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Biology of leafy spurge

CALVIN G. MESSERSMITH, RODNEY G. LYM, and DONALD S. GALITZ

Professor and Assistant Professor, Department of Agronomy, and Professor, Department of Botany, North Dakota State University, Fargo, North Dakota 58105

I. Introduction

Leafy spurge (*Euphorbia esula* L.) has spread to become a particularly troublesome weed problem in the upper Great Plains of North America. It is toxic to some animals and is unpalatable to most livestock, so it thrives when competing plants are grazed. Leafy spurge is an introduced plant in this region and thus is largely devoid of the insect and disease pests that apparently keep the weed controlled in its native areas of Europe. It has a deep root system that is very difficult to control, which contributes to the survival of the plant. Seed maturation often coincides with hay harvest, so seeds can be distributed widely through the activities of man. These and other biological features of the growth and development of leafy spurge will be discussed in this chapter. We will begin with an overview of the phenology of the weed, and then closely examine reproduction both by seed and vegetative parts, dispersal and population dynamics by seed and vegetative parts, and briefly discuss leafy spurge physiology.

II. Phenology

Leafy spurge is one of the first plants to emerge in the spring. It emerges generally in early April in North Dakota (9), during March in Iowa (2) and Wisconsin (23), and between April 17 and May 1 in Saskatchewan (23). The plants are 15 cm tall by the middle of April in Iowa (2), but it generally is the last week of April before the weed reaches a similar height in North Dakota (9). Apparently, development in Saskatchewan is about 1 week later than in North Dakota. Stem elongation and vegetative development is very rapid as the temperature warms during late April through early June.

Initiation of the leafy spurge inflorescence is indicated by swelling of the stem apex within about 1 week after stem emergence (3). The terminal umbel forms at the stem apex, with each branch producing additional pairs of opposite branchlets (Figure 1). The branching can continue until each original floral branch has divided into 8 to 16 branchlets (23). Each branchlet has its own pair of yellow to yellowish-green bracts. The first yellowish bracts at the base of the terminal inflorescence appear from early to late May across the region, depending upon geography and the temperature for that growing season. The yellow bracts of the inflorescence are most visible from late May through June in most of the region. The bracts change from yellow or yellowish-green to pale yellowish-green or mostly green as the inflorescence matures. Thus, patches of leafy spurge are most conspicuous during peak flower development and become less conspicuous as flowers and seed mature.

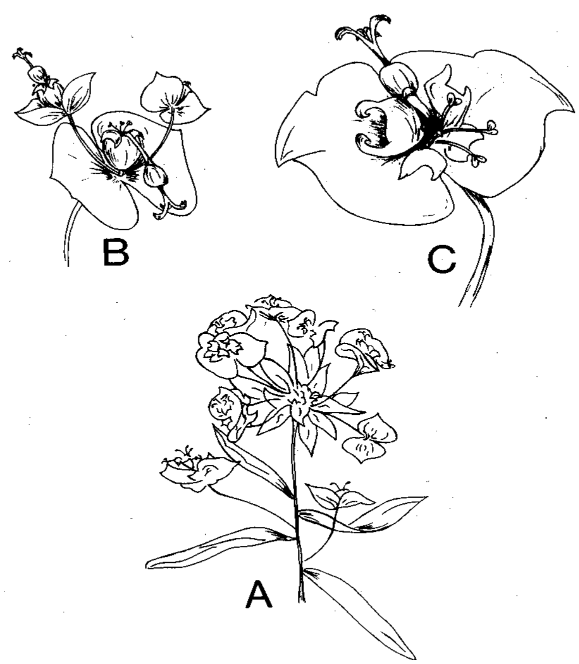

Figure 1. The inflorescence of leafy spurge: A. A terminal umbel at the stem apex with two flowering branches developed below the umbel; B. A branch of the umbel with basal yellow-green bracts, a terminal cyathium with the pistallate flower after inversion, and two branchlets each bearing a cyathium; C. A cyathium with basal bracts, single pistillate flower after inversion, three staminate flowers, and four nectar-secreting glands.

Flowering in the terminal inflorescence generally ceases between the end of June and early July (23). Seed development and maturation continue for approximately 30 days after appearance of the last flower. Thus, flower production and seed development are continuous from late May or early June on through late July into early August, depending upon geography and the growing conditions for that season. Some stems can continue to produce seed until frost under favorable conditions, but the plant often ceases to grow and bloom during the hottest and driest parts of the year in July and August. Flowering and seed development can be renewed later in the fall (2); however, the fall season in most infested areas usually is too short to complete viable seed development.

Often the terminal umbel will die during the hot, dry period, but new vegetative branches form below the terminal umbel when favorable cool and moist growing conditions occur in the fall. As the plant matures, either during hot, dry periods after seed production in midsummer or due to senescence in the fall, the stems and leaves often turn from a bluish-green to reddish-brown, red, or yellow; most leaves fall from the plant prior to a killing frost.

Each branch of the inflorescence of leafy spurge produces a cyathium, which is a special flower-type characteristic of the *Euphorbia* genus (Figure 1). The cyathium has a single terminal pistil with a long stalk and a compound ovary containing three chambers. The pistil is surrounded by 11 to 20 staminate flowers, each with a stalk and a single anther (23). The pistillate and staminate flowers are surrounded by a cup-like structure known as the involucre. The cyathium is enclosed by five involucral bracts alternating with four nectar-secreting glands. The fifth gland is absent. The pistillate flower emerges before the staminate flowers. The stigma opens and becomes receptive to pollen from 1 to 3 days after emergence of the female flower (23). The glands of the cyathium begin secreting nectar from 3 to 8 days later. Then, the female flower inverts in the space of the absent nectar gland, and the first one or two male flowers appear. Occasionally a male flower appears prior to inversion. An additional two to five male flowers appear on the day after inversion, and a total of 11 to 20 male flowers appear within 3 days. The interval between appearance of the female and male flowers varies from 2 to 13 days under field conditions, depending upon environmental conditions, especially temperature. The stems from seedlings or new root buds generally do not produce a flower until the second year (19, 23), although plants grown free of interference from other vegetation have flowered the first year. (19).

