		Seed Lot					Seed Lot				
Planting	Recovery	RC86B	RC88B	SS86	SS88	Mean	RC86B	RC88B	SS86	SS88	Mean
Late Fall 88	Winter 89	76.5	76.8	75.9	79.9	77.3a[1]	8.2	9.0	8.5	8.0	8.4b
Dry Seed[2]		2.9	6.3	6.1	2.5	4.5b	21.5	16.3	19.2	17.1	18.6a
Winter 89	Early	34.0	50.7	47.0	37.6	42.3a	8.3	7.4	7.3	7.8	7.7b
Dry Seed	Spring 89	5.7	12.5	11.9	7.2	9.3b	19.8	17.9	19.0	17.7	18.3a
Mean		19.8C	31.6A	29.4AB	22.4BC						
Early Spring 89	Late	23.2Ba	32.9Ba	48.5Aa	24.4Ba		7.7	5.0	5.9	11.3	7.5b
Dry Seed	Spring 89	6.8Ab	11.8Ab	8.1Ab	8.8Ab		20.5	17.7	22.1	22.8	20.8a
Mean							11.0AB	9.1B	11.2AB	13.2A	
Early Spring 89	Early	6.2	5.4	7.2	7.1	6.5	21.7	17.5	16.0	21.4	19.2
Late Spring 89	Summer 89	6.5	8.3	3.2	7.6	6.4	18.2	20.3	17.0	19.5	18.7
Dry Seed		7.2	5.4	4.3	2.2	4.8	24.0	19.6	24.9	20.4	22.20
Mean		6.6	6.4	4.9	5.6	5.9n.s.	21.3	19.2	19.3	20.5	20.0n.s.

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[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

Table II.9. Percent moisture content and percent viability for 4 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Reynolds Creek 1988-89 plots, southwestern Idaho.

Date		Percent Moisture Content					Percent Viability				
		Seed Lot					Seed Lot				
Planting	Recovery	RC86B	RC88B	SS86	SS88	Mean	RC86B	RC88B	SS86	SS88	Mean
Late Fall 88	Winter 89	35.2	35.1	33.3	36.3	35.0a[1]	80.8	87.2	71.6	77.2	
Dry Seed[2]			6.8	6.8	7.1	6.9	6.9b	79.6	88.4	79.2	80.0
Mean							80.2B	87.8A	75.4B	78.6B	
Winter 89	Early Spring 89	36.1	37.7	36.8	38.1	37.2a	76.4	86.0	74.0	78.0	
Dry Seed		6.5	6.3	6.9	6.5	6.5b	77.6	86.4	77.6	77.2	
Mean		32.2B	37.4AB	35.2B	37.9A		77.0B	86.2A	75.8B	77.6B	
Winter 89	Late Spring 89	55.0	53.6	56.7	54.8	55.0a	72.2Ab	59.4Bb	69.6Aa	74.8Aa	
Early Spring 89		42.4	46.2	42.6	44.7	44.0b	80.8ABa	87.2Aa	72.8Ba	76.6Ba	
Dry Seed		5.4	5.9	5.5	5.3	5.5c	82.0Aa	86.8Aa	76.8Ba	77.2Ba	
Early Spring 89	Early Summer 89	18.7	18.2	18.8	21.3	19.3a	78.0	84.8	75.2	74.8	78.2b
Late Spring 89		21.9	22.5	19.7	21.9	21.5a	74.0	85.2	66.8	79.2	76.3b
Dry Seed		6.3	6.7	6.7	7.9	7.0b	80.4	89.6	78.4	82.0	82.6a
Mean							77.5B	86.5A	73.5C	78.7B	

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[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

Table II.10. Total percent germination and days to 50% germination for 4 spiny hopsage seed lots placed in the field in nylon bags on 4 planting dates and recovered after selected intervals from Reynolds Creek 1988-89 plots, southwestern Idaho.

Date		Total Percent Germination					Days to 50% Germination
		Seed Lot					Seed Lot
Planting	Recovery	RC86B	RC88B	SS86	SS88	Mean	Mean
Late Fall 88	Winter 89	72.0	74.3	68.2	81.9	74.1a[1]	7.3b
Dry Seed[2]		2.9	6.3	6.1	2.5	4.5b	18.6a
Winter 89	Early	55.5	73.5	70.3	64.6	66.0a	7.8b
Dry Seed	Spring 89	5.7	12.5	11.9	7.2	9.3b	18.3a
Mean		30.6C	43.0A	41.1AB	35.9BC		
Winter 89	Late	57.0	74.0	70.1	58.3	64.8a	6.4c
Early Spring 89	Spring 89	29.6	41.3	47.8	26.8	36.4b	10.1b
Dry Seed		6.8	11.8	8.1	8.8	8.9c	20.8a
Mean		31.2B	42.3A	42.0A	31.3B		
Early Spring 89	Early	11.8Ba	6.3Bb	7.2Bb	20.6Aa		20.5
Late Spring 89	Summer 89	14.5Aa	16.2Aa	18.3Aa	17.5Aa		20.1
Dry Seed		7.2Aa	5.4Ab	4.3Ab	2.2Ab		22.2
Mean							20.9n.s.

[1] Seed lot means within planting date, recovery date, and seed characteristic followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within recovery date and seed lot followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

[2] Seed stored in sealed containers at room temperature since harvest.

Table II.11. Density of spiny hopsage seedlings on 1988-89 Birds of Prey and Reynolds Creek plots, southwestern Idaho.

		Planting Site						
	Birds of Prey						Reynolds Creek	
		Seedling Density						Seedling Density
		Seed Lot						Seed Lot
Planting Date	Counting Date	RC86B	RC88B	SS86	SS88	Mean	Counting Date	Mean
		--------no./m^2--------						--no./m^2--
Late Fall 88	12 March	59.6	52.8	51.6	67.2	57.6a[1]	11 March	12.8a
Early Spring 89		0.0	0.0	0.0	0.0	0.0b		0.0b
Late Fall 88	23 March	102.8ABa	86.4Ba	114.4Aa	108.8ABa		20 March	39.2a
Early Spring 89		3.6Ab	0.4Ab	0.0Ab	4.0Ab			0.8b
Late Fall 88	18 April	93.2Aa	69.6Ba	88.4ABa	74.4ABa		11 April	93.8a
Early Spring 89		12.4Bb	16.4Bb	31.6Ab	24.4Ab			8.8b
Late Spring 89		0.0Ac	0.4Ac	0.4Ac	0.0Ac			0.0c
Late Fall 88	6 July	43.6	39.6	63.6	56.8	50.8a	3 July	41.0a
Early Spring 89		4.8	4.0	13.6	11.6	8.4b		1.6b
Late Spring 89		0.0	0.4	0.0	0.0	0.1c		0.0b
Mean		16.0B	14.8B	25.6A	22.8A			

[1] Seed lot means within planting date, counting date, and planting site followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Planting date means within counting date, seed lot, and study site followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

