

Reprinted from: Leafy Spurge, Monograph series of the Weed Science Society of America. ed. Alan K. Watson, 1985. Chapter 9 (3):93-104. ill.

Published by: Weed Science Society of America. <http://www.wssa.net/>

Integrated management of leafy spurge

A. K. WATSON

Department of Plant Science, Macdonald College of McGill University, Ste-Anne-de-Bellevue, Québec, Canada H9X 1C0

- I. Introduction
- II. Leafy Spurge Problem
- III. Population Dynamics
- IV. Simulation of Leafy Spurge Populations
 - Infestation
 - Control
 - Limitations
- V. Leafy Spurge Management
 - Literature Cited

I. Introduction

Integrated pest management (IPM) has been defined and interpreted in various ways, usually to suit the specific situation, which has led to confusion and misinterpretation of the concept. A generally accepted definition is "...a desirable approach to the selection, integration, and use of (pest-control) methods on the basis of their anticipated economic, ecological, and sociological consequences" (1, 18, 33). Two recent publications, the special issue of *Bioscience*, Volume 30, No. 10, 1980, on "Integrated Pest Management" and the *Weed Science Supplement to Volume 30*, 1982, on "Integrated Weed Management Systems (IWMS)" provide excellent reviews on integrated pest management systems. The IPM concept is complex and involves basic research, control methods research, various levels of integration, extension (delivery), education and economic analysis.

The IPM systems concept is relatively new to the Weed Science discipline. In recent decades herbicides have been the mainstay of weed control, but development of herbicide resistance, registration problems, and environmental concerns have helped spawn a greater interest in integrated weed management systems (IWMS). Shaw (33) defined IWMS as "...directed agro-ecosystem approach for the management and control of weed

...populations at threshold levels that prevent economic damage in current and future years.” IWMS includes all methods of control: preventive (such as use of weed-free seed), managerial (techniques used to favor growth of crop species and to the detriment of weed species, such as optimum plant populations, timely fertilizer applications and appropriate crop rotations), physical (such as suitable seedbed preparation and timely cultivation), chemical (effective herbicide application) and biological (use of insects and pathogens). The integration of various control methods against one weed or a complex of weeds is termed vertical integration. Horizontal integration involves the integration of management systems across more than one class of pests. IWMS can be focused on a weed, a crop or an agroecosystem with the following objectives: a) to reduce losses caused by weeds, costs of control, energy, and labor requirements; b) to reduce tillage and soil erosion caused by water and wind; c) to assure an adequate supply of quality food, feed, and fiber-safeguarded against poisonous weed seeds and contaminants; d) to improve environmental quality and reduce hazards to man; and d) to maximize producer profits (33).

The objective of an integrated management system for leafy spurge would be to manage leafy spurge populations below certain economic thresholds by using any or all control methods available in a sound ecological and sociological manner. This objective can only be realized through a comprehensive understanding of the population biology of leafy spurge, an awareness of the advantages and limitations of various methods of control, and the development and implementation of the optimum control strategy or management system to prevent further spread of this noxious weed and to reduce leafy spurge infestations in North America.

The implementation of an IWMS for leafy spurge requires supportive information on the importance of the problem and potential threat, detailed information on the population biology of the species, awareness of the strengths and weaknesses of available control technology, and the resources to operate the program.

II. Leafy spurge problem

Leafy spurge is a major noxious weed in the northern Great Plains of the United States and the bordering prairie provinces of Canada. This aggressive perennial weed infests nearly 2 1/2 million acres in North America (22) and although capable of prolific seed production, the persistence of leafy spurge is due to the reproductive capacity of the numerous vegetative buds on its extensive, well-developed root system (8, 9). The biology of leafy spurge has been widely studied and reported (3, 4, 12, 19, 32, see also Chapter 5). The aggressive noxious nature of leafy spurge has been referred to in most publications concerning this species. For example, in 1934 Hanson (11) stated, “Many fields have become solid patches of leafy spurge...” and “...that other kinds of plants, even alfalfa and sweet clover, cannot compete with leafy spurge.” In a review on the biology of leafy spurge, Best *et al.* (4) stated “...it is difficult to grow crops in infested areas” but no further discussion of yield losses attributable to leafy spurge was given. Derscheid and Wrage (10) suggested that leafy spurge infestations caused 10 to 100% reduction in crop yields, and Baker [as reported by Reilly and Kaufman (26)] observed a 75% reduction in rangeland carrying capacity due to leafy spurge with 50% yield reduc-

tion and 25% loss in forage utilization due to presence of leafy spurge. The effect of leafy spurge on grass yield is illustrated in Figure 1. It is unfortunate that more comprehensive data on yield loss and the combined detrimental effects of leafy spurge are not available. Perhaps this deficiency can be explained or accounted for by the lack of resources in weed science to provide the necessary data to support the obvious. The seriousness of this weed and further justification for directing resources into an IWMS for leafy spurge control is evident by legislation in Canada and the United States directed toward the reduction of leafy spurge spread and its control.

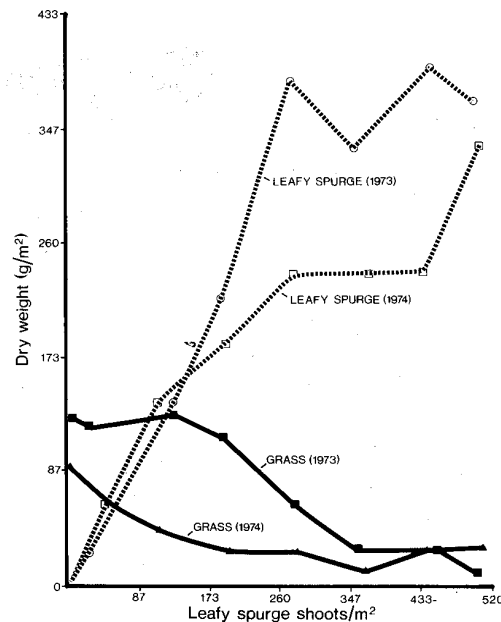


Figure 1. Effect of increasing leafy spurge density on grass yield. Redrawn with permission from Bowes (unpublished).