III. Reproduction

Pollination. Leafy spurge pollen is sticky, so most of the pollination is by insects. The immature pollen is yellow and becomes orange and sticky when mature. The pollen is most viable approximately 24 hours after emergence of the male flower (23). The female is most receptive to pollen when the stigma opens while the pistil is erect, but fertilization can occur after the pistil has inverted. The general mechanism of flower development minimizes self-pollination because the female develops prior to the male flowers and the female is less receptive to pollen after inversion. The preference for cross-pollination was confirmed in artificial pollination experiments by Selleck *et al.* (23), who observed that 28% of the flowers produced seed when pollinated by males on the same cyathium while 56% of the flowers produced seed when pollen was obtained from a different plant.

Pollen and nectar are important sources of protein required for ova development in many insects. Many insects have been observed feeding on the pollen and nectar of leafy spurge. Insects apparently account for most of the pollination in the field. It was demonstrated that wind may cause pollination through accidental contact of male and female flowers but not by wind transport of pollen (23). Bakke (2) observed a soldier beetle (*Chauliognathus pennsylvanicus* De. Gur) regularly on leafy spurge, and leafy spurge pollen was nearly always found on its body. A ground-dwelling ant (*Lasius* spp.) has been observed feeding on the nectar of leafy spurge in Saskatchewan (23). A survey near Esterhazy and Mortlach, Saskatchewan, during late June and early July 1955 showed 8 orders, 39 families and 60 species of insects on leafy spurge (3). Diptera and Hymenoptera predominated. Weekly insect collections at Jameson, Saskatchewan, from late May through early September 1976 showed 196 species associated with leafy spurge, representing 9 orders, 41 families, and 104 species of phytophagous insects and 4 orders, 43 families, and 92 species of predators and parasites.

Honeybees feed on leafy spurge flowers and probably aid in pollination. Commercial honey producers can utilize leafy spurge as an early season food source to maintain honeybee colonies, because it flowers prior to the prime honey-producing months. Also, leafy spurge honey does not granulate quickly in cold weather, so it makes a good honey to feed bee colonies over winter.

Seed production. The leafy spurge fruit develops from a superior three-celled ovary, which has central placentation. Capsules with four and five cells and a clone that produced female flowers only have been observed (23). The capsule dehisces when ripe to distribute the seeds. The number of seeds per fruit varies. Hanson and Rudd (9) observed that nearly 50% of the fruits produce only one mature seed, about 35% produce two seeds, and only 15 to 20% of the fruits produce three seeds. The individual seed stalks produce from 10 to 50 fruits under normal conditions (2). Selleck *et al*. (23), in Saskatchewan, reported an average yield of 252 seeds/shoot in competition with native grass and yields of 212 and 196 seeds per flowering shoot in competition with annual weeds and crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult.], respectively. The fact that leafy spurge seed production was high when grown in competition with several perennial grasses indicates the high competitive ability of the weed.

The fruits are ripe enough to dehisce beginning about July 10 and continuing until late fall (3, 9). The peak period for seed maturity is from mid-to-late July in most locations. The average seed weight of bulk samples ranges from 250 to 350 mg/100 seeds (3, 23, 26). The seed yield within various Saskatchewan leafy spurge patches was calculated to range from 27 to 3800 kg/ha (23). The highest yield occurred when a stand in native grass had been mowed. Mowing removed the apical meristem and stimulated development of inflorescences on numerous lateral branches. The average seed production in the center of leafy spurge patches was 2500 seeds/m^2, with a range from 790 to 8020 seeds/m^2 (3).

Leafy spurge seed has various colors, depending upon the maturity of the seed when harvested. Wicks and Derscheid (28), in South Dakota, reported that the seed color changes from yellow, to yellow with brown tips, to brown ends with narrow yellow band, to brown with an orange band, to reddish-brown, brown, gray-brown, gray, and finally mottled (Figure 2). Selleck *et al*. (23), in Saskatchewan, concurred with the description by Wicks and Derscheid. Also, Hanson and Rudd (9), in North Dakota, indicated that the typical mature seed color is light gray tinged with purple, while the less mature seeds are purplish-brown with very little of the gray tinge. Conversely, Bakke (2) reported that the gray color belongs to the immature seeds, while the mature seeds are brown. The differences in seedcoat color at maturity as reported by these authors may be due to differences in individual classification or to differences in seed color due to environmental or biotype variability at the various locations.

Figure 2. Mature leafy spurge seeds are mottled with a gray to gray-brown background. A caruncle is present at the narrow end and a brown line extends from the caruncle to the opposite end.

Wicks and Derscheid (28) reported that the brown, gray-brown, gray and mottled seeds were viable. Ripened seed samples invariably included both gray and mottled seeds. The rate of seed development within a capsule usually was uniform (23). The more advanced stage of maturity resulted in significant increases in seed weight, as indicated by 373 mg/100 seeds for mottled seeds compared with 316 mg/100 seeds for gray seeds. Mowing of leafy spurge to prevent viable seed production must be done while the seeds are lightweight before they turn brown (28). Brown seeds appeared 10 to 13 days after fertilization, depending upon seasonal conditions.

Seed bank in soil. Viability of leafy spurge seed has varied depending upon the seed source used. Hanson and Rudd (9) reported germination from 51 to 70% in one experiment and up to 84% in another experiment. Bakke (2) reported germination from 52 to 76% in one experiment and an average of 67% in another experiment. Bowes and Thomas (5) observed 62 to 75% germination of leafy spurge seed. Overall, these reports suggest that fresh leafy spurge seed generally is 60 to 80% viable, but the germination among several seed sources can be quite variable.

Viability of seeds in a Saskatchewan soil depended mostly upon the depth of burial (3). The seed source initially was 87% viable, but the viability after 3 years of burial was 12, 18, 43, and 64% at depths of 2.5, 5, 10, and 20 cm, respectively. Thus, seed near the soil surface lost viability most rapidly. Bowes and Thomas (5) estimated a 13% annual loss of leafy spurge seed viability in undisturbed pastures (Figure 3).

Dormancy of leafy spurge seed permits germination for at least 5 years following maturity (23) and perhaps up to 8 years after the seed is deposited (5). Selleck *et al.* (23) reported that germination of individual samples of seed collected from several sites during the first year varied from less than 1 to 44%. Dormancy was indicated in another experiment because germination of 1-year-old seed exceeded that of newly harvested seed at nearly every soil depth. In subsequent experiments, Selleck *et al.* (23) observed considerable variation in the percentage germination of seed from different sources, ranging from 4.2 to 38%. The variability in germination of different leafy spurge seed lots could be due to genetic differences in seed dormancy or viability, environmentally induced dormancy, or an afterripening phenomenon. Selleck *et al.* (23) felt there were genetic differences in dormancy and (or) viability of seeds, because seed from some sites never germinated more than 7 or 8%, while seed from other sites consistently germinated between 60 and 85%.