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MANUSCRIPT III

LABORATORY GERMINATION OF 2 SPINY HOPSAGE POPULATIONS FROM THE SHRUB STEPPE

Abstract

Inclusion of spiny hopsage (*Grayia spinosa* [Hook.] Moq.) in shrub plantings in Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle and A. Young] Welsh) and salt desert shrub communities in the northern shrub steppe would contribute to the forage, cover, and soil stabilization values of the resultant vegetation. Use of the species is presently limited as seeds are only rarely available commercially and planting requirements have not been determined. This laboratory study was conducted to develop pretreatments for enhancing germination for nursery and greenhouse plantings and to examine the nature of dormancy in utricles and seeds of 2 spiny hopsage populations from southeastern Oregon and southwestern Idaho. Utricles and seeds responded to cold stratification at 3-5°C. Minimum treatment duration for optimizing the germination response was approximately 60 days. Mean total germination at 5/15°C (44.1%) was similar to the greatest constant temperature germination which was obtained over the 20-30°C (36.8-39.8%) range. Stratification and the low temperature alternation may act to release dormancy and permit germination in early spring when soil moisture conditions are favorable for emergence. Excising embryos or piercing seeds through the perisperm area released inhibition to germination imposed by the elastic inner layers of the testa. Moist-heat treatments of 96 hours at 35°C applied following 1-, 15-, or 30-day incubations at 15°C or 6 hours at 35°C following a 30-day incubation at 15°C reduced dormancy, with the effect greater for seeds than utricles. Dry-heat and freeze-thaw treatments were ineffective in relieving dormancy. Leaching did not alleviate the inhibition of utricle germination resulting from the presence of the papery bracts. Bracts did not decrease water uptake or provide mechanical restraint to embryo emergence, hence they may act by reducing oxygen uptake. Both stratification and moist-heat treatments could be utilized as germination pretreatments for nursery or greenhouse production of planting stock.

Key Words: chenopod shrubs, coat-imposed dormancy, *Grayia spinosa*, germination, shrub steppe, utricles

Introduction

Spiny hopsage (*Grayia spinosa* [Hook.] Moq.) is a summer deciduous chenopod shrub endemic to the interior western United States (Welsh et al. 1987). In the northern shrub steppe it is commonly associated with drier portions of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & A. Young] Welsh) communities and a variety of salt desert shrub communities (Daubenmire 1970, Welsh et al. 1987). Reestablishment of spiny hopsage populations depleted or lost as a result of livestock grazing practices and other human activities is desirable due to the species forage, cover, and soil stabilization values (Dasmann and Blaisdell 1954, Gullion 1964, USDA-SCS 1968, Krysl et al. 1984).

Limited knowledge of seed germination requirements has restricted use of seed from northern spiny hopsage populations for production of nursery stock or rangeland seedings. Southern populations produce nondormant seeds that germinate rapidly on imbibition (Wallace et al. 1970, Wallace and Romney 1972, Wood et al. 1976). Although Glazebrook (1941) found seeds from eastern Washington required no pretreatment for germination, King (1947) reported seeds from the same area were dormant. Preliminary germination tests indicated seeds of a number of southern Idaho and southeastern Oregon populations were also dormant (N.L. Shaw, file data, 1984-87).

Utricles and seeds of shrubby chenopods in related genera, including *Atriplex* L., *Ceratoides* Gagnebin, and *Sarcobatus* [Hook.] Torr. exhibit a variety of dormancy-inducing mechanisms (Young et al. 1984). Approaches developed for alleviating dormancy in these species include leaching to remove chemical inhibitors (Nord and Van Atta 1960) or soluble salt accumulations in the bracts (Twitchell 1955, Cornelius and Hylton 1969), mechanical scarification (Beadle 1952, Eddleman 1979, Warren and Kay 1984), dry storage to promote afterripening (Springfield 1968, 1970), and stratification (Ansley and Abernethy 1985). Treatment combinations are required to relieve multiple forms of dormancy in Gardner's saltbush (Atriplex gardneri [Moq.] D. Dietr.) (Ansley and Abernethy 1985). Intraspecific variation in nature and degree of dormancy, common among chenopods, is considered an adaptation to local site conditions (Clark and West 1971, Meyer and Pendleton 1990, Sanderson et al. 1990), but can complicate efforts to develop techniques for enhancing germination.

Seed pretreatments to improve both total germination and uniformity of germination in spiny hopsage are essential for efficient greenhouse and nursery production of transplant stock. An understanding of germination requirements in this species is also prerequisite to development of successful systems for establishing the species by direct seeding on rangelands. The major objective of this study was to determine methods that improve utricle or seed germination of 2 spiny hopsage populations from the northern shrub steppe. A secondary objective was to investigate the nature of dormancy in these populations.

Materials and Methods

Utricle Harvest

Utricles were harvested by hand at Sponge Springs, Malheur Co., Oregon ($43^{o}47'42''N;117^{o}25'59''W$) in 1988 (SS88 utricle lot) and at Reynolds Creek, Owyhee Co., Idaho ($43^{o}15'31''N;116^{o}12'37''W$) in 1984 and 1988 (RC84B and RC88B utricle lots) (Table III.1). Harvested utricles were air-dried for 2-4 weeks, and twigs, large leaves, and some empty bracts were removed with an air-screen cleaner. Conditioned utricles were stored in plastic containers at room temperature. Moisture content of the 3 seed lots ranged from 8.6 to 9.8%.

Testing Procedures

The term "utricle" as used in these experiments refers to the utricle enclosed within the papery bracts. Utricle lots were examined over a light table, and empty bracts not removed by scalping were discarded. Seeds were obtained by carefully hand rubbing utricles between sheets of polyurethane foam mounted on wooden blocks to remove the bracts while minimizing embryo damage. Chaff was removed with a seed blower. Unless otherwise specified, experiments were conducted using the following general procedures: Utricles and seeds were stratified and germinated on 2 layers of blotter paper moistened with distilled water in 110 X 110 X 30-mm germination boxes. During incubation, samples were exposed to 16 hours of darkness alternating with 8 hours of light. The light period coincided with the high temperature period of alternating temperature regimes.

Germination experiments were completed between April 1989 and March 1990. All germination trials were conducted in 4 blocks with time of run used as a blocking factor. Each sample unit consisted of 50 utricles or seeds. Pretreatments were scheduled to permit a 30-day incubation period to begin simultaneously for all sample units within each block. Dishes were randomly placed on germinator shelves and replaced randomly following germination counts made at 1- or 2-day intervals. Viability was estimated separately for 4 replications of 50 utricles and seeds of each lot at the beginning of each experiment, using techniques recommended by AOSA (1970) and Belcher (1985). Total germination was quantified as percentage of viable utricles or seeds producing normal seedlings after 30 days of incubation. Seedlings were considered normal if all essential structures for development were present, the hypocotyl arch was raised, and the radicle was 10 mm long. Unless otherwise specified, seedlings not meeting these criteria were classified as abnormal. Germination rate was calculated as days to 50% of 30-day germination.