Because of the noxious nature of leafy spurge, major effort has been directed toward its control. Preventive methods are required to reduce the spread of this weed into habitats prone to invasion, whereas eradication should be the objective for small, localized infestations of leafy spurge. However, for the majority of leafy spurge infestations in North America, the only practical program objective is control. In any control program it is important to define the level of control desired, and with leafy spurge the level of control, or population threshold to be tolerated, will vary depending on such socioeconomic factors of an area as land value, land use, method of control, costs of control, control efficacy and so forth.

The different control strategies used to combat leafy spurge have their strengths and weaknesses. The progress of cultural, chemical and biological control of leafy spurge has been described in detail in the previous three chapters. The goal of an IWMS for leafy

spurge is to utilize the available control technology to reduce infestations and prevent further spread of this weed. This integration of control technology is complex and must be supported by an understanding of the population dynamics of the weed.

III. Population dynamics

Models are commonly used to illustrate the interacting elements of a biotic system, and these models can be relatively simple or complex. A simple or general model illustrates the more important elements interacting in the system and does not include all the complexities involved. Therefore, a general leafy spurge model should effectively illustrate the major factors affecting the size of the leafy spurge population, which include the influence of man, interference with associated vegetation, the effect of the abiotic environment, and the effect of herbivores (Figure 2).

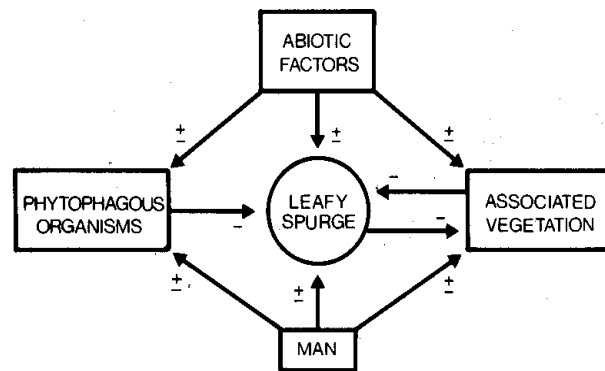


Figure 2. A general leafy spurge population model [adapted from Zwölfer (39)].

Man has a major impact, both positive and negative, on the spurge system. These influences range from the initial introduction of leafy spurge into North America and subsequent spread to control with herbicides, cultural practices and introduction of biological control agents. Management practices that either increase or decrease the competitiveness of associated vegetation influence the spurge population and, conversely, the negative influence of the leafy spurge population on crop species, are also illustrated in Figure 2. The negative impact of weed-feeding organisms (sheep and phytophagous insects) and disease on spurge populations, as well as the positive and negative influences of the abiotic component of the environment on the system, are illustrated in this model. Obviously, the overall goal of a control program would be to maximize the negative influences on the spurge population, and therefore the success of any control program may ultimately depend on an understanding of the mechanisms that regulate the size of the weed population. The importance of a comprehensive knowledge of the life cycle and population dynamics of a weed species has been stated by many authors (14, 21, 27, 28, 29, 30).

IV. Simulation of leafy spurge populations

Modeling techniques have had limited application in weed research in North America (23, 30), but Bowes and Thomas (6) used a population model as the basis for their discussion of leafy spurge control. Their model was a flow diagram, which represented the relationships among the various components (seeds, roots and shoots) of a leafy spurge population but was not designed to predict the flux of individuals from one component to another over time.

Using demographic data, Mortimer and colleagues from the University of Liverpool have described a modeling approach for predicting weed populations and evaluating weed control practices (17, 20, 21). A life table is prepared, composed of the various age states of the weed population, and then translated into a modified Leslie matrix model consisting of a transition matrix and column vectors. When the transition matrix is multiplied by the column vector of the number of individuals in each age state at one time period, the number of individuals in each age state present in the next time period is given. Through repetitive multiplication of successive column vectors by the transition matrix, the dynamics of the population can be simulated. The development and use of the Leslie matrix model has been described in detail elsewhere (35, 37).

The model presented here for leafy spurge utilizes the approach of Mortimer *et al.* (21) and McMahon and Mortimer (17). The diagrammatic life table uses the five age states (seeds, seedlings, vegetative shoots, flowering shoots and root buds) within the life cycle of leafy spurge (Figure 3). The life table also depicts the changes that may occur between the different age states. For example, ' P_s ' **represents the proportion of seeds that remain as seeds** and ' a ' represents the proportion of seeds that germinate and become seedlings. Similarly ' e ', ' f ' and ' g ' are fecundity values of the number of seeds and root buds produced per shoot. The life table is translated into a matrix model consisting of a transition matrix and column vectors (Figure 4). When, this matrix is multiplied by the number of individuals in each age state at one time period (1st column vector), the result is the number of individuals in each age state at the next time period (2nd column vector).

Despite the many studies on the biology and ecology of leafy spurge, much of the demographic data required for the model are incomplete. Values used in the simulation were obtained directly from the literature or calculated from data presented in the literature (3, 4, 5, 6, 7, 12, 19, 31, 32, 34). Simulations were aided by the use of a microcomputer with six transition matrices that changed throughout the season, which simulated the development of the spurge population throughout the year (Figure 5). The initial age state distribution (Figure 6) represents the number of seeds [from Bowes and Thomas (6)] and the number of root buds per m^2 in the top 30 cm of soil (determined in a local population at Ste-Anne-de-Bellevue, Quebec) in the field prior to the commencement of growth in the spring.

Although the model is not very sophisticated and does not include density-dependent functions, a feature in the program partly accounts for this limitation. Because of the tremendous reproductive capacity of leafy spurge, populations that have been suppressed by herbicide treatment or some other form of control quickly return (often within 1 year) to the carrying capacity of the habitat after the control is removed (5,7,32). Values ex-

ceeding the carrying capacity are not realistic and can quickly be obtained through simulation of the spurge population. Therefore, limits on the maximum number of seeds, seedlings, vegetative shoots, flowering shoots and root buds were incorporated into the computer program. Values of 300000, 1000, 1000, 500, and 20000 per m^2 for seeds, seedlings, vegetative shoots, flowering shoots and root buds respectively were used in the program.