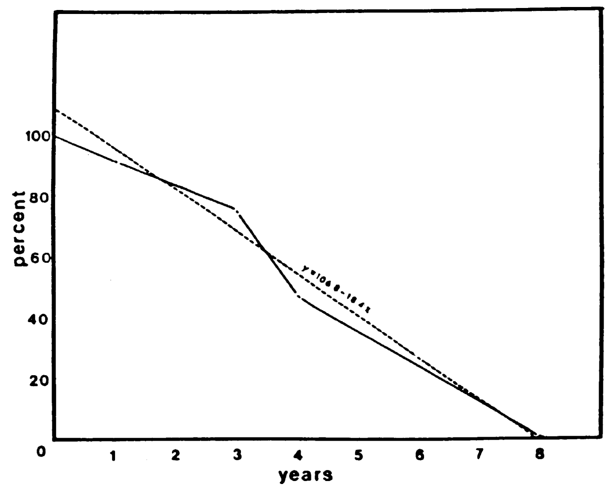

Figure 3. Viability of leafy spurge seed in soil when seed production was prevented by picloram, expressed as percentage of the untreated areas [from Bowes and Thomas (5), used with permission from J. Range. Manage.]

Germination requirements. Temperature probably is the most important environmental factor affecting leafy spurge seed germination. Hanson and Rudd (9) observed that an alternating 20 and 30° C temperature produced the highest germination of 84%, whereas constant 30 and 20° C produced 74 and 4% germination, respectively. Bakke (2) observed no germination of leafy spurge seeds on moist blotting paper or soil at temperatures between 1 and 3° C. Germination at 18 to 20° C was 8% on moist blotting paper and 20% in soil, whereas germination at 28 to 31° C was 43% on moist blotting paper and 24% in soil. Selleck *et al.* (23) observed that only 1 of 400 seeds germinated when temperature varied between 8 and 12° C. Samples representing three different seed ages germinated more completely at 32 than at 22° C during a 2-week period, but the highest germination percentages were obtained from alternating exposure to 22 and 32° C. Similar results were obtained in an experiment involving 1400 seeds at temperatures of 20 and 30° C. Most seed germinated within a 2-week period, but an additional 2 weeks at the highest temperatures promoted further germination. This observation suggested a progressive breakdown of seed dormancy. Bowes and Thomas (5) observed about 47% germination of freshly harvested seed in the laboratory at near optimum temperatures of 30° C for 8 hours and 10° C for 16 hours. Leafy spurge seed failed to germinate when extreme alternating temperatures of 40° C for 8 and 10° C for 16 hours were used. Also, germination of leafy spurge seed was reduced greatly when extreme alternating temperatures preceded near optimum temperature conditions. Thomas, as reported by Best *et al.* (3), germinated 3-month-old seeds in darkness under controlled conditions and found that alternating temperatures of 10/30° C for 16/8-hour cycles gave 55% germination, while less than 5% germination occurred with constant temperatures of 10, 20 or 30º C. In summary, the reports consistently indicate that the best leafy spurge germination can be expected with alternating temperatures in the range of 20 to 30º C, and a temperature of approximately 30º C appears optimum if a constant temperature is used.

Other environmental factors can affect leafy spurge seed germination. Selleck *et al*. (23) found that light was a significant factor in retarding germination over a temperature range from 20 to 40º C. Also, seed scarification reduced germination compared with untreated seed. Thus, the intact seedcoat apparently did not contribute to dormancy. Stratification of seed for 4 weeks at 2 to 5º C caused slightly better germination than seed that were not stratified when tested at alternating 10/30º C (3). However, seed germination increased greatly when the same stratification process preceded the constant 20º C temperature. The seed receives a cold treatment under field conditions, so nondormant seed can germinate in the spring as soon as temperature and moisture conditions are favorable.

Water is imbibed quickly by seed, which contributes to rapid germination. Imbibition resulted in a 30 to 45% gain in seed weight during the first 6 hours and continued for an additional 42 hours (23). Maximum imbibition occurred just prior to radicle emergence from germinable seed and after the same period of soaking for seed that failed to germinate. Alternate wetting and drying periods at 48-hour intervals in petri plates at 20 and 30º C did not affect germination significantly. Bakke (2) reported that leafy spurge seeds can float and germinate on water.

Leafy spurge germination in the field can occur throughout the growing season whenever adequate moisture is available (2); however, early spring is the most favorable period for germination. In Saskatchewan, 14% of the seedling emergence for 1 year occurred in April and 82% in May, with occasional emergence until October 15 (23). The next year, 23% of the seedlings appeared in May, 76% during the first 10 days of June, and 1% between June 10 and October 10. Maximum emergence for the first year took place after 10 days with a maximum air temperature of 21º C or higher in late April. During the next year, similar temperatures were not reached until the last week of May, which apparently accounted for the maximum rate of emergence in early June. Thomas, as reported by Best *et al*. (3), observed that nearly all seedlings emerged within a 3-week period in the early spring. Emergence at later periods in the growing season followed heavy rains.

Seedling establishment. Seeds can absorb water, germinate, and emerge relatively rapidly with favorable temperatures. Absorption of water by a germinable seed often causes the testa to break within 12 to 24 hours, and the radicle can appear as early as 12 hours after the rupture (23). Root hairs develop from 12 to 24 hours later when the radicle is approximately 1 cm long. The hypocotyl develops within 12 hours after appearance of the root hairs. The hypocotyl arch is the first structure to emerge from the soil surface and becomes erect within 24 hours to reveal the cotyledons enclosed within the seedcoat. The seedcoat is sloughed off within another 24 hours. The cotyledons expand to look like and function as true leaves. The hypocotyl often is pink or reddish but turns green soon after exposure to sunlight. The latex system develops within the embryo of the seed and is present in the stem at emergence.

Leafy spurge seedlings can emerge through several centimeters of soil even though the seed is not large. Selleck *et al.* (23) reported that maximum leafy spurge emergence occurred from seeding depths of 1.3 to 5 cm, although occasionally a seedling emerged from 15 cm deep. Seedling emergence from the upper 1 cm of soil was low, perhaps due to low moisture or high temperatures near the soil surface.

