Leafy Spurge Physiology and Anatomy

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The first step in developing a control program for any troublesome weed is to recognize the nature and the magnitude of the problem. The second step, on the basis of existing knowledge about that weed, is to try to develop an explanation for the persistance and competitiveness of the weed and for why existing weed control practices are not effective. If such an explanation is available, then one has a basis for developing a strategy for the control of the pest. If an explanation is not readily available and present control measures are not effective against the troublesome species, additional information regarding the morphology (the external appearance), the anatomy (internal structure) and the physiology (function) of the troublesome species must be obtained. Such is the case with leafy spurge.

This plant species has been growing and flourishing in noncultivated areas at an alarming rate and with significant economic impact, as has been brought out elsewhere in this issue. This has occurred because there has not been a control program developed that is both effective and cost efficient to the owners of the rangeland and other noncultivated lands infested by spurge. Consequently, the productivity of vast acreages of North Dakota's lands is reduced because of growing infestations of untreated spurge.

Leafy spurge possesses nearly all the qualities attributed to an ideal weed. Characteristic of this species is the fact that large numbers of seeds with high viability are produced, and these germinate over an extended period of time. If seedlings from one flush of germination do not survive, other viable seeds remain in the soil to provide seedlings at other times. Spurge seeds are believed to be spread by birds and other animals. The seeds vary in color from yellow to a variety of greys and browns to a mottled appearance (Figure 1). Yellow seeds are immature and do not germinate. The mottled seeds are mature and are the most viable. A close-up of a seed is shown in Figure 2.

Figure 1. Seeds of leafy spurge, showing varying colors ranging from yellow immature (left) to more mature grey stages (center) to mature seeds that are speckled, or mottled (right). (X15)

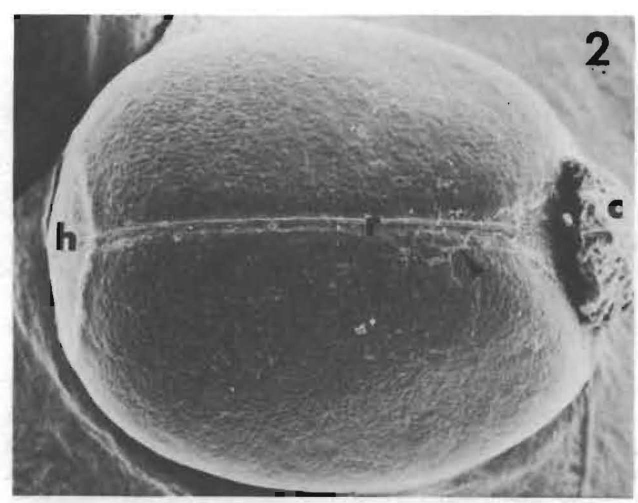

Figure 2. A scaning electron microscope view of a seed, showing the rachis (r), the point of attachment to the plant known as the hilum (h) and a water absorbing structure called the caruncle (c). Fungal hyphae (arrowhead) can also be seen.

Upon germination, which may occur over a wide range of environmental conditions from early spring to fall, seedlings will grow rapidly through the vegetative phase of growth to maturity and flowering. By mid-June a patch of spurge viewed from a distance develops a characteristic yellow-green hue, indicating that flowering is in progress and mature seeds will soon be dispersed. The leafy spurge flower is distinctly different from the usual concept of a flower. Figure 3 is a close-up of the flower showing the developing seeds and the nectaries that are conspicuous features.

A somewhat uncommon characteristic of the spurge seed pod is its dehiscence (sudden rupturing as it dries)

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which can propel individual seeds up to 15 feet from the parent plant. This mechanism of early seed dispersal may account for reinfestation of the spurge patch and its rapid enlargement from one year to the next. A spurge patch can increase in diameter by 30 feet in a single season due to seed dispersal.

