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Application of Modelling to Biological Weed Control

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Abstract

The type of model that can incorporate dynamic demographic information and take into consideration the various plant growth stages is the modified Leslie matrix model. The amount of stress inflicted by biocontrol agents on distinct plant growth stages can easily be integrated in such models. Its use is illustrated in the evaluation of the biocontrol of *Centaurea diffusa* and *C. maculosa* in North America. The model predicts that 99.5% control of seed production is required to reduce diffuse knapweed infestations. Other predictions are made where both seed and seedling control are considered. The forecasts made by the model follow reported trends in the field and prove that this type of approach would be of greatest benefit if it was included in the early phases of the development of biological weed control programs.

Introduction

Biological weed control programs are by nature long-term (Harris 1986) and are subject to periodic review. There is often limited additional empirical information available between project evaluations because of the usually slow rate of establishment and spread of biological control agents. Harris (1985) mentioned that it is currently difficult or nearly impossible to predict the level of control required to reduce a weed infestation level or to establish the effective level of a specific agent. We suggest that a simple demographic model of the target weed should be developed early in a biological weed control program to help solve these problems. Such a model could help predict the repression level required to control the weed population. Also, this model could forecast the impact of potential biological control agent(s) against a specific weed thereby making the selection of appropriate agents less risky (Myers 1985). In the context of evaluating a biological weed control program, a model could either help explain the lack of noticeable effects on a weed population or provide reference levels to compare observed population reductions.

Models are useful tools because they provide a precise, concise, and simplified description of a population and of the mechanisms that regulate it. The development of models usually increase understanding of the processes affecting a population, helps in organizing the available information, and helps identify knowledge gaps (Cousens *et al.* 1987).

The purpose of this work was to demonstrate the feasibility and usefulness of demographic models of weeds and their application in the development and evaluation of biological weed control programs.

Modified Leslie Matrix Model

One of the most useful and simple demographic models used in plant population studies is the modified Leslie matrix model. It relies on the use of life-tables where individuals are classified by age and/or development stage (Mortimer 1983). The properties of this model will be reviewed and examples of its application for the control of knapweeds (*Centaurea* spp.; Asteraceae) will be presented.

Plant population processes can be presented as a simple algebraic equation that describes the change in numbers of a population between two points in time:

$$N_{t+1} = N_t + B - D + I - E \qquad (1)$$

where N = the number of individuals;
t = time;
B = the number of new individuals produced between t and t+1 (fecundity);
D = the number of individuals that died between t and t+1 (mortality);
I = the number of individuals that immigrated into the area; and
E = the number of individuals that left the area through emigration.

Since most studies cannot include the whole population of a species, this equation is usually based on densities rather than absolute numbers and N is expressed on a m^{-2} or other area basis (Begon and Mortimer 1981). Equation 1 is very general and must be converted to a form that reflects the complexities of plant populations in the field (Begon and Mortimer 1981). Sagar and Mortimer's (1976) diagrammatic life-table incorporated the diversity of plant life cycles. The plant population is separated into classes of plant stages (seeds, buds, seedlings, and adults) for which numbers are assessed at the beginning and end of each time period. The mortality and fecundity of each of the classes change with their age. It is a simple matter to express in algebraic terms the changes in numbers of individuals changing class. For example:

$$N_{t+1} = N_t{*}p_1{*}p_2{*}p_3{*}p_4{*}p_5{*}f \qquad (2)$$

where p = the proportion of the individuals that reach the next stage;
N_{t+1} = the number of seeds at time t+1;
N_t = the number of seeds at time t;
p_1 = seeds that survive;
p_2 = seeds that germinate;
p_3 = individuals that establish seedlings;
p_4 = individuals that survive to maturity;
p_5 = individuals that survive to produce seeds; and
f = number of seeds produced.

This is a simplified example but the principles remain the same for more complex situations where fecundity and surviving proportions might change with density, growth stage, and individual size as a function of time. The number of algebraic expressions increase as the number of equations and classes increase, and they become more difficult to manage. Matrix algebra allows the use of the same equations but in a more compact and simpler form:

$$A{*}\,a_t = a_{t+1} \qquad (3)$$

where a_t is a column vector representing the population stage structure at time t; and
A is a matrix representing the proportion of individuals changing class (survival) and the production of new individuals (fecundity) (Usher 1972).