Seedling development is rapid after emergence. The cotyledons and first two leaves are opposite, but the remaining leaves are distinctly alternate (Figure 4). Seedlings under greenhouse conditions produced 4, 6, 8, 10 and 12 leaves within 6 to 10, 10 to 21, 13 to 24, 17 to 26 and 21 to 31 days, respectively, after seedling emergence (23). The stem at 24 days was 6 cm tall and the roots were 18 cm long. Seedling roots can be 61 cm long and the stem 13 cm tall within 2 months after the cotyledons expand (9).

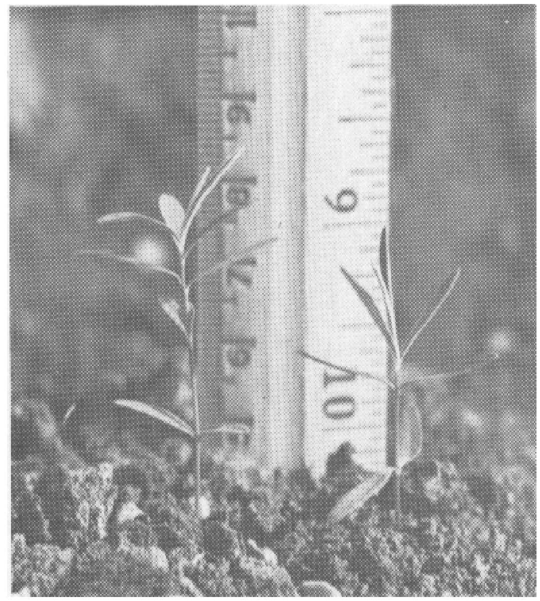

Figure 4. Leafy spurge seedlings. The cotyledons are at the first node, the first true leaves are opposite at the second node, and subsequent leaves are alternate.

Vegetative buds developed on each seedling just above the soil surface 10 to 12 days after emergence or when six leaves were present (23). The seedlings averaged 4.7 buds at 15 days and 5.6 buds at 35 days when the shoots were 10 and 16 cm tall, respectively. When seedlings were cut 1.2 cm below the soil surface, 50% of the seedlings in the six-leaf stage and all of the seedlings in the ten-leaf stage produced new shoots. Despite the rapid vegetative establishment, seedlings do not flower the first year under field conditions (19, 23), although seedlings growing without competition occasionally flower the first year (19).

The density of leafy spurge seedlings varies considerably from site to site and from year to year. One patch in a favorable location supported a mean of 92 seedlings/m^2 during a 5-year period, while the driest habitat at the same location averaged 1.6 seedlings/m^2 (23). Seedling densities paralleled densities of vegetative leafy spurge shoots with 1073 seedlings/m^2 in quadrats with dense leafy spurge stands compared with 31 seedlings/m^2 in sparsely populated quadrats. Seedling densities were particularly low when in competition with native grass and in quadrats with small leafy spurge populations in competition with crested wheatgrass. Seedling survival at all locations is low, as is discussed later in the seedling mortality segment of this paper.

The rate of spread of leafy spurge from seedlings varies with competition. Morrow (19) reported that plants from seed produced only a single stem in the seedling year when grown with and without competition, and no plant grown with competition produced more than the original shoot during the second growing season. However, plants from seed grown without competition averaged 170 shoots per plant and a distance of 174 cm from the point of the original shoot by the end of the second growing season. Selleck *et al*. (23) reported that seven seedlings only occupied 0.2 m^2 after the first growing season but had increased to occupy nearly 44 m^2 after 5 years.

Vegetative reproduction. Vegetative reproduction of leafy spurge is by buds that survive over winter under the soil surface. The types of vegetative buds that produce stems are crown buds and root buds.

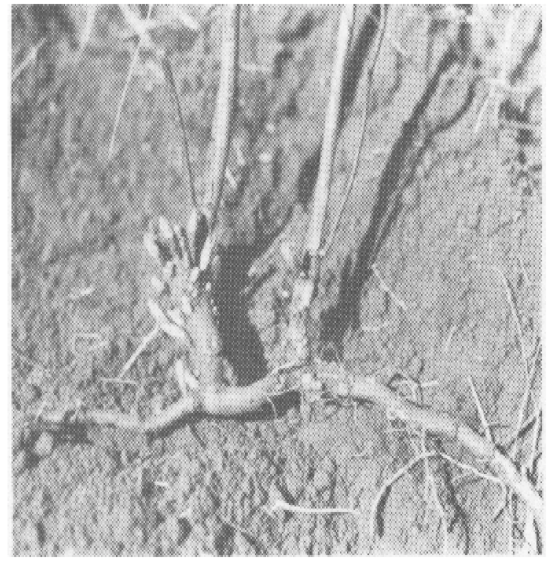

Figure 5. Underground stem and roots for vegetative reproduction of leafy spurge. A crown develops at the base of stems and forms buds to produce new stems annually. The horizontal long roots can form adventitious shoot buds at almost any point along the root.

The crown of leafy spurge develops at the base of the stem and consists of buds that produce new stems at the same location annually (Figure 5). Visible buds were present on underground plant parts at all times during the growing season (18). Buds that did not sprout in the spring apparently sloughed off during the season and were replaced by new buds. Death of older buds was most apparent around flowering time when large unemerged buds were deteriorating and new buds were appearing. The new buds reached full size by late summer. Some buds grew into shoots that emerged during the late summer and fall months but failed to grow beyond 2.5 to 7.6 cm tall. The crown region can produce roots that contribute to the spread of leafy spurge. Leafy spurge crowns live for several years, but the number of years is not known (4).

The root system of leafy spurge is the primary contributor to the persistence of the weed when control practices have been initiated. The root system is deep and spreading and can produce shoot buds at almost any point along any root segment. Leafy spurge has a heterorhizic root system composed of both "long" and "short" roots (21). The long roots have cambial activity and can give rise to new root and shoot buds. Short roots do not have cambial activity and do not give rise to shoot buds. The long roots have been excavated to 4.8 m (2) and have been reported as deep as 9 m (3). Coupland and Alex (6) reported that the maximum depth of penetration was 2.5 m, and the roots penetrated deeper than 1.2 m in all instances except one. The oven-dry weight of the underground leafy spurge parts to a 1.2 m depth was equivalent to 9518 kg/ha. The proportion of this weight contributed by plant material in the upper 15-cm soil layer was 56%, while that contributed by each layer decreased steadily with depth from 17% in the 15- to 30-cm layer to 2.4% in the 107- to 122-cm layer.