Effects of pretreatments on total percent germination, percent abnormal germination, germination rate, final viability, and seedling axis length were evaluated by analyses of variance. Means were separated using Fisher's least significant difference. Percentage data for viability, germination, and abnormal germination were transformed with arcsin $\sqrt{p}$ for analyses of variance (Snedecor and Cochran 1980). Polynomial response curves were developed to describe the effect of stratification period on total germination and germination rate using untransformed data (Peterson 1985). All statistical tests were conducted with $p \leq 0.05$.

Treatments

Stratification

The effects of 0-, 30-, 60-, and 90-day stratification periods at 3-5°C on 5-year old RC84B utricles (56% viability) and seeds (70% viability) and 1-year old RC88B and SS88 utricles (viability 81% for RC88B and 68% for SS88 utricles) and seeds (viability 87% for RC88B and 72% for SS88 seeds) were examined. Germination was determined by incubating stratified utricles and seeds at 5/15 (16 hours/8 hours) or 25°C.

Temperature

Germination of the RC84B, RC88B, and SS88 utricle collections was measured at 10, 15, 20, 25, 30, 5/15, and 2/10°C. Nonstratified and stratified (45 days at 3-5°C) utricles and seeds were monitored. The stratification and temperature experiments were conducted concurrently, thus viability for the 3 seed lots was as described for the stratification experiment.

Leaching

Samples of RC88B utricles (82% viability) and seeds (88% viability) were either (i) imbibed on moist blotters or (ii) leached with running tap water for 24 hours. After pretreatment, bracts and pericarps were removed (debracted seeds) from one-half of the utricle samples. Pretreated utricles, seeds, and debracted seeds were either (i) placed in incubation at 15°C, or (ii) stratified at 3-5°C for 30 days before being placed in incubation at 15°C to determine potential germination.

Mechanical Scarification

Mechanical scarification was accomplished by piercing through the bract, pericarp, and testa on both flat surfaces of imbibed RC88B utricles (78% viability) and seeds (85% viability) using a sharp needle. Care was taken to pierce through the perisperm area to prevent embryo damage. Scarification was applied to both nonstratified and stratified (45 days at 3-5°C) utricles and seeds. Scarified samples and corresponding controls were incubated in germinators at 15°C for 19 days. Germination of some mechanically scarified utricles and seeds occurred when the radicle or cotyledons protruded through one of the pierced surfaces. Cotyledons often emerged first, in which case the radicle frequently remained within the enclosing structures. Germinants in this condition at the conclusion of the 19-day incubation period were dissected from the enclosing structures and classified as normal or abnormal.

Embryo Excision

Sample units consisting of 25 normal embryos were randomly selected from groups of 50 RC88B utricles (78% viability) or seeds (85% viability) as follows: (i) embryos were excised from utricles or seeds imbibed for 24 hours at room temperature; (ii) embryos excised from imbibed utricles or seeds were stratified at 3-5°C for 45 days; and (iii) embryos were excised from imbibed, stratified utricles and seeds. A fourth treatment consisted of utricles and seeds stratified at 3-5°C for 45 days. Excised embryos from the first 3 treatments and and utricles and seeds from the fourth treatment were incubated at 15°C for 19 days. Response to treatments was determined by measuring axis length (tip of epicotyl to tip of radicle or primary root) of each of the 25 excised embryos or 25 germinated utricles or seeds from each sample unit.

In a second experiment, 25 normal embryos excised from groups of 50 imbibed seeds were incubated at 15°C for 19 days (i) on moist blotters, (ii) on blotters moistened with distilled water containing ground bracts of 25 utricles, or (iii) each embryo was incubated within an empty set of imbibed bracts placed on blotters with the slit surface of the bract placed upward. Response to treatments was determined by measuring the axis length of each embryo or seedling.

Moist-Heat

After a 1-, 15-, or 30-day incubation at 15°C, RC88B utricles (79% viability) and seeds (86% viability) were incubated in closed germination dishes at 35 or 45°C for 6- or 96-hour moist-heat treatments. Pretreated samples were returned to 15°C for further incubation. For each experiment, the moist-heat treatment plus subsequent incubation at 15°C totaled 30 days. Germination of all sample units, including controls incubated at 15°C, was counted over the total incubation period (31, 45, or 60 days) for each experiment. Final viability was calculated as percent germination plus percent viable, nongerminated utricles or seeds remaining at the end of the incubation period.

Dry-Heat

RC88B seed (85% viability) was oven-dried in open or sealed containers at 15 (controls), 35, or 45°C for 15, 30, or 45 days. Pretreated seed was incubated at 15°C.

Freeze-Thaw

RC88B utricles (79% viability) and seeds (86% viability) incubated at 15°C for 1, 15, or 30 days were treated by freezing at -10°C for 24, 48, or 96 hours or by freezing for either two or three 8-hour periods at -10°C separated by 16 hour periods of thawing at 15°C. Pretreated samples were returned to 15°C for further incubation. For each experiment, the freeze-thaw treatment plus subsequent incubation at 15°C totaled 30 days. Germination of all sample units, including controls incubated at 15°C, was counted over the total incubation period (31, 45, or 60 days) for each experiment.

Results and Discussion

Stratification and Temperature Experiments

Stratification

Nonstratified utricles and seeds were highly dormant. Total germination and germination rate increased with longer stratification treatments (Fig. III.1). Significant interactions containing the stratification factor were not examined as their contributions to the reduction of the sum of squares for both total germination (0.9-1.8%) and the germination rate (0.0-1.0%) were dwarfed by the reduction contributed by the stratification main effect (69.8% for total germination and 75.4% for germination rate).

The 3 collections collections responded differently to incubation temperature (Table III.2). Total germination of the RC88B collection was similar at 5/15 and 25°C, but germination of the RC84B and SS88 collections was greater at 5/15°C than at 25°C. Germination was greater for the RC84B and RC88B collections compared to the SS88 collection at both incubation temperatures.

Utricles and seeds also differed in their response to incubation temperature. Total germination of seeds was similar at 15/5 and 25°C (mean 59.4%) ($p \leq 0.05$). Germination of utricles did not differ from seeds at 5/15°C (mean 57.8%). At 25°C, however, germination was lower for utricles (39.9%) than for seeds (58.5%).

Rate of germination was greater at the higher incubation temperature. Days to 50% germination averaged 13.5 at 5/15°C and 9.3 at 25°C ($p \leq 0.05$). Rate of germination was similar for seeds of the 3 utricle collections, but RC84B utricles germinated more rapidly than

RC88B or SS88 utricles (Table III.3). Within each RC collection, utricles and seeds germinated at similar rates. By contrast, SS88 seeds germinated more rapidly than utricles.