It is called a transition matrix and is referred to as a modified Leslie matrix (Mortimer 1983, Usher 1972).

Modified Leslie matrix models have been used in several plant population studies where the plant stages were separated in classes such as seeds, seedlings, immature plants, mature plants, and flowering plants, with overwintering buds for perennials, and in some cases with size classes (McMahon and Mortimer 1980, Mortimer 1983). These models are frequently used because they are simple, concise, do not require extensive mathematical knowledge, and have well known properties (Usher 1972).

The models using modified Leslie matrices rely on demographic studies to obtain estimates of the parameters used in the matrix. The modelling process and the use of modified Leslie matrices will be illustrated using two weeds that have been the subject of intensive biological control studies in the last two decades.

Modelling of Diffuse and Spotted Knapweed

Diffuse knapweed (*Centaurea diffusa* Lamarck) and spotted knapweed (*Centaurea maculosa* Lamarck) are herbaceous weeds introduced from Europe and/or Western Asia into North America. These knapweeds are dominant rangeland and pasture weeds in British Columbia, Washington, Oregon, Idaho, and Montana (Maddox 1979, Watson and Renney 1974). Spotted knapweed is also a problem weed in parts of eastern Canada and the northeastern United States. Diffuse and spotted knapweed, although not poisonous to grazing animals, are of major economic importance because they rapidly invade rangeland and pasture habitats replacing desirable forage species.

Different control strategies have been attempted for diffuse and spotted knapweed with varying degrees of success (Watson and Renney 1974). It is apparent that the only long-term solution over most of the range of these introduced species will be biological control (Maddox 1979, 1982, Harris and Cranston 1979). Significant progress has been made towards biological control of diffuse and spotted knapweed (Harris 1980*a*,*b*, Harris and Myers 1984, Maddox 1982, Story *et al.* 1987). The two seed head flies introduced from Europe, *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae), are well established on knapweed and broadly distributed over much of the knapweed range in western North America. Other biological control agents, including *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae), *Sphenoptera jugoslavica* Obenberger (Coleoptera: Buprestidae), and *Agapeta zoegana* L. (Lepidoptera: Cochylidae) have also been established on some knapweed populations in western North America. Additional insects and rust fungi (*Puccinia* spp.; Uredinales) (Watson and Clement 1986) are being investigated as possible biological control agents for diffuse and spotted knapweed.

The effect of the two *Urophora* flies has been a reduction of approximately 80-94% of seed production of both knapweed species (Harris 1980*b*, Harris and Myers 1984, Roze 1981). The quantity of seeds not destroyed is more than adequate to maintain knapweed populations in western North America and therefore additional agents are required if knapweed populations are to be reduced. In most instances the effects of the other released biological control agents on diffuse and spotted knapweed populations have not been documented, but Harris (pers. comm., 1987) suggests that each agent, in addition to the *Urophora* flies, reduces seed production by one half. Harris and Cranston (1979) have previously estimated that six established biological control agents would be necessary to reduce knapweed densities.

A comprehensive knowledge of the biology and population dynamics of the target weeds is essential for the development of a model. Demographic and population dynamics information for diffuse and spotted knapweed can be obtained from the literature and utilized in the models although it is incomplete (Berube and Myers 1982, Boggs and Story 1987, Chicoine and Fay 1984, Myers and Berube 1983, Roze 1981, Schirman 1981, Watson 1972, Watson and Renney 1974). The life cycles of diffuse and spotted knapweed as considered in the models developed here are presented in Figure 1. The demographic information for both species is presented in Table 1.

Diffuse knapweed was used to illustrate the use of modified Leslie matrices as an example. The following plant growth stages were used in the column vector:

$$a_t = \begin{bmatrix} \text{number of seeds} \\ \text{number of seedlings} \\ \text{number of rosettes} \\ \text{number of vernalized rosettes} \\ \text{number of flowering shoots} \end{bmatrix}$$

where rosettes are produced in the first year, are vernalized over winter, and flower the following season. The transition matrices have the following general appearance:

$$A_i = \begin{bmatrix} P & F & F & F & F \\ T & P & O & O & O \\ O & T & P & O & O \\ O & O & T & P & O \\ O & O & O & T & P \end{bmatrix}$$

where A_i is the transition matrix for the i^{th} time period;
P is the proportion of either seeds, seedlings, rosettes, vernalized rosettes, or flowering shoots surviving to the next time period;
T is the proportion of plant growth stage classes reaching the next classes; and
F is the fecundity of the various plant growth stage classes.