The distribution of reproductive buds underground on leafy spurge is a major reason for species persistence (7). Vegetative buds were counted at various levels on 65 roots from 13 excavations (Figure 6). The roots from different excavations tended to fall into three groupings based on number of buds. The mean number of buds per root was 35, 72, and 272 for the three groups. Differences in habitat, and possibly genetic stock, were responsible for the wide variation observed. The maximum depth to which buds were found varied from 30 cm for one group to 17.3 cm for another group. The A-horizon of soil contained 62% of the buds. There was a high association between the weight of root material and the number of buds at each soil depth.

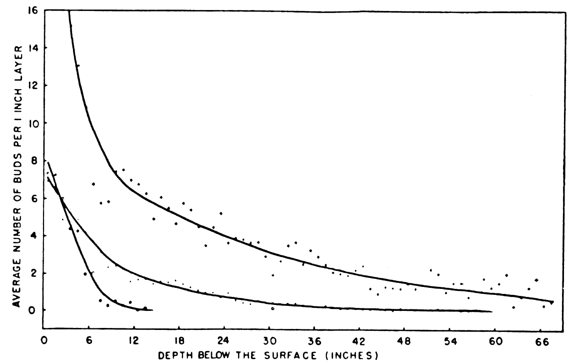

Figure 6. Distribution of vegetative buds on the underground parts in three groups of excavations [from Coupland and Alex (7)]. Each point represents the weighted average number of buds per 2.54 cm (1 inch) layer per excavation in each group.

Regeneration of stems from roots. The principles concerning the regenerative ability of leafy spurge from roots was illustrated by the research of Hanson and Rudd (9) in 1933 (Figure 7). The upper portion of the plant can be injured or killed by tillage or herbicide treatment, but the remaining root system either below the treatment or from detached root segments can develop adventitious buds that will send up new shoots from a depth of 30 cm or more. Undisturbed leafy spurge usually produces shoots from underground plant parts within a few centimeters of the soil surface (8). However, shoots under undisturbed conditions have emerged through up to 43 cm of soil from the point of origin on the roots. Shallow cutting of leafy spurge, such as by cultivation, may stimulate development of many buds and result in a net increase in the number of stems (9). Selleck *et al.* (23) showed that leafy spurge regrowth following rototilling averaged 316 shoots/m^2, compared with 134 shoots/m^2 in the undisturbed check. The authors have observed similar large increases in numbers of shoots when leafy spurge is treated with herbicides that control the topgrowth without leaving an effective soil residual.

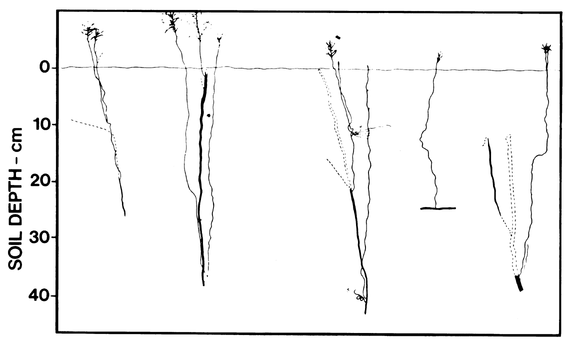

Figure 7. Shoots of leafy spurge arising from roots and root pieces after a sodium chlorate treatment [from Hanson and Rudd (9)]. The killed root parts are indicated by broken lines, and new shoots are arising from surviving roots at depths of 30 cm or more.

The enormous ability of leafy spurge roots to produce new shoots is illustrated in research by Coupland *et al.* (8). They covered leafy spurge roots with 30, 60, or 90 cm of weed-free soil by two methods: a) burying the plants by piling and tamping soil to the desired depth on top of a leafy spurge patch, and b) excavating all the soil in a leafy spurge patch to the desired depth and tamping clean soil over the remaining roots. Shoots emerged through 30 cm of dense soil within 116 to 133 days at some sites and produced seed the same season. Shoots penetrated 60 cm of soil within 12 months at every location with both treatments. Only at two sites were shoots able to emerge through 90 cm of soil in either the buried or excavated plots. The density of shoot regrowth was not decreased by 30 cm of soil in buried plots (58 shoots/0.25 m^2), but the density in the excavated plots was decreased by 13%. Crown tissue was formed near the soil surface following regrowth of shoots in the 30- and 60-cm plots, and regrowth from crown buds occurred the following year. However, shoots that emerged from the 90-cm level each year did not develop crowns. Roots produced vegetative shoots for five successive years from a 90-cm depth after the major portion of the root system had been removed by excavation.

The ability of leafy spurge to produce new shoots from small root segments was demonstrated in several experiments by Hanson and Rudd (9). They divided 0.3- to 0.5-cm-diam roots into 0.6- to 10-cm lengths and buried them 5 to 7.5 cm deep in soil. The segments produced new shoots within 3 weeks, except the 0.6- and 1.3-cm-long lots. No shoots were produced from the 0.6-cm-long segments, but 60% of the 1.3-cm segments produced new shoots within 3 weeks. Also, Hanson and Rudd buried root segments 7.6 cm long and 0.6 cm in diameter in soil at depths ranging from the surface to 60 cm. New shoots were produced by 70, 90, 50 and 70% of the root segments buried 2.5, 5, 10 and 15 cm deep, respectively, but shoots were not produced from the 25-, 36-, and 60-cm depths.

Leafy spurge root tissue is fairly resistant to drying because of the well-developed cork on the root surface and the large amount of latex within the tissues. However, Hanson and Rudd (9) demonstrated that 10-cm-long root segments could be killed by about 3 hours of exposure to hot, dry weather. A longer drying period would be required on cooler and moist days.

Rate of vegetative spread. The ability of leafy spurge to spread vegetatively was documented for eight habitats by Selleck *et al*. (23). They mapped the perimeter of each patch annually from 1951 to 1958 at a similar time each year. The weed spread every year in competition with all other species in the study areas. The average annual radial spread within a stand of introduced grass was less (50 cm) than in unseeded abandoned cropland (64 cm) and in ungrazed native grasslands (64 cm). Considerable variation occurred in the average radial spread in different habitats in different years; the range was 8 to 126 cm. Also, considerable variation occurred in the rate of radial increase on different sides of the same patch, between different patches in the same, type of habitat, and in different habitats. The maximum increase in radius for a patch rarely occurred in the same direction in consecutive years. The greatest spread in nearby patches usually occurred in different directions in the same year. The fluctuation in the boundary was even greater for flowering shoots than for nonflowering ones. Occasionally, the boundary of a patch retreated at some locations from its position the preceding year. These recessions were temporary and were not associated with deterioration of underground parts. Patches under favorable moisture conditions continued to extend their borders throughout the growing season.