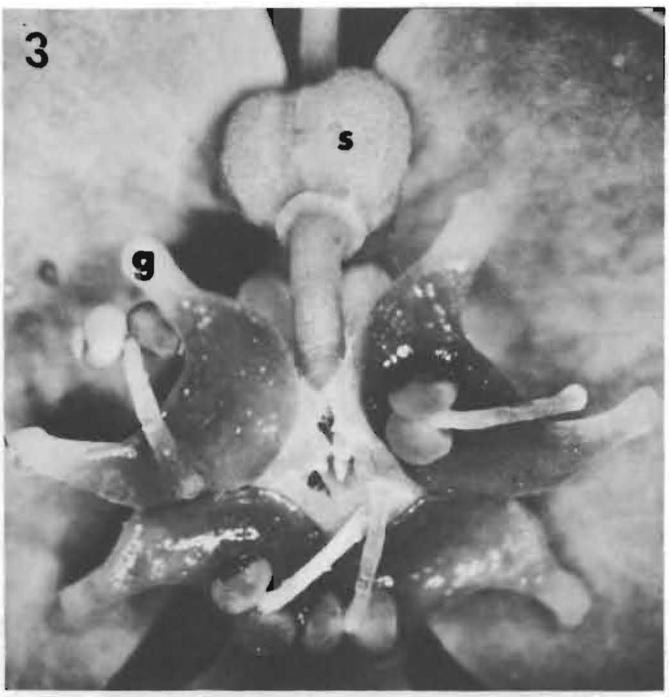


Figure 3. A close-up of a single flower of leafy spurge, showing the developing seed (s) contained in the carpels, and glands (g) that contain nectar. (X26)

The persistence and rapid expansion of a spurge patch is greatly enhanced by the perennial roots and crown which produce many underground vegetative buds. These buds possess a tremendous regenerative capacity and may be induced to produce new shoots at any time, depending on what happens to the shoot portion of the plant during the growing season. In anatomical studies of seedlings, Raju et al. (4, 5, 6) described the presence of shoot buds in the transition zone between the shoot and root as early as the second week after germination. These buds provide a means of shoot regeneration at a very young age should the initial shoot be damaged or cut off. If the plant is left to grow undisturbed, these first buds develop into a crown just below the surface of the ground. Such crowns are the source of shoots early in the spring of the next year. The growth of these crown buds is controlled in part by the presence of the plant hormone indoleacetic acid (IAA). This growth regulator is produced in the apex or tip of each vegetative shoot and is transported toward the base of the plant. IAA in the stem suppresses the growth of lateral buds located on the stem at the base of each leaf as well as the crown buds. Consequently, mowing, grazing or chemical destruction of the shoot apex causes a drop in the IAA concentration and the remaining shoot buds begin to grow, producing a branched plant. If the entire stem is destroyed the crown buds will begin to grow.

Numerous buds are produced throughout the extensive root system of a spurge plant (Figures 4 and 5) that are responsible for the tremendous regenerative capacity of leafy spruge. Hanson and Rudd (2) demonstrated that root buds are produced to depths exceeding 4 feet into the soil and are abundant on the many horizontal roots found throughout the top 12 inches of soil. Root fragments as small as an inch in length contain enough energy reserves that a bud located on it can grow and produce a viable shoot. Consequently, operations such as disking, plowing, etc., which break up the root system into many small pieces, in reality may produce many new plants. Undisturbed, the horizontal roots with their many shoot and root buds are the vegetative system by which a spurge plant spreads and reproduces. Excavation of a spurge patch reveals that many of the shoots throughout an entire spurge patch are interconnected and have arisen from a single original seedling.