Five time periods were used: winter, spring, summer, late-summer/early-fall, and fall. The transition matrices are presented in Figure 2. The parameter values used are averages or estimates and should not be considered absolute. To simulate the populations changes in time, the transition matrix is multiplied by the column vector to obtain the next column vector:

$$* \; a_{i,\,t} = a_{i+1,\,t}$$

where i stands for the i^{th} time period listed above. For diffuse knapweed:

$$A_1 * a_{1,t} = a_{2,t} ,$$

where A_1 is the winter transition matrix and $a_{1,t}$ the population vector at the beginning of winter,

$$A_2 * a_{2,t} = a_{3,t} ,$$

where A_2 is the spring transition matrix and $a_{2,t}$ the population vector at the beginning of spring, and so on.

However,

$$A_5 * a_{5,t} = a_{1,t+1} ,$$

because there are five transition matrices. The new column vector is the following year's column vector ($a_{1,t+1}$ rather than $a_{6,t}$). This last column vector then contains the number of seeds, seedlings, rosettes, vernalized rosettes, and flowering shoots after one year of growth.

Simulations

For all simulations, maximum values were specified for each class of plant growth stage in the model to have a more realistic population response. For diffuse knapweed, the maxima were set at 150,000 seeds, 1,000 seedlings, 400 rosettes, 400 vernalized rosettes, and 50 flowering shoots/m^2. For spotted knapweed, the maxima were: 100,000 seeds, 1,000 seedlings, 400 rosettes, 400 vernalized rosettes, 100 flowering shoots, 500 crown buds, and 500 vernalized crown buds. The initial column vector for all the simulations done in this work was the fall column vector (beginning of winter) and, unless stated otherwise, had a starting seed density of 100 seeds/m^2 and no seedlings, rosettes, or flowering shoots. This decision was arbitrary and any time-period vector could have been used as a starting point although spring or fall values are more indicative. All simulations were done for a period of 25 years.

The first simulation was done to observe the number of seeds produced in an uncontrolled diffuse knapweed population originating from either 1 or 100 seeds/m^2 (Fig. 3). The reduction in seed number between years 2 and 3 for the population originating from a 100 seeds/m^2 and between years 4 and 5 for the other population is caused by the biennial life cycle of this species. The variation disappears as the population reaches the carrying capacity. The 100 fold difference in initial infestation level resulted in only a two year lag before the population reached the carrying capacity, demonstrating the reproductive capacity of diffuse knapweed.