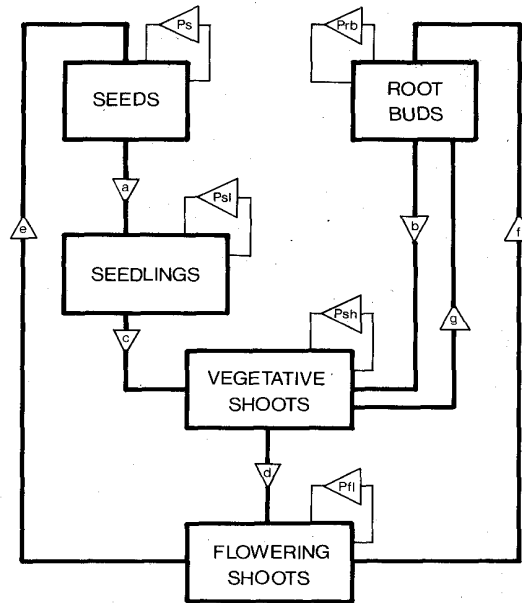


Figure 3. Diagrammatic life table of a leafy spurge population, where

- P_s - proportion of seeds surviving as seeds
- P_{sl} - proportion of seedlings surviving as seedlings
- P_{sh} - proportion of vegetative shoots surviving as vegetative shoots
- P_{fl} - proportion of flowering shoots surviving as flowering shoots
- P_{rb} - proportion of root buds surviving as root buds
- a - proportion of seeds germinating
- b - proportion of root buds germinating
- c - proportion of seedlings surviving to become vegetative shoots
- d - proportion of vegetative shoots surviving to become flowering shoots
- e - number of seeds produced by each flowering shoot
- f - number of root buds produced by each flowering shoot
- g - number of root buds produced by each vegetative shoot

$$\begin{array}{c} \text{Transition Matrix} \\ \left[\begin{array}{ccccc} P_s & 0 & 0 & e & 0 \\ a & P_{sl} & 0 & 0 & 0 \\ 0 & c & P_{sh} & 0 & b \\ 0 & 0 & d & P_{fl} & 0 \\ 0 & 0 & g & f & P_{rb} \end{array} \right] \end{array} \times \begin{array}{c} \text{Column Vectors} \\ \left[\begin{array}{c} S_t \\ SL_t \\ SH_t \\ FL_t \\ RB_t \end{array} \right] \end{array} = \begin{array}{c} \left[\begin{array}{c} S_{t+1} \\ SL_{t+1} \\ SH_{t+1} \\ FL_{t+1} \\ RB_{t+1} \end{array} \right] \end{array}$$

Figure 4. A matrix model of the life table of leafy spurge, where

- S_t and S_{t+1} - the number of seeds at time t and $t + 1$.
- SL_t and SL_{t+1} - the number of seedlings at time t and $t + 1$.
- SH_t and SH_{t+1} - the number of vegetative shoots at time t and $t + 1$.
- FL_t and FL_{t+1} - the number of flowering shoots at time t and $t + 1$.
- RB_t and RB_{t+1} - the number of root buds at time t and $t + 1$.

Infestation. To illustrate the use of the model in predicting the spread or population growth of leafy spurge, values of 10 seeds/m², 1 seed/m², 1 seed/1000m² and 1 seed/ha were used to simulate various levels of seed introduction into a previously uninfested area. This was accomplished by placing the appropriate value for the seed age state in the initial age state distribution (see Figure 6) with all the remaining age states, including the root buds being zero. A similar simulation was performed with root buds as the introduced propagule.

Results of these simulations (Figures 8 and 9) demonstrate the rapid colonizing ability of this noxious, aggressive weed. An initial introduction of 1 seed/m² theoretically will reach the carrying capacity within 6 years, and even when only 1 seed/ha is introduced, the leafy spurge infestation will reach the carrying capacity in 10 years (Figure 7). Because of the greater survival of shoots arising from root buds compared with seedlings, the corresponding time to reach the carrying capacity of the habitat is reduced when root buds are the introduced propagule (Figure 8). When 1 root bud/m² is introduced, the resulting spurge population will attain the carrying capacity in 4 years, and when only 1 root bud/ha is introduced, the spurge population will reach the carrying capacity in 8 years (Figure 8).