Dispersal of seed. The initial dispersal of seed is by dehiscence of the seed capsule. The capsule consists of several layers of columnar cells that lose water upon maturity (2). The drying tends to pull all edges of the locule together, which puts a strain on the whole capsule until it breaks with an explosive force. The explosive force can throw the seed up to 4.6 m (2,9) and distribute the seed fairly uniformly from 0.3 to 4 m from the shoot (9). Usually the carpel segment splits free of the seed and resembles a twisted winglike structure (23).

Seeds can float on the water surface (2, 23). This feature probably accounted for seedlings appearing first in the washed areas of a field (2). The ability of seed to float and germinate in water appears to be an advantage for leafy spurge establishment in areas that flood occasionally. Ditch, stream and river banks often are the location for new leafy spurge infestations in an area.

Birds have been implicated in spreading leafy spurge seed, starting with early scientific reports (9), but documentation is limited. Bakke (2) reported that mourning doves devour an enormous quantity of seed, but undigested seeds were not found in the intestine. Thus, mourning doves are beneficial by destroying many seeds. However, doves may distribute some seed because they regurgitate when feeding the young, so there is an opportunity for seeds to drop to the ground (23). Sharptail grouse may be important distributors of leafy spurge on rangeland areas because viable seeds have been found in their droppings (20). Also, leafy spurge patches in uninfested fields frequently appear first in primary grouse habitat, such as draws and hilltops.

Large and small animals probably spread leafy spurge seed. Undoubtedly, some leafy spurge seed is carried in mud on feet and hair of wild and domestic animals. Some leafy spurge seed fed to sheep was excreted in the manure and was viable.[1] Indirect evidence of distribution by animals comes from the report that leafy spurge plants occurred along the path where buried deer entrails were accidentally spread by tillage (23). Ants are important for dispersal of some seeds, and both ground ants (*Lasius* spp.) and mound ants (*Formica* spp.) are common in many leafy spurge patches (23). However, ants showed no inclination either to feed on leafy spurge seeds or to store them in their burrows.

Man has had a major role in the dispersal of leafy spurge seed. Probably the widest distribution has been as a contaminant in seed, feed grain and forages. Leafy spurge seed has been reported as a contaminant in oat (*Avena sativa* L.) seed in Minnesota and Iowa (2) and Saskatchewan (23), smooth brome (*Bromus inermis* Leyss.) seed in Saskatchewan (23), and alfalfa (*Medicago sativa* L.) in North Dakota. Ranchers frequently report that they first noticed leafy spurge in pastures after they had purchased hay from other areas during a drought period. Contaminated tillage and harvest machinery can distribute leafy spurge seed within a field or along roads when the equipment is being transported.

Dispersal of root fragments. Roots account for the spread of a patch as the plants grow, but natural dispersal of roots to establish new patches has not been reported. However, man can spread root segments to new locations through his activities. Tillage can spread root segments to new locations through his activities. Tillage can spread root segments around a field, or root segments can wrap around machinery and be transported to a new field. Roots can be transported in landfill soil, building and road excavations, and through landscaping, such as transplanting of sod or nursery plants. Dispersal of roots is usually a minor factor compared with dispersal of seeds in the spread of leafy spurge.

[1] Fay, P. K. 2983. Personal communication. Montana State University, Bozeman, Montana 59717.

IV. Population dynamics

Climatic and community requirements. Leafy spurge possesses a broad ecological range of habitats, from xeric to subhumid and from subtropic to subarctic (3). The species is most common in mesophytic areas, but the greatest rate of spread is in the more humid sites within an area. Leafy spurge can survive under unfavorable conditions within an area. Some examples of habitats where leafy spurge has been reported include dry meadows, native ungrazed grassland, grain fields, waste areas, sand deposits, bushes and woods, stony hillsides and rocky forest lands, railway embankments, roads, drainage ditches and riverbanks (23).

Leafy spurge is widely distributed in Europe and Asia, but it is not considered a particularly noxious weed there (23). This may be due to the type of agriculture that is practiced, the combination of weather conditions, or competing species and natural predators that keep the weed in check. However, leafy spurge in North America is a vigorous and strongly competitive plant, reproducing actively from both seed and roots. There is a marked similarity in the environments where the species has been found in Europe, Asia, and North America.

Density relations. The density of leafy spurge varies with habitat. Selleck *et al.* (23) counted the number of leafy spurge shoots in 139 m^2 quadrats annually from 1951 through 1958 in 13 locations with four basic habitats (3 smooth brome, 2 crested wheatgrass, 3 native grasses, and 5 abandoned land). They reported that the average density ranged from 8.7 to 217 shoots/m^2 in the habitats that were observed for eight consecutive years. The density of leafy spurge fluctuated considerably during this period and no apparent trend was observed. The densities nearly doubled in some habitats from one year to the next with favorable conditions, and declines in density were nearly as great some other years. In most situations, the density of stems did not increase after a population of 200 shoots/m^2 had been reached. Smooth brome evidently was not able to compete effectively against leafy spurge, because spurge densities varied from 988 stems/m^2 in the center of the patch to 20 shoots/m^2 at the perimeter. Crested wheatgrass apparently was no more effective than smooth brome in reducing the density of a thick leafy spurge stand, but it did limit the rate of increase of sparse stands.

The density of leafy spurge can be reduced by heavy grazing pressure with sheep. Bowes and Thomas (5) reported that 3 or more years of continuous sheep grazing were necessary to greatly reduce the shoot density of leafy spurge (Figure 8). Also, 5 to 10 shoots/m^2 still were growing from perennial roots after 8

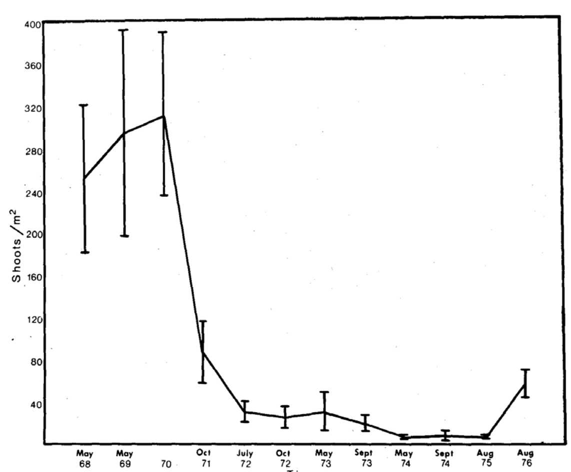

Figure 8. Effect of continuous grazing by sheep on the shoot density of leafy spurge [from Bowes and Thomas (5), used with permission from J. Range Manage.].

years. The number of shoots did not increase until the second year after sheep grazing was discontinued. It was not known how many years were necessary for the leafy spurge density to return to the preexperiment level. The reduction of leafy spurge density by sheep grazing was also reported by Helgeson and colleagues (10, 11) in North Dakota and by Johnston and Peake (12) in Alberta.