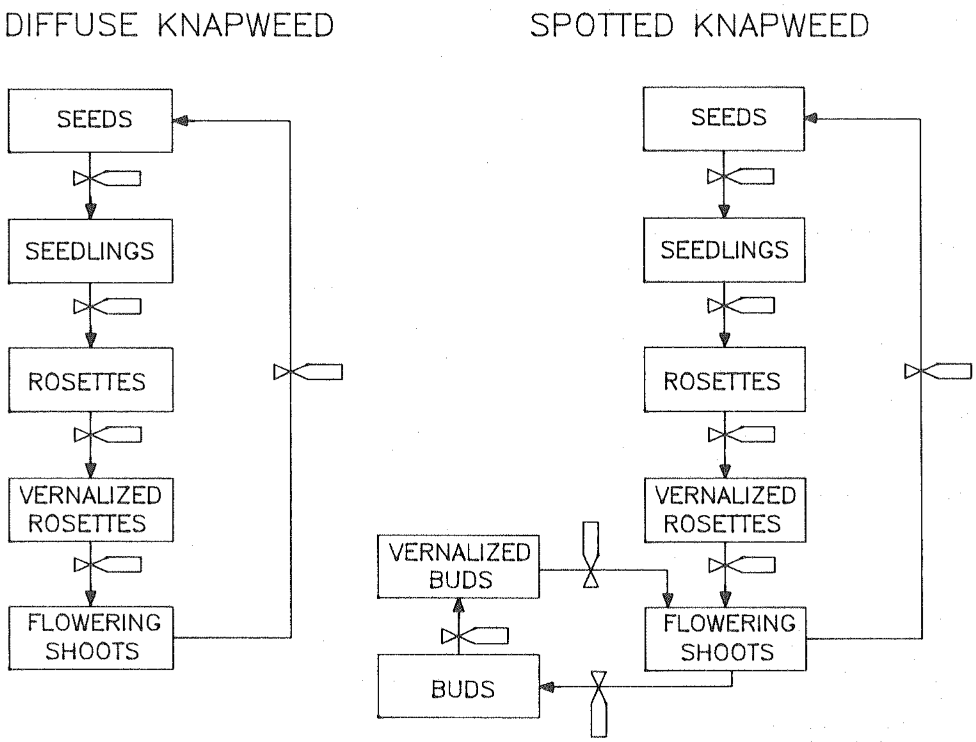

Figure 1. Diagrammatic life cycle of diffuse and spotted knapweed.

The next two simulations forecast the effects of different levels of seed production control over time (Figs. 4 and 5). The control levels were 0, 40, 60, 94 and 96% (Fig. 4) and 99.1-99.6% (Fig. 5). They correspond to different levels of seed destruction by biological control agents. In general, as observed in the field, in spite of substantial seed reduction, a sufficient number of seeds remain to maintain knapweed infestations (Harris and Myers 1984). Diffuse knapweed populations are reduced when there is >99.5% control of seed production (Fig. 5). Levels of seed control above 99.1% will stabilize the diffuse knapweed seed population at levels below 700 seeds/m^2. This level of control, however, to our knowledge, has never been reported in the literature.

The level of control achieved by *Urophora* spp. is reported to be up to 94% (Harris and Myers, 1984). A simulation was done to see the combined effect of biological control agents attacking different plant parts such as seeds and seedlings (Fig. 6). The hypothesis was that a combination of agents might increase the pressure on the weed population. According to our model, approximately 90% of the seedlings would have to be destroyed in order to stabilize the population under 500 seeds/m^2. This value is very high and it is impossible to verify its validity at the present time. According to this prediction, an agent that affects seedlings will have to destroy a large proportion of the seedlings to show any measurable effect.

The life cycle of diffuse and spotted knapweed are similar with the exception that knapweed produces crown buds (Fig. 1). Results of simulations for spotted knapweed were similar to diffuse knapweed results and therefore are not presented. Spotted knapweed is a perennial that reproduces mostly by seeds although some crown buds are produced and give rise to flowering shoots. The final simulation predicts the unlimited growth of spotted knapweed with or without the contribution of crown buds. According to the model, the presence of crown buds only contributed an additional 1.5% of seed production (Fig. 7). Therefore, insects that attack crown buds should be given low priority in a biological weed control program.

Table 1. Demographic information on diffuse and spotted knapweed.

Centaurea diffusa	*Centaurea maculosa*
Winter	
95% of seeds survive the winter 0.01% of seedlings survive the winter 87% of the rosettes are vernalized and survive 0.1% of the vernalized rosettes survive the winter	95% of seeds survive the winter 0.01% of seedlings survive the winter 87% of the rosettes are vernalized and survive 0.1% of the vernalized rosettes survive the winter 95% of crown buds survive and become vernalized 0.1% of vernalized crown buds survive a subsequent winter
Spring	
35% of seeds survive the spring 60% of seeds germinate 80% of seedlings survive the spring 7% of seedlings produce rosettes 87% of vernalized rosettes survive the spring 0.1% of the vernalized rosettes produce shoots	35% of seeds survive the spring 60% of seeds germinate 80% of seedlings survive the spring 7% of seedlings produce rosettes 86% of vernalized rosettes survive the spring 0.1% of the vernalized rosettes produce shoots 80% of vernalized crown buds survive the spring 15% of vernalized crown buds establish flowering shoots
Summer	
89% of seeds survive the summer 10% of seeds germinate 10% of seedlings survive the summer 40% of seedlings establish rosettes 87% of rosettes survive the summer 5% of vernalized rosettes survive the summer 80% of vernalized rosettes produce flowering shoots 95% of flowering shoots survive the summer Flowering shoots produce 50 seeds	89% of seeds survive the summer 10% of seeds germinate 10% of seedlings survive the summer 40% of seedlings establish rosettes 87% of rosettes survive the summer 5% of vernalized rosettes survive the summer 80% of vernalized rosettes produce flowering shoots 95% of flowering shoots survive the summer 90% of vernalized crown buds produce flowering shoots Flowering shoots produce 50 seeds Flowering shoots produce 0.5 crown buds
Late Summer/Early Fall	
95% of seeds survive this period 1% of seeds germinate 10% of seedlings survive this period 40% of seedlings establish rosettes 87% of rosettes survive this period 0.1% of vernalized rosettes survive this period 80% of vernalized rosettes produce flowering shoots 95% of flowering shoots survive this period Flowering shoots produce 750 seeds	95% of seeds survive this period 1% of seeds germinate 10% of seedlings survive this period 40% of seedlings establish rosettes 87% of rosettes survive this period 0.1% of vernalized rosettes survive this period 80% of vernalized rosettes produce flowering shoots 95% of flowering shoots survive this period 95% of crown buds survive this period Flowering shoots produce 275 seeds Flowering shoots produce 0.5 crown buds
Fall	
95% of seeds survive the fall 1% of seeds germinate 5% of seedlings survive the fall 40% of seedlings establish rosettes 87% of rosettes survive the fall 0.1% of vernalized rosettes survive the fall 95% of flowering shoots survive the fall Flowering shoots produce 350 seeds	95% of seeds survive the fall 1% of seeds germinate 5% of seedlings survive the fall 40% of seedlings establish rosettes 87% of rosettes survive the fall 0.1% of vernalized rosettes survive the fall 95% of flowering shoots survive the fall 95% of crown buds survive the fall Flowering shoots produce 175 seeds Flowering shoots produce 0.5 crown buds