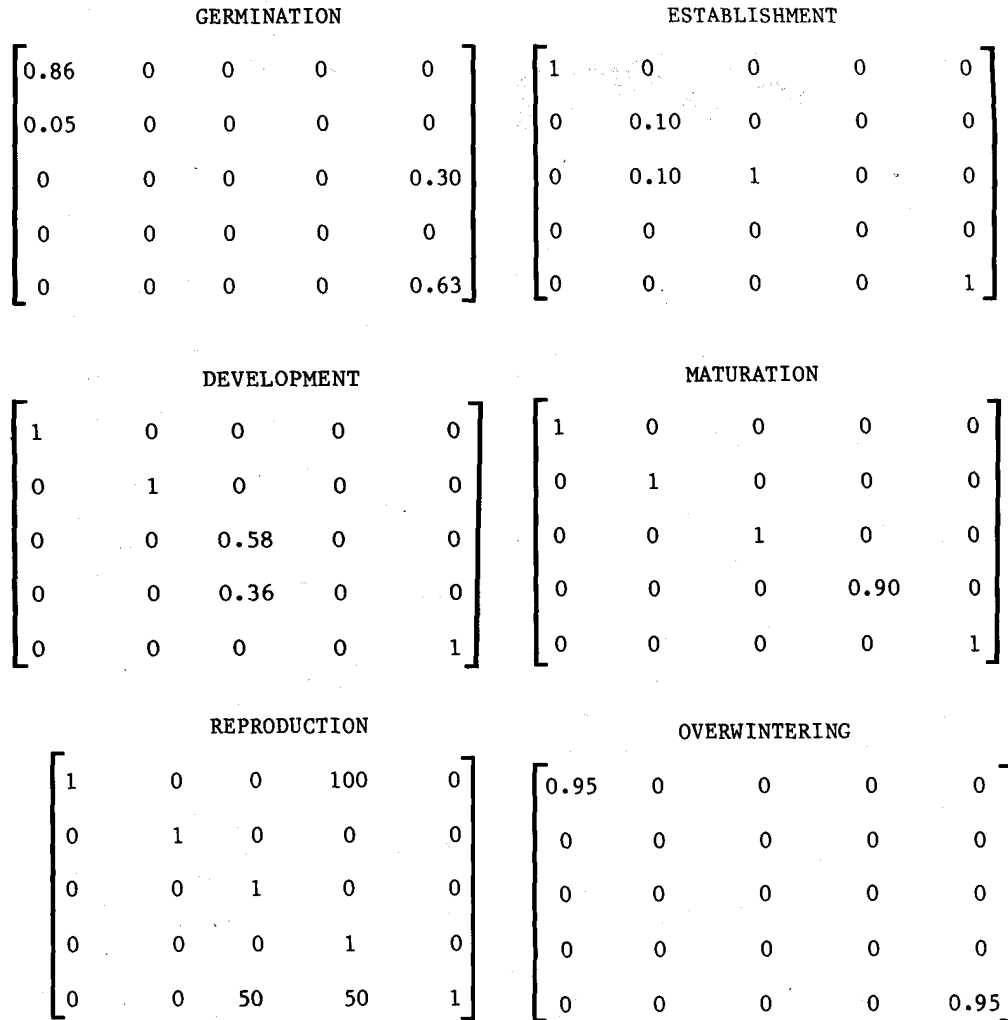


Figure 5. Transition matrices for the simulation of a leafy spurge population.

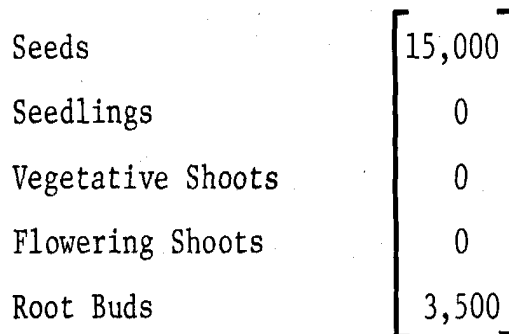


Figure 6. Initial age state distribution of leafy spurge representing the numbers present (per m²) in the field prior to commencement of growth in the spring.

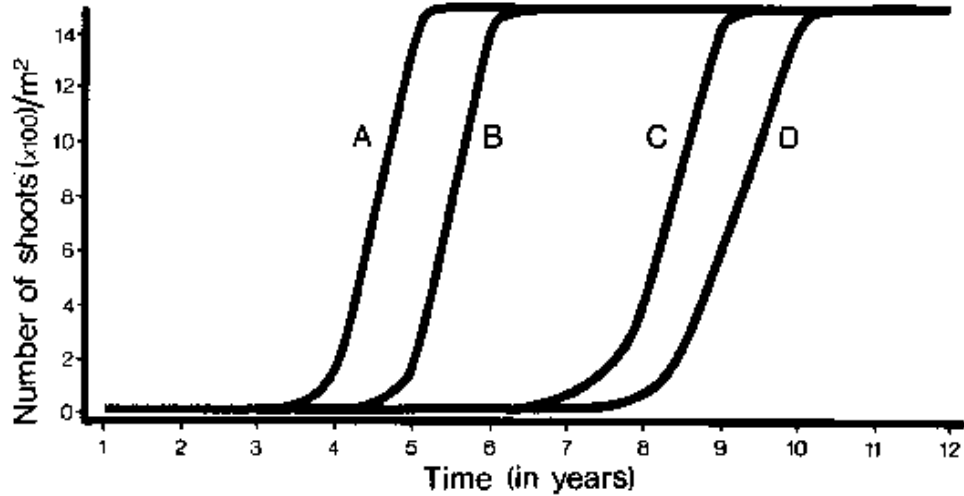


Figure 7. Time required for a simulated leafy spurge infestation to reach the carrying capacity of the habitat (1500 shoots/m²) when 10 seeds/m² are introduced (A), 1 seed/m² is introduced (B), 1 seed/1000 m² is introduced (C), and 1 seed/ha is introduced (D).

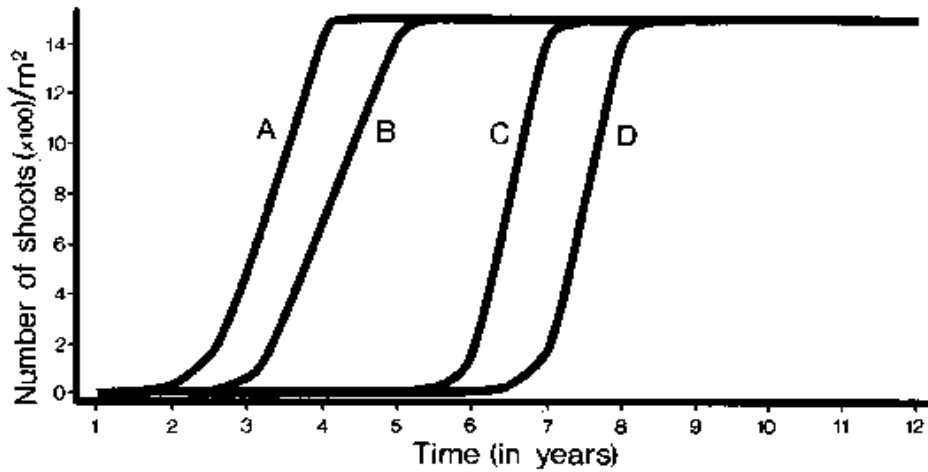


Figure 8. Time required for a simulated leafy spurge infestation to reach the carrying capacity of the habitat (1500 shoots/m²) when 10 root buds/m² are introduced (A), 1 root bud/m² is introduced (B), 1 root bud/1000 m² is introduced (C), and 1 root bud/ha is introduced (D).