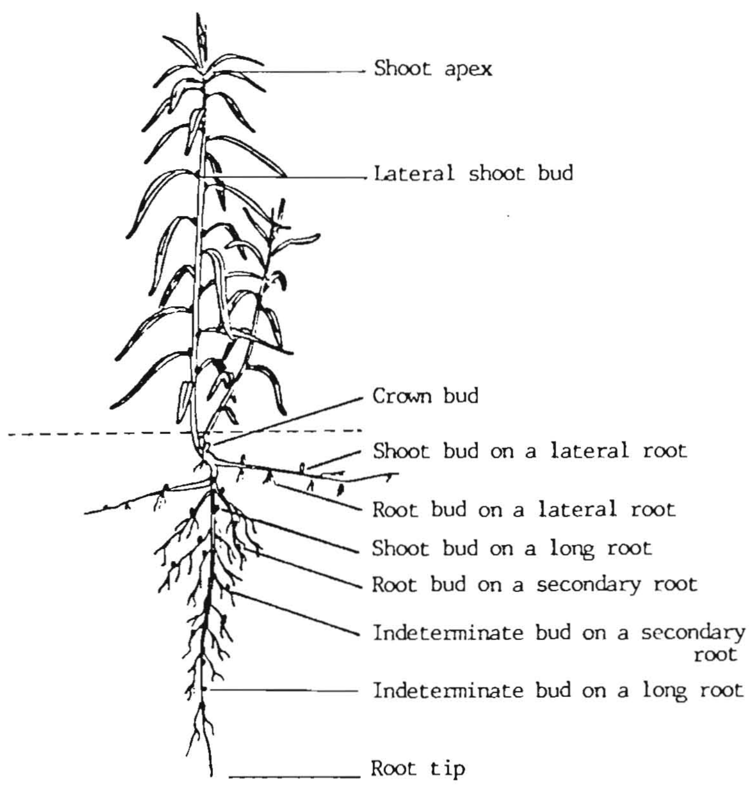


Figure 4. Diagram of a typical spurge plant showing the location of the various types of buds which can give rise to new shoots or entire plants.

There are other physiological characteristics of leafy spurge that contribute to the difficulties encountered in developing a satisfactory control program. One of these is the apparent poor absorption and translocation of foliarly applied herbicides. If a chemical is applied to

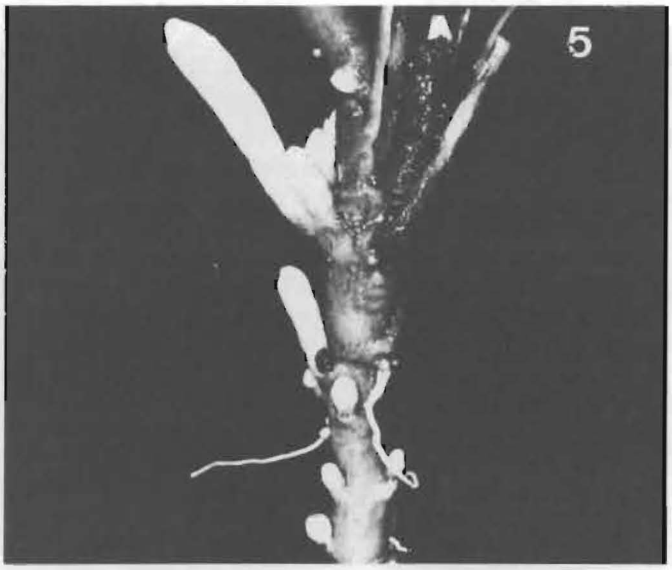


Figure 5. The crown, or base, of the shoot (at soil level) showing numerous buds in varying stages of growth. (X1.8)

the shoots of leafy spurge, the first barrier to penetration is a heavy layer of wax covering the cuticle of leaves and stems. The semi-crystalline wax formations on young and mature leaves are shown in Figures 6 and 7, respectively. Because of the wax, it is necessary to add surfactants or wetting agents to a spray to get the chemical to adhere to and spread over the surface of the leaves and stems. The wax is present as a protection from the weather and aids the plants in retaining moisture.