Seedling mortality. Leafy spurge seedling mortality is high under most conditions. Hanson and Rudd (9) reported that less than 10% of the seedlings that emerged were alive by May 15. Selleck *et al*. (23) reported that a natural infestation had 2800 seedlings/m^2 on May 27, 1951, but the number of seedlings had decreased to 500 seedlings/m^2 by September 12, representing a decrease of 82%. Bowes and Thomas (4) observed that approximately 1.5% of the seed produced from 1 year successfully germinated and became established as vegetative seedling shoots the following year. The survival was reduced to less than 1% if it was assumed that 40% of the seedlings survived the winter, as indicated by other research. They suggested that the seedling component contributed 9 to 16% of the individual shoots to a stable population of leafy spurge.

Best *et al*. (3) monitored seedling emergence and survival during two growing seasons in artificially seeded plots on a native grassland habitat, cultivated plots and a patch of western snowberry (*Symphoricarpos occidentalis* Hook.) near Regina, Saskatchewan. Leafy spurge emergence on the cultivated plots was only slightly more than on plots dominated by western snowberry but was eightfold greater than on the undisturbed grassland. The seedling survival, expressed as percent of seed sown, was 5.1, 1.5, and 0.4% for the cultivated, western snowberry, and native grassland habitats, respectively. The mortality of seedlings, expressed as percentage of emergence, was 26, 73, and 45% for the cultivated, western snowberry, and native grassland habitats, respectively. The greatest seedling mortality was on the western snowberry plots, presumably because the seedlings emerged early in the season before the western snowberry leaves were fully expanded. The dense western snowberry canopy later in the season reduced the light intensity, so the seedlings were greatly elongated and weak.

Plant communities. Leafy spurge is adapted to many plant communities. Best *et al*. (3) indicated that leafy spurge has been reported in association with 69 other plant species in cropland, abandoned fields, tame grass pastures, native grasslands and areas among trees and shrubs. Leafy spurge even withstood flooding for 4.5 months or more when the depth of water did not prevent emergence of the shoots above the surface (23).

Leafy spurge seems to grow most commonly in soils of coarse texture. Selleck *et al*. (23) mapped 3979 ha of leafy spurge in 945 quarter sections of land in 87 municipalities of Saskatchewan. They reported that 48% of the infested quarters were in the coarse-textured group of light loam to sand, 42% were in the intermediate group of loam to clay loam, and 10% were in the clay to heavy clay soils. Fifty-one percent of the infested acreage occurred in the loam to clay loam textures. The mean size of the patch was 3.5 ha in the coarsest textural group, 5.1 ha in the medium group, and 4.6 ha in the finest textured group. When the figures were compared with the proportion of each textural group available for infestation, the highest percentage of infested quarters was in the coarsest soil texture class. However, the fine-textured soils appear more conducive to germination and establishment of seedlings than coarse-textured soils (3).

Although there is a preference of leafy spurge to grow on coarse-textured soils, Coupland and Alex (6) reported that soil texture had only a small effect on underground plant development. However, there tended to be more plant material below 60 cm in coarse- than fine-textured soils. The ability of leafy spurge roots to penetrate dense soil was noted at one site where they grew through 76 cm of clay to reach a total depth of 127 cm. A preliminary investigation did not detect a relationship between the abundance of buds and soil hardness in any one layer or in the soil profile as a whole (7). A relationship was not found between the calcium carbonate content and the number of buds occurring at any level in the soil.

Competitive ability. Leafy spurge can survive in most environments and management systems, although its vegetative and reproductive development may be retarded by heavy competition or cultivation. Coupland and Alex (6) indicated that cultivation was more effective than a competing grass in reducing the vigor of the root system. Production of underground plant parts averaged 31% greater under seeded crested wheatgrass/smooth brome than under cultivation. Morrow (19) observed that leafy spurge plants arising from root segments, transplanted seedlings, or seeds growing in perennial grass sod were capable of maintaining themselves but did not reproduce during the first two growing seasons. He indicated that an early emerging crop, such as a crested wheatgrass/smooth brome sod that uses the available moisture early in the season, may limit the spread and establishment of new leafy spurge infestations.

Selleck *et al*. (23) observed leafy spurge development under several habitats, including native grasses, crested wheatgrass, and smooth brome sod. The density of leafy spurge varied from year to year and was not influenced consistently by competing factions of the vegetation. Smooth brome evidently did not compete effectively against leafy spurge. Crested wheatgrass apparently was no more effective than smooth brome in reducing the density of a thick leafy spurge stand, but it did reduce the rate of increase of sparse stands. Pavlychenko, as reported by Selleck *et al*. (23), demonstrated that crested wheatgrass under certain conditions substantially reduced the density of leafy spurge in 4 years. The vigor of competing species apparently had a profound effect upon the proportion of flowering shoots of leafy spurge. The proportion of flowering shoots averaged almost 80% in competition with native grasses compared with 4% in competition with crested wheatgrass. Competition from leafy spurge and grasses reduced the number of species and shoots of other forbs and shrubs in the infestations. Annual species virtually disappeared at all study sites.

Competition by leafy spurge reduces the production of desirable forage. Effective control of leafy spurge nearly doubled forage production during 2 consecutive years in North Dakota (14). The forage production averaged 5929 kg/ha for the four best treatments compared with 3594 kg/ha for the untreated control. Vore and Alley (27), in Wyoming, observed forage production of approximately 706 kg/ha in leafy spurge-infested areas, but there was an additional 538, 564, 463, 674, and 428 kg/ha air-dry grass produced in areas treated with picloram (4-amino-3,5,6-trichloropicolinic acid) at 0.56, 1.12, and 2.24 kg/ha and dicamba (3,6-dichloro-*o*-anisic acid) at 4.5 and 9 kg/ha, respectively.

Allelopathy. Allelopathy by leafy spurge on other plants is indicated by the small number of forbs in leafy spurge patches even when bare ground is visible between shoots.