Control. The consequence of a single management practice or a combination of several management practices on the resulting population size of leafy spurge can be modeled by deliberately manipulating the proportions surviving and the fecundity values (see Figure 5). Therefore, the effect of various levels of control on the spurge population can be predicted by altering aboveground shoot survival, seed production and root bud production within the matrices. Seed bank and bud bank survival values could also be manipulated, but these aspects will not be discussed further here. The resulting effect on the leafy spurge population over time can be evaluated by comparing values of the seed bank, root bud bank and shoots/m², or by comparing the calculated λ values. The λ is the finite rate of increase of the population in an unrestricted environment when the population has reached a stable age-state distribution (17, 35). When the $\lambda > 1$ the population is increasing, $\lambda = 1$ the population is stable, and when $\lambda < 1$ the population is decreasing. From a weed management perspective, control programs should be designed with a maximum λ value of 1 (containment) or preferably a λ value of < 1 (weed population decline).

Results of the simulation of leafy spurge control are presented graphically in Figures 9 to 13. In these spurge control simulations annual aboveground shoot control would be analogous to a paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) application or hoeing at ground level with no effect on root bud survival.

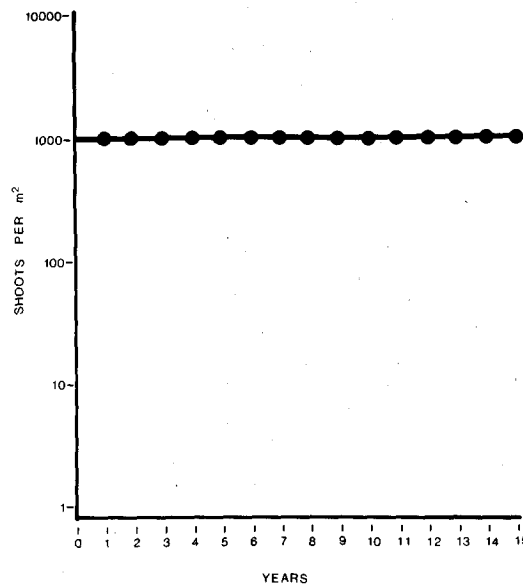


Figure 9. Simulation of a leafy spurge population when 100% of seed production is controlled each year.

Seed reduction would be analogous to a predispersal biological control agent destroying a certain proportion of seeds. Root bud control would be analogous to the death of root buds due to the translocation of picloram (4-amino-3,5,6-trichloropicolinic acid) or 2,4-D [(2,4-dichlorophenoxy)acetic acid] or to a root-boring insect, such as *Oberea erythrocephala* (Schrank), that destroys a certain proportion of the root buds (31). When

100% of the seed production is controlled, an established leafy spurge population is unaffected (Figure 9). Similarly, 80% control annually of the aboveground shoots, with additional reductions of 95% of the seed production and 20% of the root bud production, does not result in a reduction of the leafy spurge population (Figure 10). Even when 90% of the shoots are controlled each year, the population declines only if the aboveground shoot control is complemented with 95% control of seed production and 80% control of root bud production (Figure 11). Stable, relatively low infestation levels can be obtained with 95% control of the aboveground shoots with additional control of seed and root bud production (Figure 12). Eradication of leafy spurge theoretically can be obtained with 99% control annually of all aboveground shoots (Figure 13).

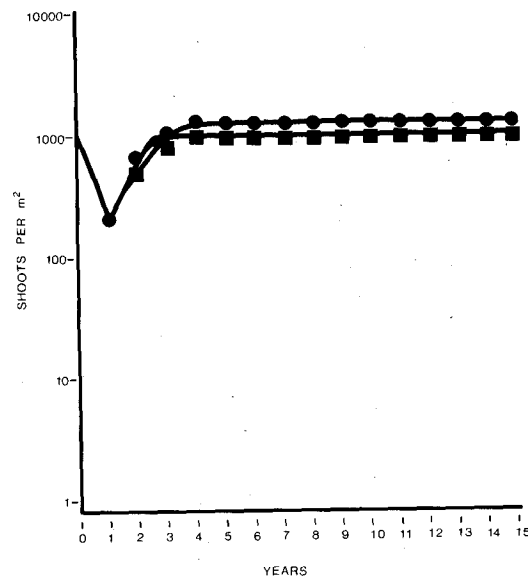


Figure 10. Simulation of a leafy spurge population when 80% of the aboveground shoots are controlled each year: (●) with no additional control of seed and root bud production, and (◆) with 95% control of seed production and 20% control of root bud production.

Limitations. The data presented and their interpretation must be viewed with some caution. Although the values used in the matrices originated from the literature and in the most part represent average values, much of the demographic data required for the precise simulation of leafy spurge populations is lacking. Some of the data used and some of the assumptions drawn from the available information may not be entirely accurate and therefore the results of the simulation may be biased. The arbitrary values for the carrying capacity of 1000 and 1500 shoots/m² are suggested as maximum values for the model even though a value of 2300 seeding shoots/m² was reported (32), but most infestations range from 150 to 500 shoots/m² (4, 6, 12, 32). Results of simulations would be similar if a lower carrying capacity value, such as 500 shoots/m², was used.

The model is limited because it does not take into account density functions. Initially, seed production and root bud production should exhibit density-dependent variation. However, studies with plant populations indicate a very narrow range of variations in seed production despite a wide range of plant densities (13, 24). Although the root system is generally more sensitive to density than seed production, variation in root bud production per unit area is also not likely to be highly variable (13). Average values from the literature were used and maximum values or upper limits for the different age states were

incorporated into the program. As a consequence, data presented are realistic and representative of leafy spurge populations. Although based on the literature, the upper limits of the population age states used in the model were high to ensure that populations were not underestimated. The high limit value for root buds of 20000/m² is likely an overestimate and the difference between 20000 and the 3500 value for the initial level (Figure 6) is responsible for the inflections in Figures 10 and 11.

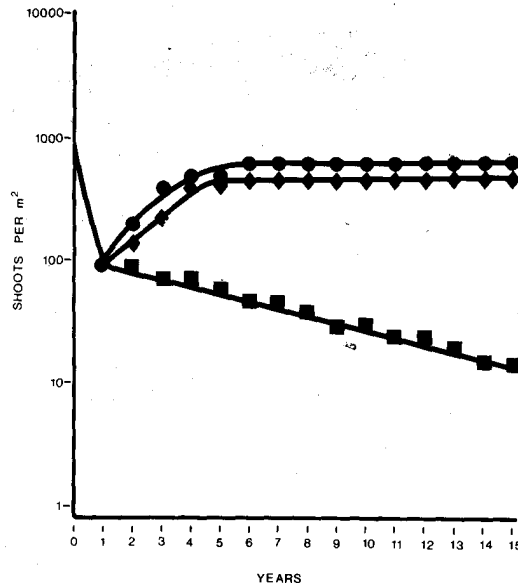


Figure 11. Simulation of a leafy spurge population when 90% of the above-ground shoots are controlled each year: (●) with no additional control of seed and root bud production, (◆) with 10% control of seed production and 20% control of root bud production, and (■) with 95% control of seed production and 80% control of root bud production.