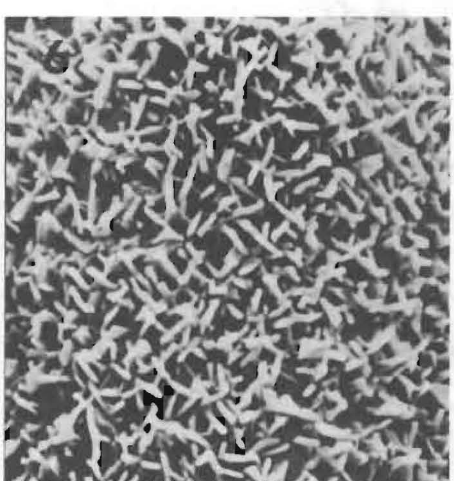


Figure 6. Crystal-like wax formations formed on the upper surface of a young leaf just starting to expand. (X9800)

Stomata (Figure 8) are important features of leaves and stems of leafy spurge. Stomata are holes in the leaf epidermis, with their size regulated by two cells (guard cells) that swell or contract according to the en-

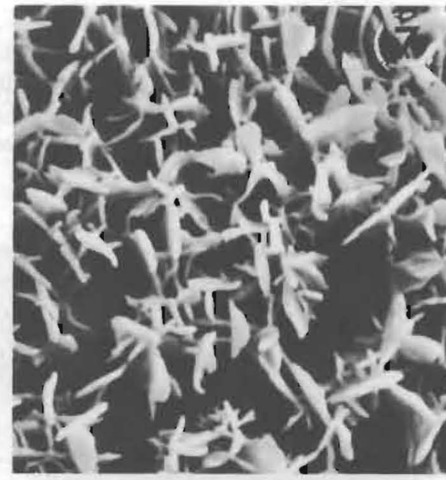


Figure 7. Mature wax formations on a fully expanded leaf about midway between the apex and base of the shoot. (× 9800)

vironmental conditions. There are few wax crystals adjacent to the stomatal opening.

The second barrier to chemicals is the cuticle, a thin membrane over the entire shoot that is thickest at the leaf tips (Figure 9) and thinner over the rest of the leaf. As the chemical moves through the cuticle it passes into the leaf at the outermost layer of cells, the epidermis (Figure 9). Some chemicals may move through the stomatal opening into the cavities below the stomata (Figures 9 and 10). The degree to which this occurs is not known.

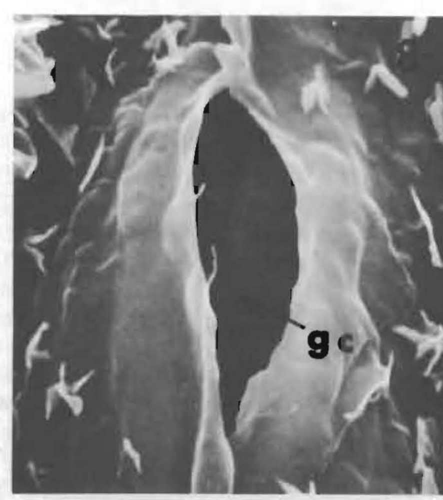


Figure 8. A surface view of a stomata showing the two guard cells (gc) that control the size of the opening. There are fewer wax crystals near the stomatal opening than over the rest of the leaf surface. (× 8500)

Once into the leaves, the chemical moves from a fairly tightly packed group of cells (palisade layer) into a more loosely arranged group of cells (spongy layer) and eventually into the main transporting structures, the veins (Figures 9, 11, and 12). The veins consist of very long cells that are arranged roughly parallel to the long axis of the leaves, stems and roots. Transportation of materials in these structures occurs in both directions. Nutrients move from roots to shoots while sucrose and other organic compounds move from shoots to roots. Ideally an herbicide would move in these same tissues throughout the plant. Once the herbicide arrives at the growing cells it should interfere with the cellular processes and eventually kill the cells. The trick, then, is to get the chemical into the conducting elements and throughout the roots without first killing the shoots. This is a very tough assignment for a single chemical because the root system of leafy spurge is very extensive and the chemical has to move several feet in some plants. The amount of chemical applied has to be regulated carefully, environmental conditions have to be just right, and the growth stage of the plant has to be one that is susceptible to the chemical. Entrapment of the chemical can occur anywhere along the pathway of travel from shoots to root buds.