Temperature

Total germination at constant temperatures increased through 20°C. No decline was noted at 30°C (Fig. III.2). Germination rate generally increased at higher constant incubation temperatures (Fig. III.3). Total germination at 5/15°C was similar to the maximum constant temperature germination obtained, while the germination rate was similar at 5/15°C and 15°C (Fig. III.2).

A 45-day stratification improved both total germination percentage and germination rate. Total germination increased from 8.9 to 63.8% with stratification while days to 50% germination declined from 24.5 to 10.7 ($p \leq 0.05$). Significant interactions containing the stratification factor were not examined as their contribution to the reduction of the sum of squares for both total germination (0.2-2.9%) and germination rate (0.0-4.0%) were very small compared to the reduction provided by the stratification main effect (53.9% for total germination and 55.2% for germination rate).

Total germination of seeds (43.5%) exceeded utricles (29.1%) ($p \leq 0.05$). Only the main effect of bract condition on total germination was examined due to its large contribution to the reduction of the sum of squares (6.1%) compared the reduction contributed by significant interactions containing this factor (0.2 to 0.4%). Seeds averaged 16.6 days to 50% germination while utricles required 18.7 days ($p \leq 0.05$).

Average germination of the RC84B and RC88B collections was 38.1% compared to 32.9% for the SS88 collection ($p \leq 0.05$). Days to 50% germination averaged 17.6 for the 3 collections ($p \leq 0.05$).

The positive response to stratification indicates fall or winter planting or laboratory stratification prior to early spring planting are necessary to relieve dormancy. A positive response to stratification is common among plants of the Great Basin, reflecting the ecological requirement for germination in early spring when soil moisture conditions are conducive to growth prior to the onset of summer drought (Vallentine 1980). Meyer and Pendleton (1990) found spineless hopsage utricles also required stratification to relieve dormancy. An 8-week treatment at $1^{\circ}C$ was required to relieve dormancy of utricles from warm and moderate-winter sites, while a 15-week stratification was required for utricles from a cold-winter site.

All 3 utricle lots examined in this study exhibited high germination in response to the $15/5^{\circ}C$ alternating temperature regime. Wood et al. (1976) reported optimum germination of nondormant Nevada and California lots occurred at alternating temperature regimes with $5^{\circ}C$ as the low alternate. These responses may also indicate an ecological adaptation for germination in early spring.

Although alternating temperatures enhance germination of many species, their physiological role is poorly understood (Bewley and Black 1982). They frequently act to reduce coat-imposed dormancy, but may also function in other phases of germination and growth. Temperature fluctuations in surface soils may provide a depth-sensing mechanism in addition to the phytochrome system permitting germination of that portion of the seedbank positioned in soil at depths favoring successful emergence (Grime 1979).

The generally greater and more rapid germination of seeds compared to utricles in both experiments could be partially, but not entirely, attributed to the additional elongation required for the radicle and hypocotyl arch to emerge beyond the perimeter of the bracts. Average diameter for seeds is 2 mm compared to 6-10 mm for bracted utricles. Results of this experiment contrast with those of Wood et al. (1976) who found bracts did not depress germination of nondormant spiny hopsage collections from Nevada and California when incubated at constant temperatures between 2-40°C, inclusive.

Inhibition imposed by structures enclosing the embryo stem from physical (reduced permeability to water, mechanical restriction, and lowered gas exchange) or chemical (presence of salts or inhibitors) causes. Total imbibition of water by seeds was not reduced by the presence of bracts at room temperature (N.L. Shaw, file data, 1989). Bracts of some chenopods, such as shadscale, may impose mechanical restraint to radicle emergence (Warren and Kay 1984). The papery bracts of spiny hopsage, however, are easily ruptured during germination; many are fractured during harvesting and conditioning.

Dry afterripening for 1 or 5 years did not relieve the dormancy of these seed lots. King (1947) obtained maximum germination of a 6-year old spiny hopsage seed lot from eastern Washington following a 2-week stratification at 5°C, while a 12-week stratification was required to maximize germination of a 4-year old seed lot. Based on these observations he concluded that older seed lots might require shorter stratification periods to relieve dormancy. Whether differences between the 2 lots were genetic or environmental in nature, however, was not determined.

Pendleton and Meyer (1990) found germination of 6 spineless hopsage collections increased with dry afterripening during the first 14 months following harvest. Initial germination and rate of afterripening varied among collections.

Leaching

Leaching did not affect total germination or rate of germination under any of the applied treatment conditions ($p \leq 0.05$). Stratification did increase germination of leached and imbibed utricles, seeds, and debracted seeds from 8.2% to 60.0% and decreased days to 50% germination from 24.2 to 5.1 ($p \leq 0.05$). Total germination, but not germination rate, was greater for seeds and debracted seeds (37.0%) compared to utricles (28.2%). Mean germination rate was 14.6 days.

Spiny hopsage accumulates postassium and other cations (Wallace et al. 1973). Sanderson et al. (1988) reported that saponins, which can function as germination inhibitors, are also present in spiny hopsage tissues. However, leaching to remove water soluble inhibitors did not improve germination of bracted utricles. It is possible that inhibition may result from the presence of insoluble inhibitors or from low permeability to oxygen or other gases.

Pendleton and Meyer (1990) concluded that bract inhibition of germination in spineless hopsage resulted from physical forces. Cations, principally sodium, and saponins at concentrations found in bract leachate did not depress germination. Sabo et al. (1979), Fernandez and Johnson (1980), and Warren and Kay (1984) found that although shadscale pericarps contain sodium chloride, leaching did not improve germination. Inhibition was attributed to low permeability of the dense, woody pericarp to water and oxygen.

Embryo Excision

Hypocotyl elongation, root hair development, and greening of cotyledons occurred rapidly in all embryo excision treatments (Table III.4). Axis length did not vary among seedlings developing from embryos excised from utricles preceding or following stratification. By contrast, axis length of seedlings developing from embryos excised from seeds was greater when excision followed stratification. Axis length was greater for seedlings developing from intact, stratified utricles and seeds compared to seedlings developing from embryos excised from the same structure.

Growth of embryos excised from nonstratified, as well as stratified utricles and seeds indicates structures enclosing the embryo are at least partially responsible for dormancy, possibly acting by imposing mechanical restraint or reducing oxygen uptake. Increased growth of seedlings from intact structures may have been related to nearly total utilization of the perisperm by the embryo observed to occur during the germination process.

Mean axis lengths did not differ among seedlings developing from nonstratified, excised embryos imbibed in distilled water, a mixture of powdered bracts and water, or in imbibed, empty bracts. These results further indicate that inhibition exerted by bracts was not related to salts or water soluble inhibitors contained within them. Mean axis length for these treatments was 25 mm.

Mechanical Scarification

Mechanical scarification increased germination of RC88 seeds from 32.6 to 92.2%, but did not affect utricle germination which averaged 30.8%. Stratification increased germination of seeds from 51.9 to 72.9% and germination of utricles from 5.0 to 56.5%. Germination of nonstratified utricles and seeds increased from 7.1 to 49.8% with scarification, while germination of stratified utricles and seeds increased from 56.5 to 73.0%.