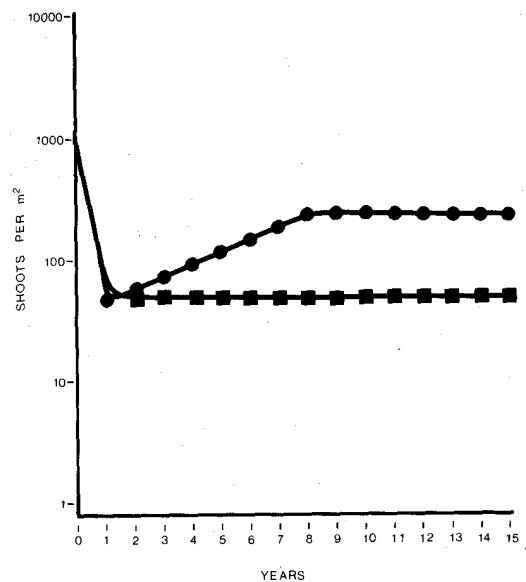


Figure 12. Simulation of a leafy spurge population when 95% of the above-ground shoots are controlled each year: (●) with no additional control of seed and root bud production, and (■) with 90% control of seed production and 40% control of root bud production.

Refinement of the simulations could be accomplished with precise data obtained from field studies designed to collect the necessary demographic data for the model. Information on the aboveground portions of the spurge populations is relatively well documented, but information on the population dynamics of the underground portions of spurge populations is generally lacking. The lacuna of information on root bud bank is the main limiting factor. For example, picloram provides excellent control of the aboveground shoots (5, see Chapter 8), is actively translocated into the root system, and must inhibit the growth and (or) kill numerous root buds. However, data on the proportion of root buds destroyed are not available.

The presentation of population models should be accompanied with verification and validation of the model (15). The model presented appears to represent the real-life spurge system but requires further testing for verification and statistical validation. Perhaps the presentation of this model will stimulate discussion and field studies necessary for the validation process.

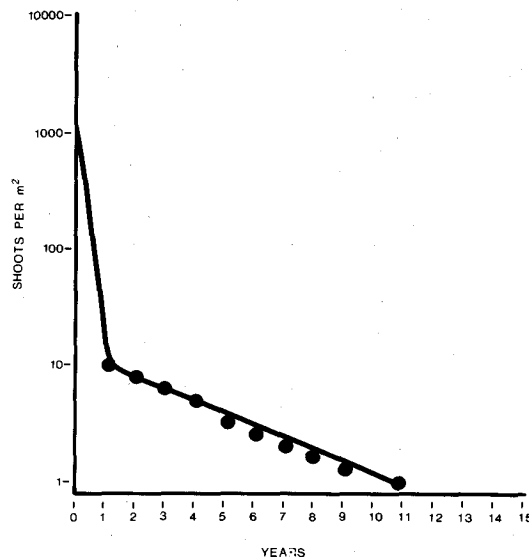


Figure 13. Simulation of a leafy spurge population when 99% of the above-ground shoots are controlled each year with no additional control of seed and root bud production.

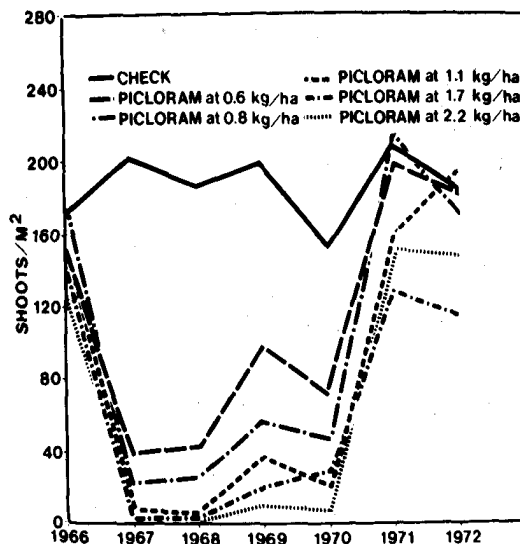


Figure 14. The density of leafy spurge following the application of five rates of picloram [from Bowes and Molberg (5) used with permission from Can. J. Plant Sci.].

V. Leafy spurge management

The problem with leafy spurge in North America is complex and widespread, and requires the integration of various control strategies since no single method seems likely to control leafy spurge over the infested range of this introduced weed. Leafy spurge apparently is not a problem in most of its native range as only small, relatively localized roadside infestations can be found in eastern Europe. Suggested reasons for the increased aggressiveness of introduced weeds include: a) more favorable environmental conditions, b) competition from associated vegetation less intense, and c) the absence of natural enemies in the new habitat (38). Since the ecologic range of leafy spurge in Eurasia is remarkably similar to the ecologic range of leafy spurge in North America and since the competition from associated species is often very similar, the increased aggressiveness of this introduced weed may be associated with the absence of natural enemies in its new habitat. Leafy spurge is attacked by few organisms in North America, but many natural enemies (over 100 different insect species and almost the same number of fungi) utilize leafy spurge in its native range (see Chapter 8). This type of analysis supports the concept of classical biological control, but more thorough investigation and comparisons between the habitats and populations in Europe and in North America may provide new insights into understanding the aggressiveness of this introduced weed and possibly lead to innovative control strategies.

All methods of control—preventive, managerial, physical, chemical, biological and, to a limited extent, integrated control—have been used against leafy spurge, but the weed continues to spread in North America. Although it has been reported that cultivation can result in increase of spurge populations by 100% on tillable land (32), cropping plus timely herbicide applications provide effective control of leafy spurge (see Chapter 7). However, most infestations of leafy spurge are on nontilled land unsuitable for extensive cultivation.