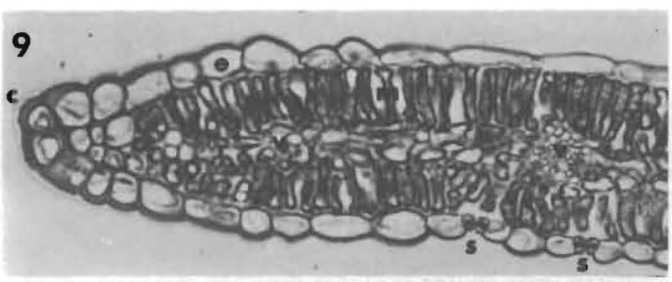


Figure 9. A cross section of a leaf tip showing the cuticle (c) that covers the entire shoot, the epidermal layers of cells (e), mesophyll cells (m), two veins (v) in different orientations and two stomata (s). (X770)

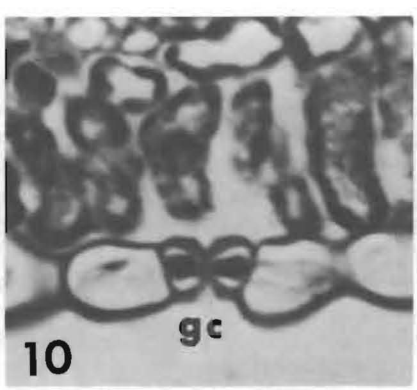


Figure 10. A higher magnification of one of the stomata shown in Figure 9. Two guard cells (gc) control the size of the opening. (X1830)

It has been demonstrated repeatedly that several herbicides, e.g. 2,4-D, are effective in killing the shoot portions of a spurge plant. However, these compounds are at best poorly translocated to the crown and root tissue, so shoots regenerate and the problem persists. Leafy spurge has a well defined laticifer system which contains large quantities of latex, a milky-colored rubber that is

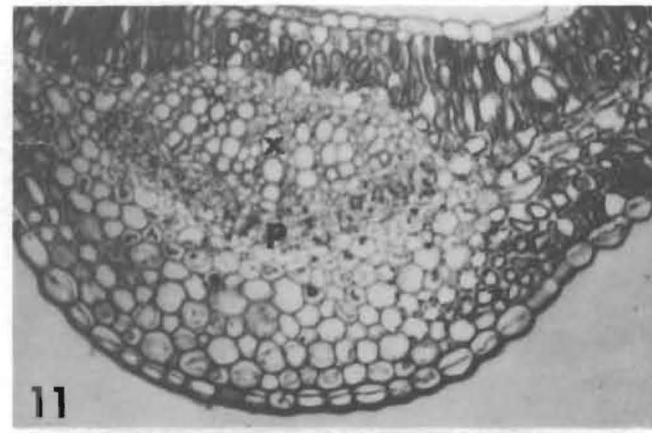


Figure 11. A cross section of the midrib of a leaf. In the center are the conducting elements of the xylem (x) and phloem (p). (X510)

Figure 12. The conducting tissues where a root bud joins the underground root, showing the variety of cell types and tissues and their orientation. (X1200)

present in all organs of a plant. If the plant is cut anywhere, small amounts of latex are exuded. The latex is encased in special cells (Figure 13 and 14) that are extremely long compared to the neighboring cells. These cells are present from shortly after germination until the plant dies. They occur close to conducting cells. It is not known whether the latex plays any role in the entrapment of chemicals because the experiments to prove or disprove this are quite difficult and have not been done. Presumably, the herbicides presently used move fairly rapidly in the shoots, or at least enough of the shoot is covered during spraying so that the amount of chemical delivered to the shoot cells is sufficient to kill the shoots. However, very little of this chemical is moved into the root tissues, either because the cells of the shoot are damaged, so they cannot move the chemical further, or there is a physical or a chemical barrier between the root and the shoot that limits herbicide movement into underground tissues. An area of future research is to study the structure of this region between the shoot and root and correlate the results of such studies with other structural and physiological data. The objective is how to overcome this bottleneck in the control of this difficult and fascinating plant.