Conclusions

The values obtained in the course of the simulations using the knapweed models do follow the same trends reported in the literature (Harris and Myers 1984). The numbers presented here, however, are not as important as the demonstration that modified Leslie matrix models are very simple to develop and to use. Also, despite their simplicity, they can be used to forecast complex situations as illustrated above. An added advantage of this type of model is that it can easily be modified as new values become available and it can be customized for specific areas or situations.

Leslie matrix models have long been used by entomologists to predict insect population levels (Usher 1972). Models of biological control agents could be developed and coupled to plant models to achieve more precise predictions. The probabilities of certain events or processes taking place in the population of the biological control agent model or in the plant population model could be included. This could be simply done by using mean and variance values of the matrices parameters and by conducting Monte Carlo simulations. Parameters could be replaced by mathematical functions. For example, a regression equation could relate the changes in seed production with the plant density changes. The patchiness of the weed population, interference of other plant species. and the effect of various agricultural production practices such as tillage and mowing could also be included. In conclusion, this class of model can be as simple or as complex as required.

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diffusa Model

Winter

Seeds	0.95	0	0	0	0
Seedlings	0	0.0001	0	0	0
Rosettes	0	0	0	0	0
Rosettes*	0	0	0.87	0.001	0
Flower	0	0	0	0	0

Spring

Seeds	0.35	0	0	0	0
Seedlings	0.6	0.8	0	0	0
Rosettes	0	0.07	0	0	0
Rosettes*	0	0	0	0.87	0
Flower	0	0	0	0.001	0

Summer

Seeds	0.89	0	0	0	50
Seedlings	0.1	0.1	0	0	0
Rosettes	0	0.4	0.87	0	0
Rosettes*	0	0	0	0.05	0
Flower	0	0	0	0.8	0.95

maculosa Model

Seeds	0.95	0	0	0	0	0	0
Seedlings	0	0.0001	0	0	0	0	0
Rosettes	0	0	0	0	0	0	0
Rosettes*	0	0	0.87	0.001	0	0	0
Flower	0	0	0	0	0	0	0
Buds	0	0	0	0	0	0	0
Buds*	0	0	0	0	0	0.95	0.001

Seeds	0.35	0	0	0	0	0	0
Seedlings	0.6	0.8	0	0	0	0	0
Rosettes	0	0.07	0	0	0	0	0
Rosettes*	0	0	0	0.86	0	0	0
Flower	0	0	0	0.001	0	0	0.15
Buds	0	0	0	0	0	0	0
Buds*	0	0	0	0	0	0	0.8

Seeds	0.89	0	0	0	50	0	0
Seedlings	0.1	0.1	0	0	0	0	0
Rosettes	0	0.4	0.87	0	0	0	0
Rosettes*	0	0	0	0.05	0	0	0
Flower	0	0	0	0.8	0.95	0	0.9
Buds	0	0	0	0	0.5	0	0
Buds*	0	0	0	0	0	0	0