Chemical herbicides, particularly picloram, provide excellent control of leafy spurge in pasture, rangeland and noncrop areas. However, retreatment after 3 to 5 years is required to maintain spurge control (Figure 14). Extensive herbicide applications are limited further by high costs, dieback of desirable forbs and tree species and possible contamination of water supplies. In fact, herbicide treatment may be more expensive than the land values (see Chapter 1).

The potential of natural enemies for the control of spurge populations is illustrated by the effect of continuous sheep grazing (Figure 15). The use of sheep, a herbivore management type of biological control, is also limited by the extent of the infestation and by the cost of fencing required for controlled grazing. Substantial progress in classical biological control has been made, but progress is hampered by the taxonomic complexity of North American spurge (see Chapter 8). Since it is assumed that at least four biotic agents are required for successful biological control of a weed species, and if there are six or more different taxa of leafy spurge in North America, significantly more research effort is required to collect and evaluate candidate agents in Europe. The use of native fungi as biological herbicides is also a possibility (16). Although these biological herbicides would be relatively host specific, their use would be limited by similar constraints that limit chemical herbicides.

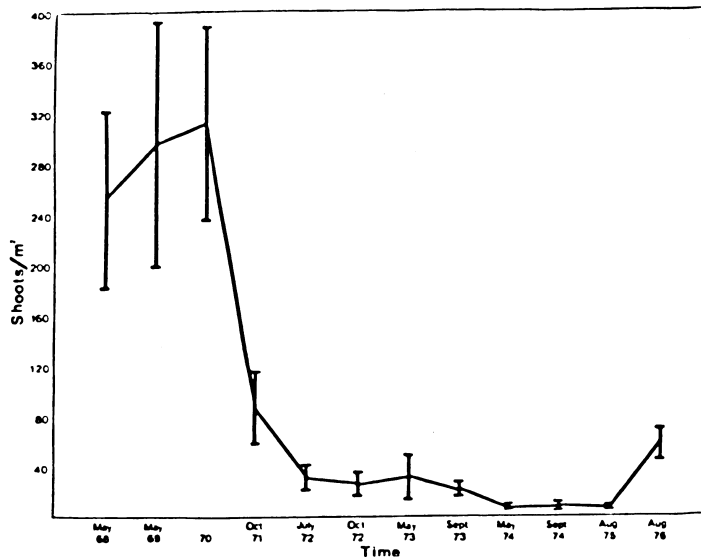


Figure 15. Effect of continuous sheep grazing on leafy spurge shoot density [from Bowes and Thomas (7) used with permission from J. Range Manage.]

Integrated weed control usually is perceived as using a multiplicity of control methods such as tillage, choice of crop, and herbicide application for the control of a weed or a complex of weeds in a specific crop. Integration at this level usually involves the appropriate implementation of different control methods over time in the same area (18, 25, 33, 36). Little attention has been directed toward integrating weed-feeding insects into these types of weed management programs and because of the living nature of the biological control agent, special considerations of the requirements of the organism must be met (2). As the biological control program for leafy spurge expands, unique opportunities to develop truly integrated systems may occur.

Integration can also include the use of one method in one area and the other methods in other areas infested with the weed (2). This integration in space would appear to be the most logical approach for leafy spurge control in North America. The recognized advantages and limitations of each method can then be utilized to maximize the negative effects on leafy spurge, with minimal adverse effects on other aspects of the system.

An integrated system for leafy spurge initially should concentrate on the small localized patches and on the fringe areas of the vast spurge infestations. It is from these small patches and the leading edges of the larger infestations that the greatest threat of spread occurs (see Chapter 1). Herbicides, such as picloram, provide excellent control of spurge and would be the control method of choice for the attempted eradication of small patches and the containment and constriction of present infestations. The benefits of the widespread use of picloram over large areas of marginally productive grassland is questionable. Because of the relative ease of controlling leafy spurge in cropland, any infestations on tillable land should be cultivated and the selected crop grown and managed to the detriment of leafy spurge. The characteristics of the weed and its widespread and abundant presence over vast areas of pasture and rangeland make leafy spurge a prime candidate for biological control. Biological control appears to be the only logical, long-term solution for the large infestations of leafy spurge in North America. Research in biological control of leafy spurge must be intensified, and more agents need to be evaluated. The simulation of spurge control presented in this chapter (Figure 9) suggests that biotic

agents that affect seed production should not be prime candidates for biological control research. It must be remembered that the development of biological control will take time, with 20 or more years required even if the program is successful. Although limited in area of application, intensive management of sheep could provide effective spurge control in some situations and should be considered where applicable.

The control components of the leafy spurge system discussed above must be accompanied by increased public awareness of the problem, improved legislation to assist in preventing further spread, and increased involvement of government agencies, with major emphasis on control and eradication of spurge on public right-of-ways. Substantial information has been accumulated on the biology and control of leafy spurge, but further research is required in such areas as repeated applications of lower rates of herbicides, biological control, spurge taxonomy and root bud dynamics. The leafy spurge problem is a formidable, expanding challenge that requires an intensified effort of all concerned to develop and implement an integrated system that ultimately will result in the control of this aggressive weed.

Acknowledgments

I wish to acknowledge the assistance of Daniel Cloutier and Sheila Forsyth in the development of the model and Daniel Cloutier for the computer program and for his comments and suggestions concerning the simulations. The assistance of Neilda Sterkenburg and André Virly in the preparation of the illustrations is appreciated.