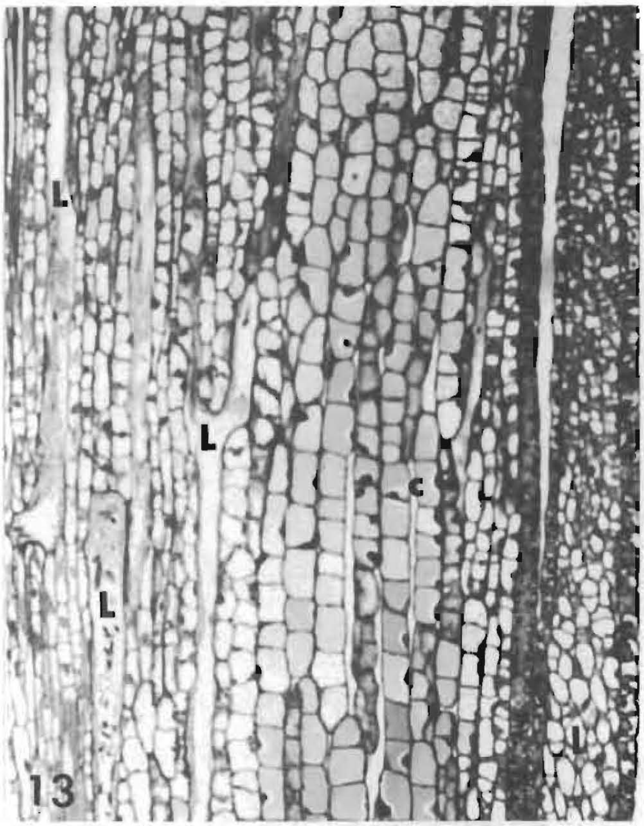


Figure 13. A longitudinal section near a stem apex, showing a young leaf (l) on the right, the epidermis (e), cortex (c) and several very long latex-containing cells (L) called laticifers. (X530)

Competition for space, water, minerals and light may not be the only factor by which leafy spurge suppresses the growth of other plant species. In some instances leafy spurge may directly retard the growth and development of a competitor through a phenomenon known as allelopathy. Allelopathy means one plant produces a chemical (an allelochem) which reaches a second plant and subsequently affects its growth or metabolism. There is evidence that leafy spurge may produce a substance(s) which reduces the growth of some of its competitors, thus giving a competitive advantage to leafy spurge. In separate experiments Le Tourneau et al. (3) and Selleck (7) demonstrated that components of various aqueous and organic solvent extracts from leafy spruge suppressed the germination and