Piercing RC88 seeds relieved the constraint imposed by the elastic inner layers of the testa. The outer layer of the testa ruptures irregularly on imbibition, but the inner layers become highly distended, delaying germination until the radicle develops adequate force to pierce the membrane, the membrane is weakened by germination processes or environmental conditions, or both. Rapid growth of excised embryos would seem to indicate that the status of the inner layers of the testa may be critical in regulating germination. The nature of the restriction provided by this layer is not known. Physical restraint, low permeability to oxygen or other gases, or presence of inhibitors are possibilities. Failure of mechanical scarification to improve utricle germination may have resulted because the small perforations made in the bracts tended to close.

The practicality of mechanical scarification treatments for artificially inducing germination is limited as utricles and seeds must be pierced individually. Use of seed scarifiers was found to produce radicle damage (N.L. Shaw, file data, 1986-9).

Moist-Heat Treatments.

The 3 moist-heat experiments were analyzed separately due to differing total incubation periods. Final viability was severely reduced and germination nearly suppressed by 96-hour moist heat treatments at 45°C. Consequently, this treatment was deleted from the analysis for each experiment. Within each experiment, germination was enhanced by the 96-hour moist-heat treatment at 35°C (Table III.7). A 6-hour moist-heat treatment at 35°C improved germination only when applied following 30 days of incubation at 15°C. Mean total germination of seeds exceeded utricles in each experiment (Table III.7).

The germination rate improved when 6- or 96-hour moist-heat treatments at 35°C were applied after a 15-day incubation ($p \leq 0.05$). Days to 50% germination averaged 22.2 for the 6-hour treatment compared to 30.0 for the 96-hour treatment and 37.6 for controls.

Within each of the 3 experiments, final viability, defined as total germination plus percent viable, nongerminated utricles or seeds remaining at the end of the experiment, was reduced relative to controls by the 6-hour moist-heat treatment at 45°C. Abnormal germination increased when this treatment was applied following 15- or 30-day incubations (Table III.9). Final viability was greater for seeds compared to utricles when moist-heat treatments were applied following 15- or 30-day incubation periods (Table III.8), but did not differ by bract condition when moist-heat treatments followed a 1-day incubation.

The 6- and 96-hour moist-heat treatments at 35°C applied following a 15-day incubation at 15°C might be used as pretreatments for nursery or greenhouse plantings. Further work may be required to refine these treatments and determine their impact, if any, on seedling emergence and development.

Treatments involving positive or negative temperature shifts may have no parallel in nature. Bewley and Black (1982) suggested the action of temperature shifts and alternating temperature regimes may be similar. Only 1 or 2 shifts of a few minutes or hours may be required to release dormancy and induce rapid germination of some species (Totterdell and Roberts 1979). Success of the treatment varies with temperature and duration of the incubation period preceding the treatment.

Dry-Heat Treatments

Subjecting RC88B seeds to dry-heat treatments at 35 or 45°C for 15, 30, or 45 days in sealed or open containers did not alter total germination, germination rate, or final viability compared to seeds pretreated at 15°C ($p \leq 0.05$). Total germination averaged 7%, days to 50% germination 24.9, and final viability 88.5%.

Dry afterripening at high temperatures may accelerate loss of dormancy (Bewley and Black 1982). Capon and Van Asdall (1967) reported dormancy in seeds of 9 annual Mojave and Sonoran Desert forbs decreased following 5 weeks of dry storage at 50°C. Meyer (1989) and Meyer and

Monsen (1989) found 4-8 weeks of dry compared to moist storage at 15 or 30°C hastened afterripening of antelope bitterbrush, a Rosaceous shrub, which, like spiny hopsage, disperses its fruits in early summer. A shorter stratification was required for germination of achenes receiving warm-dry compared to warm-moist treatments. The possibility that dry-heat treatments altered the stratification requirement of spiny hopsage seeds was not examined.

Freeze-Thaw Treatments

The 3 freeze-thaw experiments were analyzed separately due to differing total incubation periods. Freeze-thaw treatments applied following a 1-, 15-, or 30-day incubation at 15°C did not improve total germination or days to 50% germination ($p \leq 0.05$). Total germination of treated utricles and seeds (5.6%) was reduced relative to controls (18.9%) when the 96-hour freezing treatment was applied following a 15-day incubation ($p \leq 0.05$). The germination rate decreased relative to controls when this treatment was applied following a 30-day incubation ($p \leq 0.05$). Treated utricles and seeds required 55.3 days to reach 50% germination compared to 44.9 days for controls.

Eddleman (1979) found 24- and 96-hour freezes at -10°C broke dormancy of greasewood utricles that failed to germinate during 30-day incubations at higher temperatures. Effectiveness of the treatment presumably resulted from rupturing of the membranous pericarp which restricted embryo emergence.

Conclusions

Dormancy mechanisms in seeds of in spiny hopsage populations from the shrub steppe and conditions required for their release provide adaptation to early spring germination when soil moisture conditions favor seedling emergence. Seed dormancy appears to be result from the inability of the radicle to pierce the elastic inner layer of the testa. Whether this results from mechanical restraint imposed by the membrane, impermeability to oxygen or other gases, or physiological status of the embryo is not clear. Stratification and alternating temperatures, effective in relieving dormancy and promoting germination, frequently act to relieve coat-imposed dormancy, but key physiological changes affecting the response have not been identified (Bewley and Black 1982). Total germination percentage and germination rate were generally reduced by the presence of the hygroscopic bracts, possibly due to a reduction of oxygen uptake. Longevity of the bracts in the field has not been examined. Further investigation of germination regulating mechanisms is warranted.

Stratification or moist-heat treatments could be utilized to increase germination percentage of dormant spiny hopsage collections. Sixty-day stratification treatments were adequate for the collections examined, but duration of effective treatments may vary among seed lots. A 96-hour moist-heat treatment at 35°C following a 15-day incubation at 15°C may provide the most rapid means of artificially relieving dormancy. The smooth, dark brown outer layer of the testa dries quickly, thus it is possible to surface-dry imbibed seeds following application of either treatment to facilitate planting through seeding devices. Use of these techniques to provide nondormant seeds for late winter or early spring seedings on rangelands would require careful field testing.