Late summer / early fall

Seeds	0.95	0	0	0	750
Seedlings	0.01	0.1	0	0	0
Rosettes	0	0.4	0.87	0	0
Rosettes*	0	0	0	0.001	0
Flower	0	0	0	0.80	0.95

Seeds	0.95	0	0	0	275	0	0
Seedlings	0.01	0.1	0	0	0	0	0
Rosettes	0	0.4	0.87	0	0	0	0
Rosettes*	0	0	0	0.001	0	0	0
Flower	0	0	0	0.8	0.95	0	0
Buds	0	0	0	0	0.5	0.95	0
Buds*	0	0	0	0	0	0	0

Fall

Seeds	0.95	0	0	0	350
Seedlings	0.01	0.05	0	0	0
Rosettes	0	0.4	0.87	0	0
Rosettes*	0	0	0	0.001	0
Flower	0	0	0	0	0.95

Seeds	0.95	0	0	0	175	0	0
Seedlings	0.01	0.05	0	0	0	0	0
Rosettes	0	0.4	0.87	0	0	0	0
Rosettes*	0	0	0	0.001	0	0	0
Flower	0	0	0	0	0.95	0	0
Buds	0	0	0	0	0.5	0.95	0
Buds*	0	0	0	0	0	0	0

Figure 2. Transition matrices of diffuse and spotted knapweed.

*** Vernalized.**

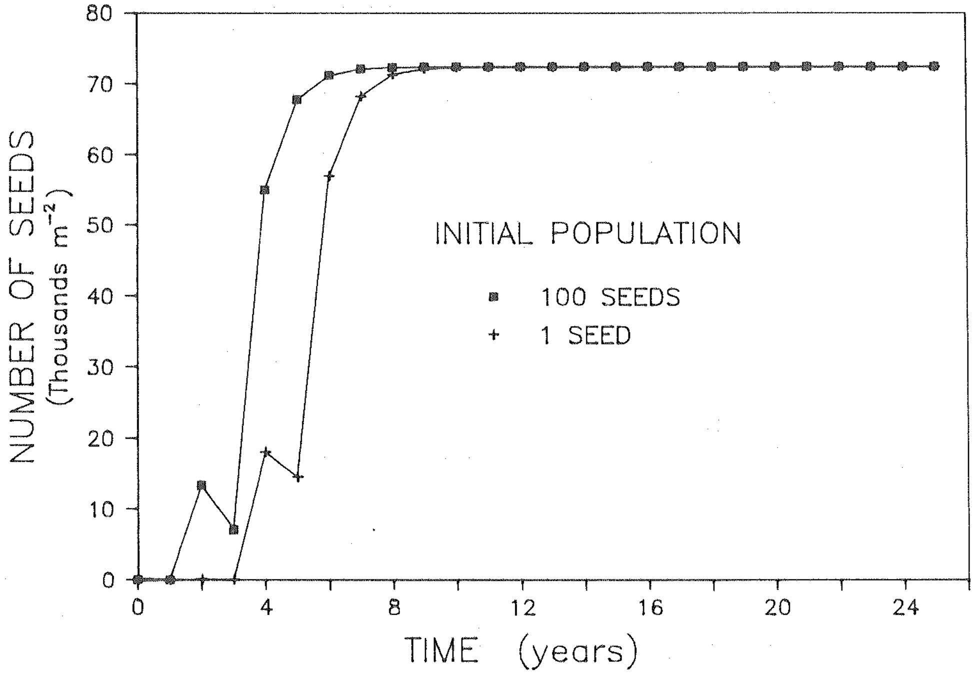

Figure 3. Simulated seed population changes in time of an uncontrolled diffuse knapweed infestation originating from either 1 or 100 seeds/m^2.