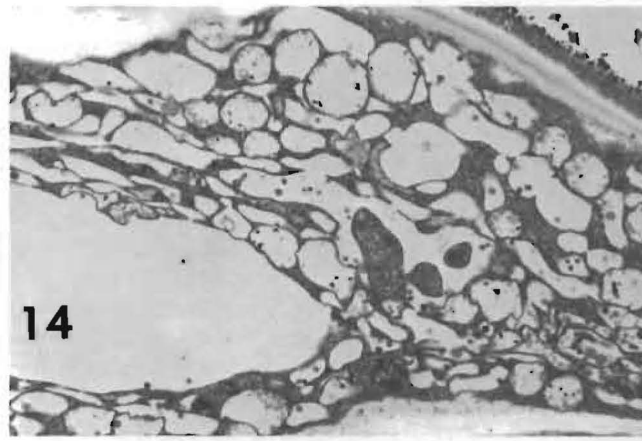


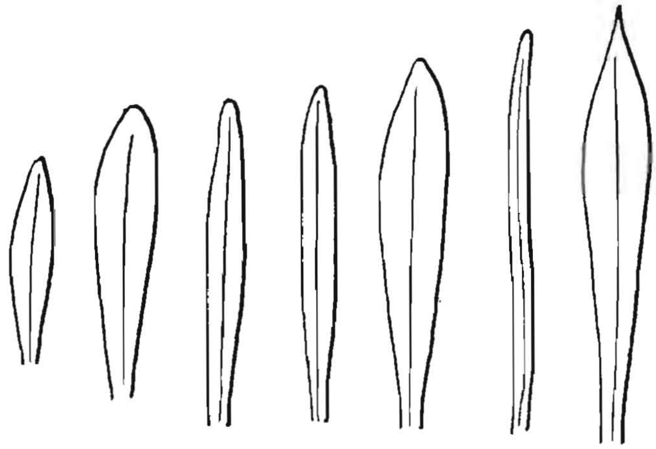
Figure 14. The cytoplasm of part of a latex cell showing numerous vesicles and some organelles. (X6150)

seedling growth of other plant species, explaining the absence of forbs in patches of spurge, even with bare ground visible between spurge shoots.

Allelopathy may work against leafy spurge as well as to its advantage. Selleck (7) reported that when leafy spurge was grown in competition with small everlasting (*Antennaria microphylla*), seed germination and seedling development of leafy spurge were reduced. The vigor of leafy spurge seedlings grown in soil taken from around the roots of small everlasting also was reduced. Under field conditions, small everlasting apparently releases a toxin which deters the establishment and development of the characteristic dense patches of leafy spurge. Uncovering the nature of such an allelochem could lead to the development of an effective class of herbicides.

Variations in local vegetative forms have been a contributing factor in the confusion over taxonomic relations among types of plants found in leafy spurge collections of the region. Some experts claim to distinguish between plant forms on the basis of leaf size and shape (Figure 15) or differences in inflorescenses. Consequently they support the concept that several species, e.g. *E. esula, E. virgata* and *E. intercedens,* are growing in the region and this acocunts for the variation that is found. The leafy spurge in North America appears to be a species other than *Euphorbia esula* that grows in Europe. The names *E. podperae* (1) and *E. pseudo x virgata* have been proposed as alternate names (See Messersmith, this issue). Other experts have not felt that they could differentiate between plant forms and therefore hold that they are all the same plant type, i.e. *E. esula,* with the observed variation due to the influence of local environments on the vegetative form. Still others feel that the variation in vegetative forms is real in the genetic sense and that the different forms should be considered as subspecies, ecotypes or biotypes of a single species. If more than one species exists, then hybridization could occur and vegetative variation be acounted for by this mechanism.

Figure 15. Two biotypes of leafy spurge about six weeks after the shoots were cut off. Numerous shoots regenerated and were grown in a greenhouse under identifical conditions. Note the variation in shoot size and numbers and in leaf size. (¼ X actual size)



Biotype number	18	17	19	13	14	1	11
Leaf surface area (mm^2) x 10^{-2}	38	65	57	66	107	51	82
Number of stomates per leaf. x 10^{-3} (upper surface)	160	160	120	110	250	130	200
Number of stomates per leaf. x 10^{-3} (Lower surface)	90	140	1	110	2	130	90

Outlines respresent fully expanded leaves from primary shoots developed from crown buds.

Figure 16. Leaf outlines, surface areas and stomatal frequencies illustrating variation which occurs amongst selected spurge biotypes.