Species diversity indices taken in the field showed that quackgrass [*Agropyron repens* (L.) Beauv] and common ragweed (*Ambrosia artemisiifolia* L.) were adversely affected by high densities of leafy spurge, while other species were unaffected (25).

Several reports provide indirect evidence that leafy spurge may be allelopathic with other plants under laboratory conditions. LeTourneau and Heggeness (13) found that aqueous extracts of fresh or dried leafy spurge foliage inhibited root growth of pea (*Pisum sativum* L.) and wheat (*Triticum aestivum* L.) seedlings. Increased extract concentrations inhibited coleoptile growth and germination of wheat. The inhibitor(s) was dialyzable, nonvolatile, and soluble in water, methanol, 50% acetone and 80% ethanol. There was indication of at least two active fractions. Selleck (22) reported that stem, root, and leaf extracts of leafy spurge depressed the elongation of radicles and stems of leafy spurge, spring wheat, smooth brome, wild mustard [*Brassica kaber* (DC.) L.C. Wheeler var. *pinnatifida* (Stokes) L.C. Wheeler] and crested wheatgrass, except that stems of crested wheatgrass were elongated by stem and leaf extracts of leafy spurge. Field soil samples from areas of moderate and high leafy spurge densities inhibited tomatoes (*Lycopersicon esculentum* Mill.) in the greenhouse (25). Dried leafy spurge to soil inhibited growth of tomatoes and large crabgrass [*Digitaria sanguinalis* (L.) Scop.], which indicated that dead or decaying plant material returned to soil may be a source of the allelopathic agent rather than live plants. However, verification of allelopathy by leafy spurge still requires isolation of an active compound(s) from plants and evidence that the chemical is phytotoxic in the soil.

V. Physiology of leafy spurge

The physiology of leafy spurge probably is the area of plant biology that has received the least attention to date. Latex is found throughout leafy spurge but is not a common characteristic of many other weeds. It has been suggested that latex contains the toxic component of leafy spurge and may be a significant inhibitor of herbicide translocation. However, the exact role of latex in leafy spurge physiology and control has not been studied extensively.

The root reserves of leafy spurge provide for long-term survival of the weed. Arny (1) observed sharp declines from late April through early May in the percentages of total sugars and total readily available carbohydrates in the storage roots of leafy spurge. The total available carbohydrates in leafy spurge roots reached low points for the season by mid-May when the plants were beginning to bloom. Then, rapid storage of available carbohydrates followed for a time and continued at a moderate rate until the growing season ended. The available carbohydrates in relation to the total reserve carbohydrates were low during mid-July. The percentage of true starch decreased markedly and sugars increased in the underground storage organs of leafy spurge as the temperature lowered in the fall. Total organic nitrogen in the underground storage organs declined early in the season, and the declines continued at a more moderate rate until August, after which increases occurred.

The influence of nitrogen supply on growth and development of leafy spurge seedlings probably has received more study than any other area of the plant's physiological processes. McIntyre and Raju (17) studied the influence of nitrogen supply from 2.1 to 210 ppm on the growth and development of leafy spurge seedlings in sand culture. Shoot height and dry weight and the shoot/root ratio were reduced substantially by nitrogen deficiency. The outgrowth of lateral buds was suppressed completely at the lowest nitrogen level. Root development of leafy spurge was very responsive to the nitrogen supply, although the heterorhizic pattern of long and short-root development observed in the field was much less evident under the experimental conditions. Long roots were more numerous and were produced at an earlier developmental stage than is usual in the field. The number of lateral long and short roots per unit length of parent roots and the number of shoot buds on the root system both were considerably greater at the highest nitrogen levels. The increase in shoot bud production, however, could be attributed mostly to associated effects on the size and mode of development of the root system. Regrowth from buds on the roots, induced by shoot removal, was suppressed extremely at the lowest nitrogen level. In subsequent experiments, McIntyre (15) observed that a nitrogen deficiency caused apical dominance to arrest completely lateral bud growth on the shoot. The root buds were inhibited but showed considerably greater activity than shoot buds. Apical dominance was reduced markedly at the highest nitrogen level, but the enhanced lateral bud growth increased the inhibiting capacity of the shoot on root bud response. The root bud growth after decapitation of the main shoot was inversely related to the nitrogen supply. Inhibition of root buds by lateral shoots was reduced significantly by growing the plants initially at a low nitrogen level to arrest the growth of the lateral buds. Then, an increase in nitrogen supply strongly promoted the growth of root buds.

Water is important for root bud growth, and there is a strong indication that internal competition for water is a factor in the mechanism of root bud inhibition (16). The water content of root buds increased by approximately 25% within 24 hours of removal of the parent shoot. Root bud length increased significantly between 24 and 48 hours after shoot removal, but some buds continued to grow while other buds apparently were reinhibited. Increasing the humidity from approximately 50 to 95% caused a significant increase in the rate of emergence and elongation of shoots from root buds following removal of the parent shoot. These observations strongly suggest that internal competition for water mediates root bud growth.

Light and temperature are other environmental factors that can strongly affect leafy spurge growth and development. Selleck *et al*. (23) reported that the percentage of flowering shoots decreased when light was limiting. Vegetative shoots of leafy spurge survived until the light reading fell below 0.28 lux in quaking aspen (*Populus tremuloides* Michx.), and few leafy spurge shoots were present at an intensity of 0.19 lux in oak (*Quercus* spp.) woods. Morrow (19) reported that leafy spurge plant height increased progressively as soil temperature increased, varying from less than 1 cm when grown for 12 weeks at a soil temperature of 3.3º C to over 35 cm at 33.3º C. Dry matter of tops exhibited the same trend, with the greatest growth at the highest temperature of 33.3º C. Root dry matter appeared to stabilize at soil temperatures of 18.3º C and above. Vigor of the plants, as indicated by a brighter green and branching, was greater at 13.3º C or warmer than at cooler temperatures.

The role of plant growth regulators in leafy spurge has not received much attention. Gibberellic acid stimulated the growth of emerged dormant buds on leafy spurge, caused branching and new shoot development on old shoots, and stimulated the emergence of new buds (24). The effects of the gibberellic acid stimulant were similar to those associated with removal of apical dominance, but the growth rate was several times that obtained when top growth was removed. The fact that decapitation of leafy spurge stems results in increased lateral bud and root bud growth (15, 16) indicates that auxins play a major regulating role on the growth and development of leafy spurge plants.

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