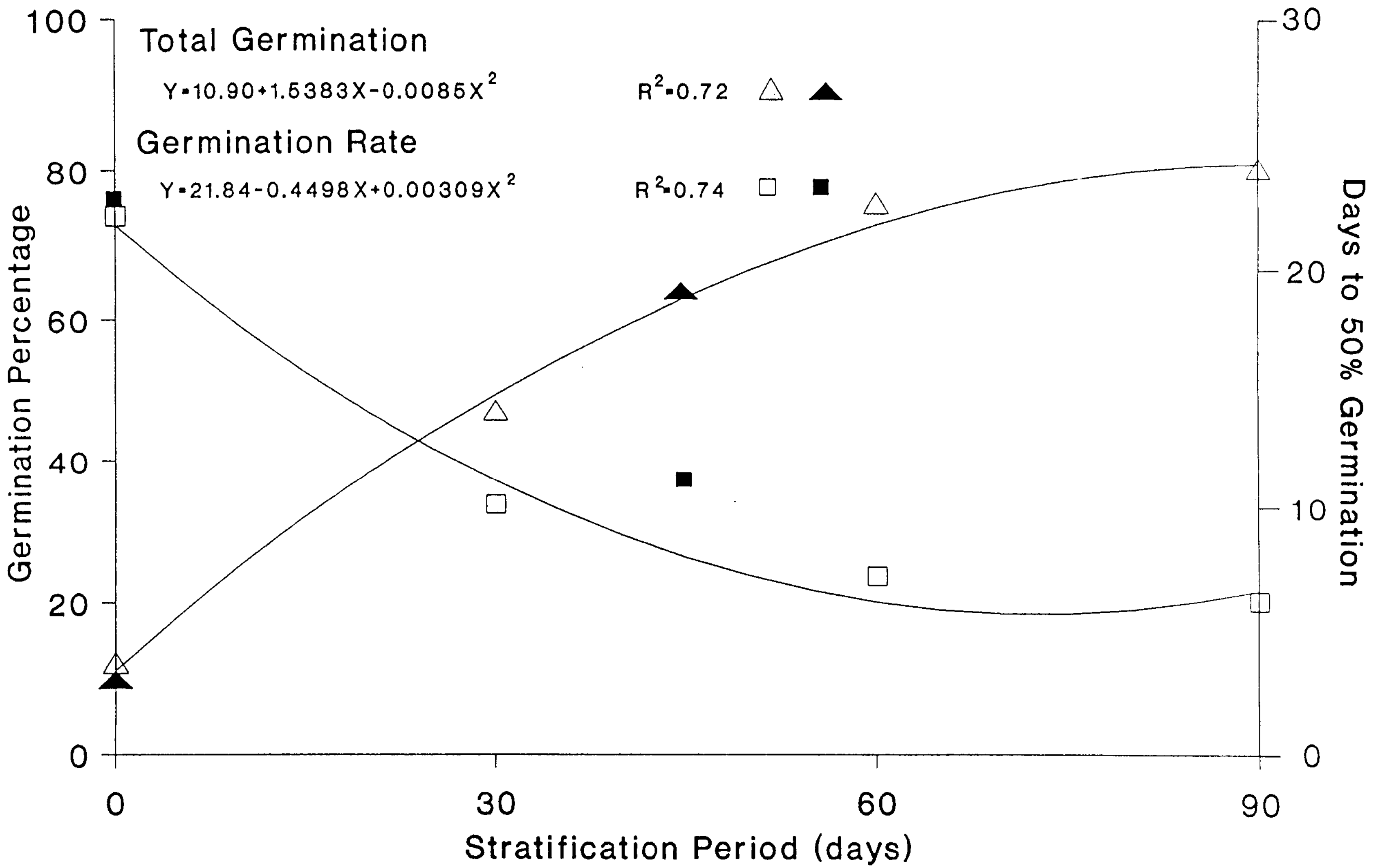

Fig. III.1. Total percent germination and germination rate of 3 spiny hopsage collections as affected by duration of cold stratification treatment. Each open symbol represents the mean of 48 replications (Stratification Experiment). Each closed symbol represents the mean of 168 replications (Temperature Experiment).

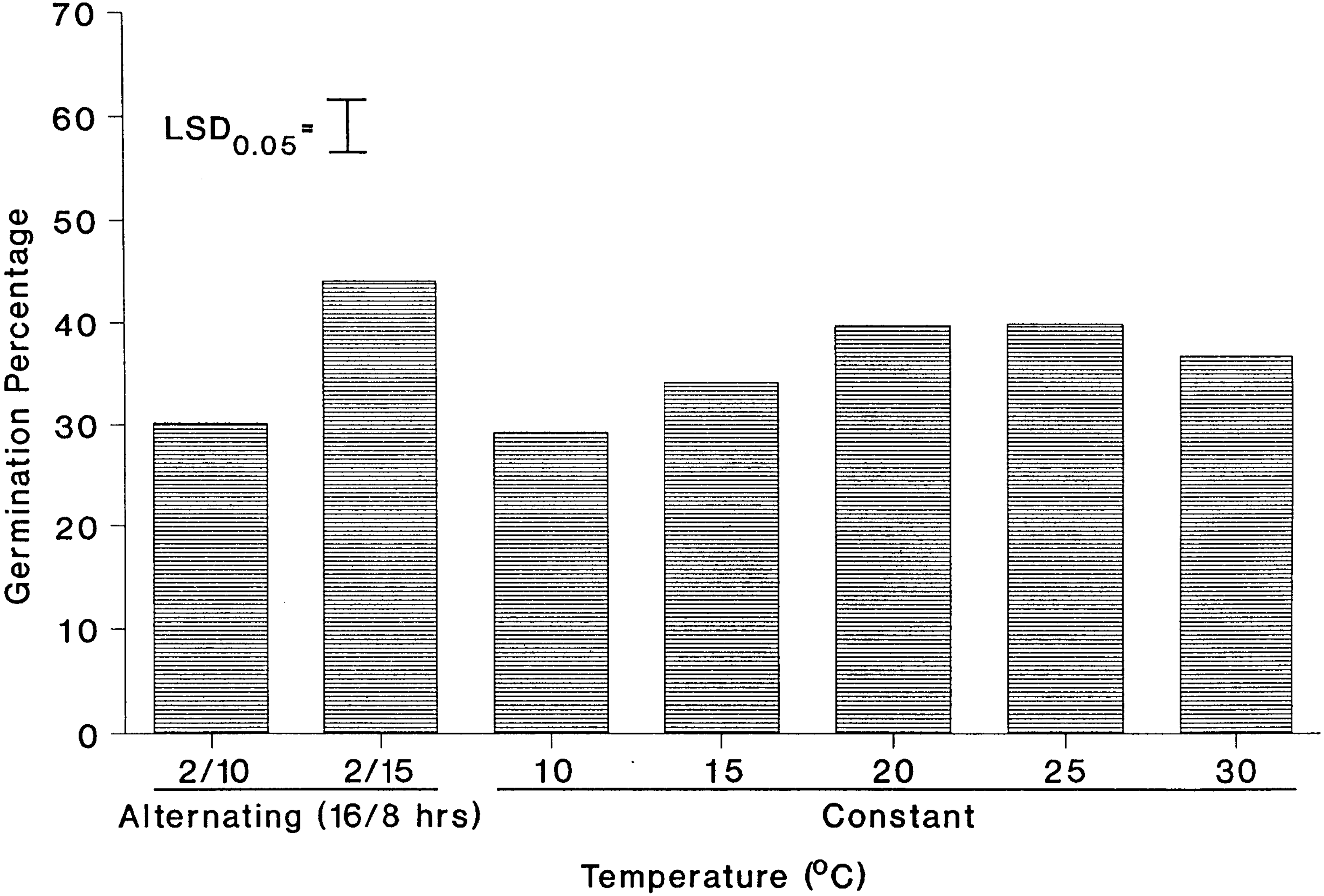

Fig. III.2. Total percent germination of spiny hopsage utricles and seeds at selected alternating and constant temperature regimes.