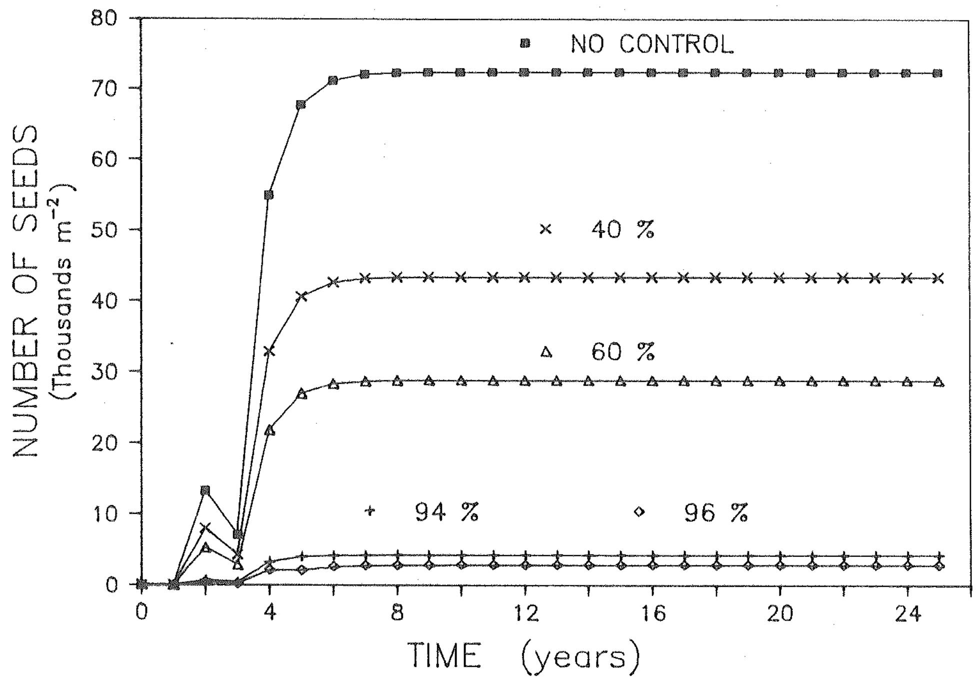

Figure 4. Simulated seed population changes in time of diffuse knapweed under 0, 40, 60, 94, and 96% control of seed production.

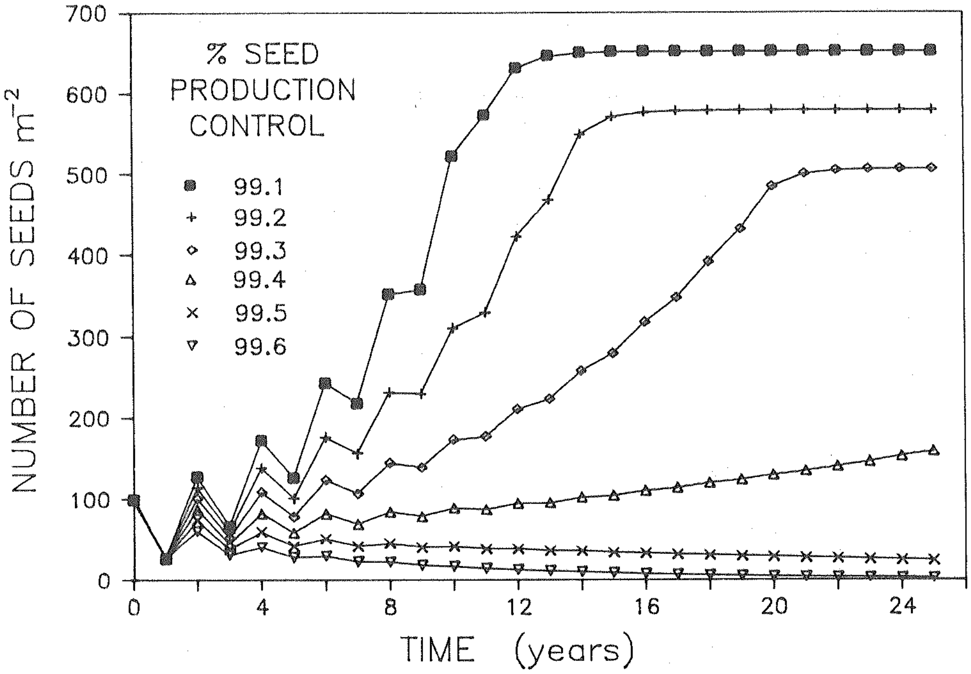

Figure 5. Simulated seed population changes in time of diffuse knapweed under 99.1-99.6% control of seed production.