Literature cited

1. Allen, G.E. and J.E. Bath. 1980. The conceptual and institutional aspects of integrated pest management. *Bioscience* 30:658-664.
2. Andres, L.A. 1982. Integrating weed biological control agents into a pest-management program. *Weed Sci.* 30(suppl.):25-30.
3. Bakke, A.L. 1936. Leafy spurge, *Euphorbia esula* L. *Iowa Agric. Exp. Stn. Res. Bull.* 198:209-246.
4. Best, K.F., C.G. Bowes, A.G. Thomas, and M.G. Maw. 1980. The biology of Canadian weeds. 39. *Euphorbia esula* L. *Can. J. Plant Sci.* 60:651-663.
5. Bowes, C. and E.S. Molberg. 1975. Picloram for the control of leafy spurge. *Can. J. Plant Sci.* 55:1023-1027.
6. Bowes, G.G. and A.G. Thomas. 1978. Leafy spurge (*Euphorbia esula* L.) control based on a population model. *Proc. 1st Int. Rangeland Congr.*:254-256.
7. Bowes, C.G. and A.G. Thomas. 1978. [Longevity of leafy spurge seeds in the soil following various control programs](#). *J. Range Manage.* 31:137-140.
8. Coupland, R.T. and J. F. Alex. 1955. Distribution of vegetative buds on the underground parts of leafy spurge (*Euphorbia esula* L.). *Can. J. Agric. Sci.* 35:76-82.
9. Coupland, R.T., G.W. Selleck, and J. F. Alex. 1955. The reproductive capacity of vegetative buds on the underground parts of leafy spurge (*Euphorbia esula* L.). *Can. J. Agric. Res.* 35:477-484.
10. Derscheid, L.A. and L.J. Wrage. 1972. Leafy Spurge. *South Dakota State Univ. Ext. FS 449.* 4 pp.
11. Hanson, H.C. 1934. Leafy spurge. *North Dakota Agric. Coll., Agric. Exp. Stn. Circ.* 55. 4 pp.

12. Hanson, H.C. and V.E. Rudd. 1933. Leafy spurge life history and habits. North Dakota Agric. Coll., Agric. Exp. Stn. Bull. 226. 24 pp.
13. Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York, 892 pp.
14. Harper, J.L. and J. White. 1974. The demography of plants. Annu. Rev. Ecol. Syst. 5:419-463.
15. Jeffers, J.N.R 1978. An introduction to systems analysis: with ecological applications. University Park Press, Baltimore, 198 pp.
16. Krupinsky, J.M. and R.J. Lorenz. 1983. An *Alternaria* sp. on leafy spurge (*Euphorbia esula*). Weed Sci. 31:86-88.
17. McMahon, D.J. and A.M. Mortimer. 1980. The prediction of couch infestations – a modeling approach. Proc. 1980 Brit. Crop Prot. Conf. – Weeds:601-608.
18. McWhorter, C.G. and W.C. Shaw. 1982. Research needs for integrated weed management systems. Weed Sci. 30(suppl.):40-45.
19. Morrow, L.A. 1979. [Studies on the reproductive biology of leafy spurge](#). Weed Sci. 27:106-109.
20. Mortimer, A.M., D.J. McMahon, R.J. Manlove, and P.D. Putwain. 1980. The prediction of weed infestations and cost of differing control strategies. Proc. 1980 Brit. Crop Prot. Conf. – Weeds:415-423.
21. Mortimer, A.M., P.D. Putwain, and D.J. McMahon. 1978. A theoretical approach to the prediction of weed population sizes. Proc. 14th Brit. Weed Control Conf.:467-474.
22. Noble, D.L., P.H. Dunn, and L.A. Andres. 1979. [The leafy spurge problem](#). Pages 8-15 in Proc. Leafy Spurge Symposium, North Dakota Coop. Ext. Serv., Fargo. 84 pp.
23. Orwick, P.L., M.M. Schreiber, and D.A. Holt. 1978. Simulation of foxtail (*Setaria viridis* var. *robusta-alba*, *Setaria viridis* var. *robusta-purpurea*) growth: the development of SETSIM. Weed Sci. 26:691-699.
24. Palmblad, I.G. 1968. Competition studies on experimental populations of weeds with emphasis on the regulation of population size. Ecology 49:26-34.
25. Quimby, P.C. Jr. and H.L. Walker. 1982. Pathogens as mechanisms for integrated weed management. Weed Sci. 30(suppl.):30-34.
26. Reilly, W. and K.R. Kaufman. 1979. The social and economic impact of the leafy spurge in Montana. Pages 21-24 in Proc. Leafy Spurge Symposium, North Dakota Coop. Ext. Serv., Fargo, 84 pp.
27. Sagar, G.R. 1970. Factors controlling the size of plant populations. Proc. 10th Brit. Weed Control Conf.:965-979.
28. Sagar, G.R. and A.M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Appl. Biol. 1:1-47.
29. Sarukhan, J. and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. J. Ecol. 62:921-936.
30. Schreiber, M.M. 1982. Modeling the biology of weeds for integrated weed management. Weed Sci. 30(suppl.):13-16.
31. Schroeder, D. 1980. Investigations on *Oberea erythrocephala* (Schrank) (Col.: Cerambycidae), a possible biocontrol agent of leafy spurge, *Euphorbia* spp. (Euphorbiaceae) in Canada. Z. Angew. Entomol. 90:237-254.
32. Selleck, G.W., R.T. Coupland, and C. Frankton. 1962. [Leafy spurge in Saskatchewan](#). Ecol. Monogr. 32:1-29.
33. Shaw, W.C. 1982. Integrated weed management systems technology for pest management. Weed Sci. 30(suppl.):2-12.

34. Thomas, A.G. and G. Bowes. 1976. An estimation of leafy spurge seed rain within and beyond a patch. Pages 561-563 in Canada Weed Committee – Western Section, Research Report. 604 pp.
35. Usher, M. B. 1972. Developments in the Leslie matrix model. Pages 29-60 in J.N.R. Jeffers, ed. Mathematical Models in Ecology. 12th Symp. Brit. Ecol. Soc. Blackwell Sci. Publ., Oxford. 398 pp.
36. Walker, R.H. and G.A. Buchanan. 1982. Crop manipulation in integrated weed management systems. Weed Sci. 30(suppl.):17-24.
37. Williamson, M. H. 1967. Introducing students to the concepts of population dynamics. Pages 169-176 in J. M. Lambert, ed. The Teaching of Ecology. Blackwell Sci. Publ., Oxford, 294 pp.
38. Wilson, F. 1964. The biological control of weeds, Annu. Rev. Entomol. 9:225-243.
39. Zwölfer, H. 1973. Possibilities and limitations in biological control of weeds. OEPP/EPPO Bull. 3:19-30.