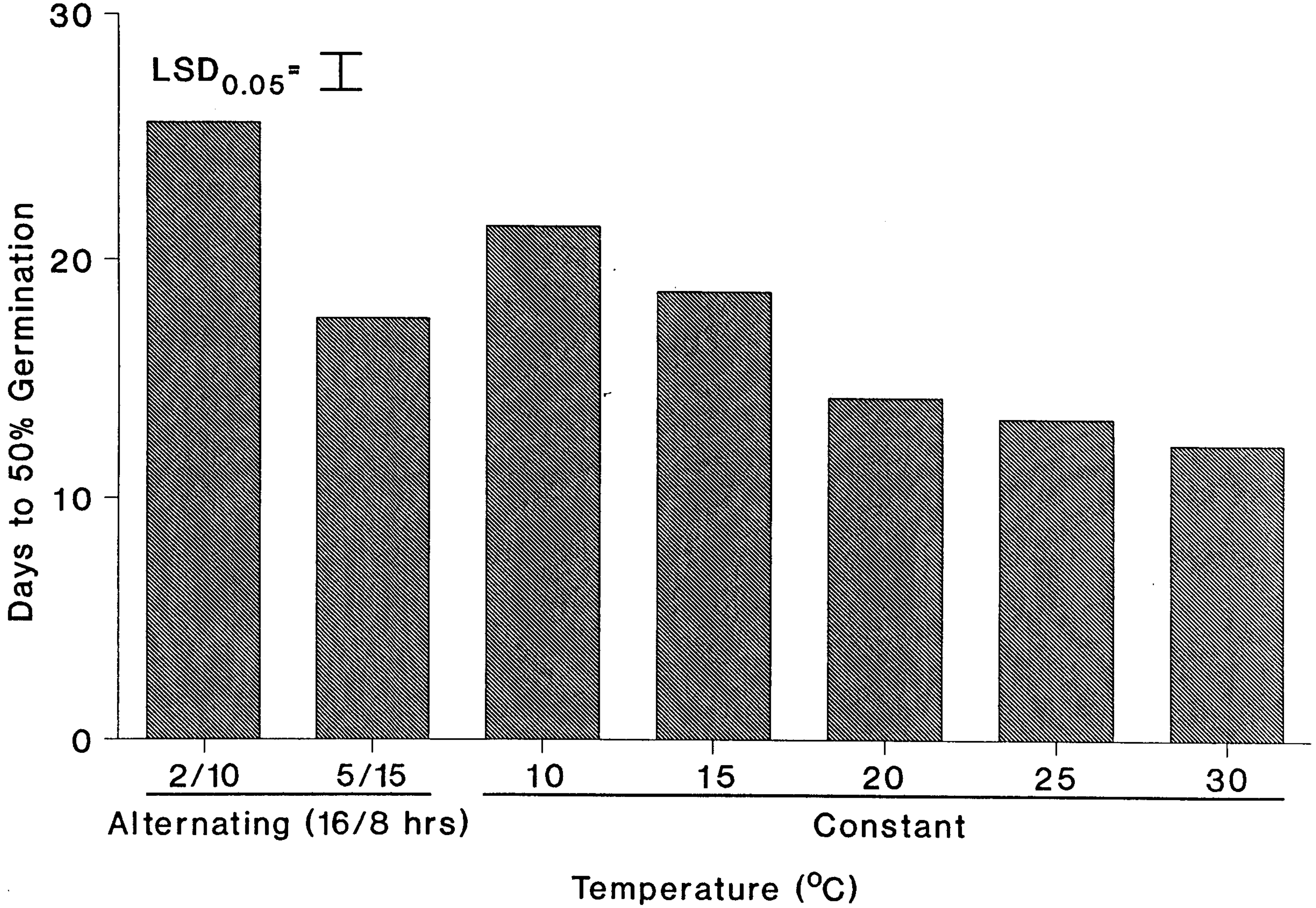

Fig. III.3. Germination rate of spiny hopsage utricles and seeds at selected alternating and constant temperature regimes.

Table III.1. Characteristics of spiny hopsage seed collection sites.

	Seed Collection Site	
	Reynolds Creek	Sponge Springs
Location	Northern foothills of Owyhee Mountains, southwestern Idaho	Malheur Basin, southeastern Oregon
Vegetation	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Sitanion hystrix*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Bromus tectorum*
Elevation (m)	1,260	991
Precipitation (mm)	249[1]	228[3]
Soil	Coarse-loamy, mixed nonacid, mesic Xeric Torriorthents[2]	Fine-loamy, mixed mesic Xerollic Durargids[4]

[1] C.L. Hanson (file data, USDA-ARS, Boise, Idaho 1992).
[2] Stephenson (1977).
[3] J.M. Findley (file data, USDI-BLM, Vale, Oregon, 1990).
[4] Oregon Water Resources Board (1969).

Table III.2. Total percent germination of 3 spiny hopsage collections by incubation temperature.

Incubation Temperature	Collection		
	RC84B	RC88B	SS88
-----°C----	-----------germination (%)-------------		
5/15	61.9Aa[1]	60.6Aa	50.2Ab
25	47.1Bb	58.4Aa	42.1Bb

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[1] Incubation temperature means within collections followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Collection means within incubation temperatures followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

Table III.3. Rate of germination for utricles and seeds of 3 spiny hopsage collections.

Bract Condition	Collection RC84	Collection RC88	Collection SS88
	------days to 50% germination-----		
Utricles	10.5Ab[1]	12.2Aa	13.2Aa
Seeds	11.3Aa	10.9Aa	10.2Ba

[1] Bract condition means within collections followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Collection means within bract conditions followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

Table III.4. Axis length of RC88 seedlings as affected by bract condition and utricle or seed pretreatment.

Bract condition	Utricle or seed pretreatment			
	Embryo excised	Embryo excised and stratified	Stratified intact embryo excised	Stratified intact
	mm			
Utricles	27Ab[1]	25Ab	29Bb	49Ba
Seeds	25Ac	25Ac	36Ab	59Aa

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[1] Bract condition means within utricle or seed pretreatment followed by similar upper case letters do not differ at $p \leq 0.05$. Utricle or seed pretreatment means within bract condition do not differ significantly at $p \leq 0.05$.