As a working hypothesis, the concept that vegetative varitions are due to the occurrence of biotypes of a single species of leafy spurge has been used and this hypothesis may account for the inconsistant responses of different infestations to the same control measures. Leaf size, leaf shape, leaf surface characteristics, and the number or distribution of stomata all could affect the efficacy of a foliar herbicide application (Figure 16). If there are morphological or anatomical differences between biotypes, biochemical differences also must exist.

To investigate the possibiilty of the occurrence of biotypes of leafy spurge, a collection was made of spurge plants with apparent vegetative differences. These plants hve been maintained in a nursery and also under greenhouse conditions for over two years. The specimens have been propagated vegetatively by periodically subdividing the root systems. Also, for experimental purposes, large numbers of genetically uniform plants of one or more of the collection plants have been produced by rooting fresh cuttings. Morphological differences have been established for plant materials obtained from this collection.

Tissue culture techniques are being employed to investigate biochemical differences in the spurge biotypes. Masses of undifferentiated cells (callus tissue) and cell suspensions of the different biotypes have been established and are being evaluated. A comparison of initial results indicates that there are significant differences between the cell suspension cultures of the different biotypes. Physical characteristics of the suspension cultures vary from a cream colored uniform suspension of apparently single to small clusters of cells to clumpy light brown suspensions of large colonies of cells. There is as much as a two-fold difference in the growth rates of some of the biotypes. The growth rate differences also are reflected by similar differences in protein content and the capacity of the suspension cultures to reduce nitrate in the medium.

These data alone do not prove genetic differences between the suspension cultures, but suggest there is justificaton for conducting additional research concerning the genetic variability of leafy spurge that may effect control methods. For example, a comparison of the sensitivity of some of the suspension cultures of different biotypes to different concentrations of the herbicide dicabma indicates that at the cellular level some biotypes of spurge are nearly twice as sensitive as others. Also, there are apparent differences in the susceptability or resistance of leafy spurge biotypes to infection by a powdery mildew identified as *Erysiphe* type *Oidium*. At this point the evidence is accumulating that there is a genetic basis for biotypes of leaf spurge.

REFERENCES

1. Galitz, D.S. 1980. **A summary of the synonomy of leafy spurge.** N. Dak. Research Report, N. Dak. State Univ., Fargo, ND 6 pp.

2. Hanson, H.C. and V.E. Rudd. 1933. **Leafy spurge — Life history and habits.** ND Agr. Expt. Sta. Bull. 266..

3. LeTourneau, D., G.D. Failes and H.G. Heggeness. 1956. **The effect of aqueous extracts of plant tissue on germination of seeds and growth of seedlings.** Weeds 4:363-368.

4. Raju, M.V.S. 1975. **Experimental studies on leafy spurge (*Euphorbia esula*L.). I. Ontogeny and distribution of buds and shoots on the hypocotyl.** Bot. Gaz. 136:254-261.

5. Raju, M.V.S. and W.N. Marchuk. 1977. **Experimental studies on leafy spurge (*Euphorbia esula*L.). III. Xylem development in relation to the hypocotylary bud growth.** Bot. Gaz. 138:305-311.

6. Raju, M.V.S., T.A. Steeves and R.T. Coupland. 1963. **Developmental studies on *Euphorbia esula* L. morphology of the root system.** Can. J. Botany 41:579-589.

7. Selleck. G.W. 1972. **The antibiotic effects of plants in laboratory and field.** Weed Sci. 20:189-194.

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3. Kidder, Daniel W. 1982. **Low volume application of dicamba for leafy spurge control.** M.S. Thesis. North Dakota State University, Fargo. 54 p.

4. Lym, R. G., and C. G. Messersmith — Unpublished data.

5. Messersmith, C. G., and R. G. Lym. 1981. **Roller and wick applciation of picloram for leafy spurge control.** Down to Earth 37(2):9-12.

6. Vore, R. E., and H. P. Alley. 1981. **Leafy spurge (*Euphorbia esula* L.), Wyoming Chemical Control Research.** University of Wyoming Agricultural Experiment Station Bulletin MP-46R. 26 p.