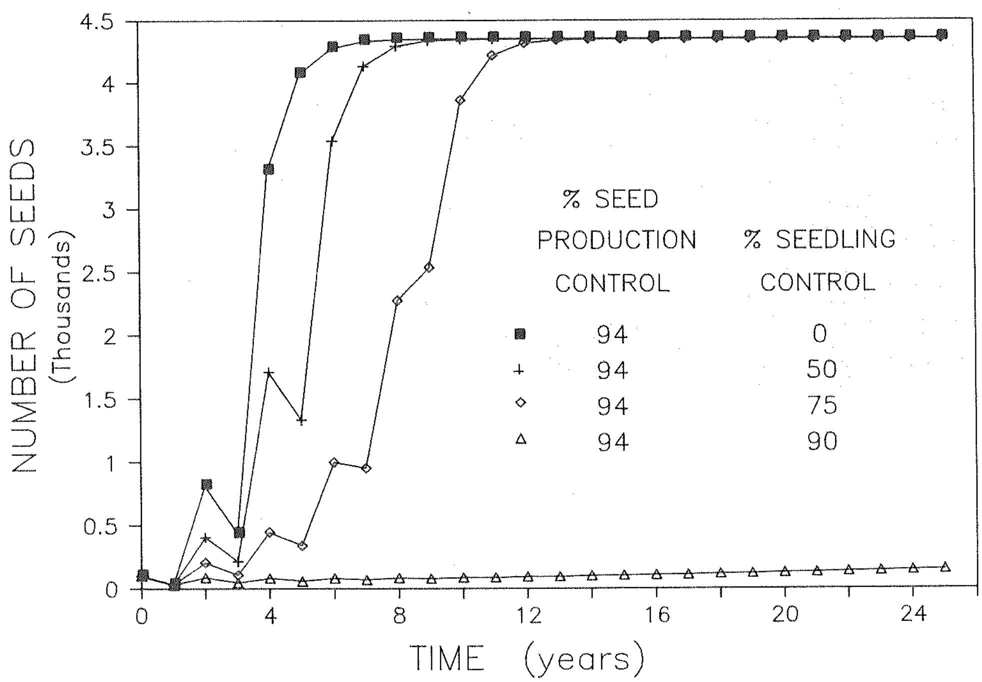

Figure 6. Simulation of the effects in time of biological control agents controlling 94% of seed production, and 0, 50, 75 and 90% of the seedling population, on the total seed population/m² of diffuse knapweed.

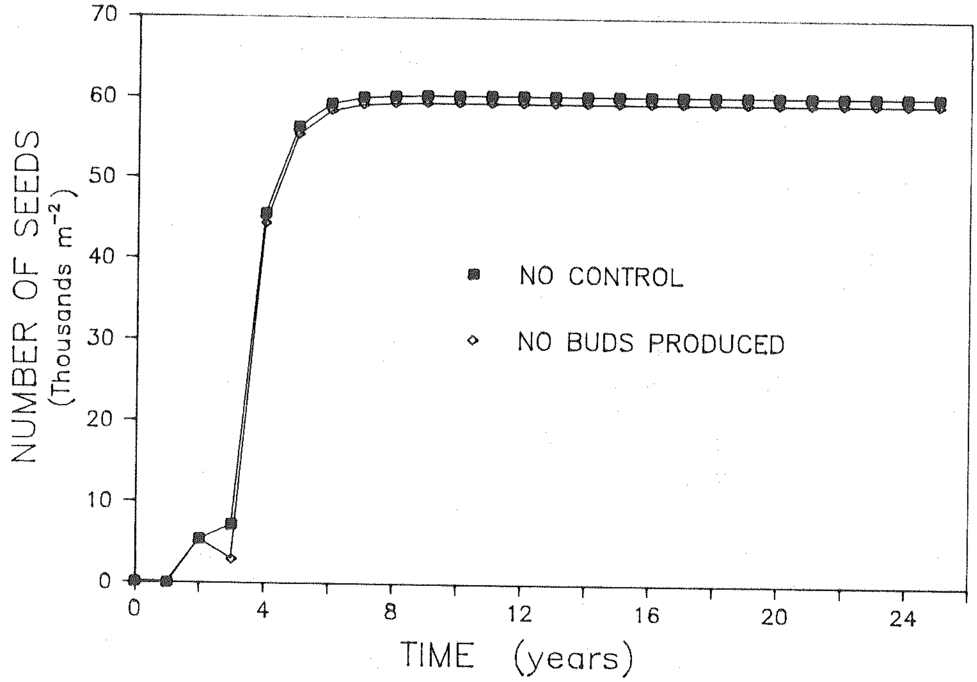

Figure 7. Simulation of seed population changes in time of an uncontrolled spotted knapweed population with or without the contribution of crown buds.

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