Table III.5. Total percent germination of the RC88 collection, utricles and seeds in response to moist-heat treatments applied following selected pretreatment incubation periods at 15°C.

Treatment	Pretreatment Incubation (days)		
	1	15	30
	-----total germination (%)------		
Moist-heat treatment, °C/hours			
Control	6.8B	15.1B	24.7B
35/ 6	7.1B	22.2B	44.5A
35/96	18.4A	40.8A	46.9A
45/ 6	10.4B	16.7B	17.8C
Bract condition			
Utricles	7.4B	17.2B	18.5B
Seeds	13.9A	31.6A	40.4A

[1] Moist-heat treatment means and bract condition means within pretreatment incubation periods followed by similar letters do not differ significantly at $p \leq 0.05$.

Table III.6. Final viability (total percent germination plus remaining viable seeds or utricles) of the RC88 collection, utricles, and seeds following moist-heat experiments.

Treatment	Pretreatment Incubation (days)		
	1	15	30
	---------final viability (%)---------		
Moist-heat treatment, °C/hours			
Control	72.5A[1]	68.0A	74.0A
35/ 6	74.0A	70.8A	69.0A
35/96	78.7A	74.0A	65.2A
45/ 6	62.5B	20.5B	26.8B
Bract condition			
Utricles	69.9A	49.1B	52.1B
Seeds	74.0A	67.5A	65.4A

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[1] Moist-heat treatment means and bract condition means within pretreatment incubation periods followed by similar letters do not differ significantly at $p \leq 0.05$.

Table III.7. Abnormal germination of the RC88 collection in response to moist-heat treatments applied following selected pretreatment incubation periods at 15°C.

	Pretreatment Incubation (days)			
	Bract Condition			
Moist-heat	1		15	30
Treatment	Utricles	Seeds	Mean	Mean
--°C/hour--	---------------abnormal germination (%)-------------			
Control	3.0Aa[1]	3.0ABa	1.8B	2.0B
35/ 6	0.5Aa	1.0Ba	1.7B	1.8B
35/96	0.5Aa	2.0Ba	4.5B	5.0B
45/ 6	2.0Ab	10.5Aa	16.0A	18.5A

[1] Moist-heat treatment means within pretreatment incubation periods and bract condition followed by similar upper case letters do not differ significantly at $p \leq 0.05$. Bract condition means within the 1-day moist-heat pretreatment followed by similar lower case letters do not differ significantly at $p \leq 0.05$.

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CONCLUSION

Spiny hopsage can be established by direct seeding in the northern shrub steppe. Shallow planting in fall or early winter is crucial. This allows adequate stratification of seeds to terminate dormancy and permit germination with emergence occurring in early spring. Germination is initiated as maximum soil temperatures rise above freezing, and seedling emergence occurs as maximum and minimum air and soil temperatures fluctuate in the 0-20°C range. Although early spring temperatures may not be optimal for growth, soil moisture conditions conducive to germination and seedling emergence are most likely to occur during this period. Emergence in early spring allows seedlings to compete more effectively with cheatgrass and other winter annuals (Vallentine 1980), and maximizes the period for vegetative growth prior to mid-summer leaf fall and dormancy which characterizes this species. During the first growing season, seedlings develop a single shoot and a strong taproot system. This contrasts with the multistemmed, intricately branched shoot system and moderate to deep, diffusely branched root system of mature plants (Wallace and Romney 1972).

In good precipitation years, germination and seedling emergence generally increased with duration of incubation of seed in soil. However, both germination and seedling emergence were severely limited by low precipitation and inadequate soil moisture. Some nondormant seeds may have entered secondary dormancy in response to these conditions. Large percentages of emerged seedlings were lost each year as a result of dry soil conditions and predation by a plant bug (Melanotrichus spp.).

Incubating seeds in soil from early spring to late spring or early summer improved laboratory germination of recovered seed in some cases. Few seedlings, however, emerged from spring plantings, probably due to inadequate stratification and poor conditions for germination.

There was some indication that seedling emergence was greater on rough compared to compact seedbeds, possibly due to better microclimate conditions. Natural seedlings emerge beneath canopies of nurse plants where temperature and moisture conditions of the surface soil differ considerably from conditions on seeded plots (Manning and Groeneveld 1990). Seedling density and growth rates varied among field planted seed collections. Factors responsible for observed differences were not investigated.

Under laboratory conditions, utricles and seeds responded to cold stratification and 60 days was found to be the treatment duration for optimizing germination. Total germination at a 5/15°C (16 hours/8 hours) alternating temperature regime equaled greatest constant temperature response obtained over the 20-30°C range. Both stratification and alternating temperatures can release dormancy when soil moisture conditions are favorable, frequently by affecting termination of coat-imposed dormancy. Both mechanisms also act to adapt the species to early spring germination and emergence. Dormancy was also relieved by excising the embryo or by piercing all layers of the testa over the perisperm, thus relieving the restraint to germination imposed by the elastic inner layers. Moist-heat treatments of 96 hours at 35°C applied following 1-, 15-, or 30-day incubations at 15°C or 6 hours at 35°C following a 30-day incubation at 15°C also relieved dormancy of many seeds and utricles. Although spiny hopsage accumulates potassium and other cations and produces saponins (Wallace et al. 1973, Sanderson et al. 1988), leaching did not alleviate inhibition of germination resulting from the presence of the papery bracts. Bracts did not reduce imbibition or provide mechanical restraint to germination, hence they may act by reducing oxygen uptake.

Both stratification and moist-heat treatments could be utilized to promote rapid, uniform germination for nursery or greenhouse production of planting stock. The smooth outer layer of the testa surface-dries quickly, thus imbibed seeds can be distributed through seeding devices. Determining the practicality of pretreating seeds for late winter or early spring plantings on rangelands would require further investigation.

Studies of seed germination and seedling establishment of spiny hopsage from field seedings are still needed. Information on natural seedling establishment would provide valuable data needed for managing the species and improving the success of artificial seedings. Determining the longevity of seeds in soil and the nature of secondary dormancy, if present in northern populations of the species, would provide additional insight into the dynamics of natural seedling establishment.

Understanding the physiological nature of dormancy requires examination of changes in the inner layers of the testa and perhaps the embryo that result in the termination of dormancy. A detailed examination of the role of the bracts in regulating both natural and artificial germination is warranted. Bracts accumulate in drifts beneath mother plant canopies, areas where seedlings are most often found. As suggested by Wood et al. (1976), their effect may be to ameliorate seedbed conditions by acting as a natural mulch and improving seedbed water relations.

Testing available seeding techniques and equipment or development of new systems for field seeding is essential to place the small seeds at the proper depth, improve seedbed water relations, and establish mixtures of species. Efficient seeding systems are critical in areas where low or erratic precipitation often create conditions marginal or unfavorable for seedling establishment (Bleak et al. 1965, Plummer 1966, and Blaisdell and Holmgren 1984).

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