WEED ECOLOGY

Implications for Management

Second Edition

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John Wiley & Sons, Inc.
New York • Chichester • Weinheim • Brisbane • Singapore • Toronto

This text is printed on acid-free paper.

Library of Congress Cataloging in Publication Data

Radosevich, Steven R.
Weed ecology : implications for management / Steven Radosevich, Jodie Holt, Claudio Ghersa.—2nd ed.
p. cm.
ISBN 0-471-11606-8 (cloth : alk. paper)
1. Weeds—Ecology. 2. Weeds—Control. I. Holt, Jodie S. II. Ghersa, Claudio. III. Title.
SB611.R33 1996
581.6′52—dc20 96-19470
CIP

Printed in the United States of America
10 9 8 7 6 5 4 3

through time until a climax community similar, but not identical, to the original pristine one appears. If disturbance occurs repeatedly, as in the agricultural system by tillage and in forests by frequent fires, succession may become cyclic such that earlier stages are favored. For example, after logging or a severe forest fire, first herbaceous pioneers then intermediate shrub communities may dominate a site for decades or more, especially if it is frequently disturbed (see Figure 1.10). Similarly, in agriculture, dominance by herbaceous annual species usually delays the establishment of perennial species that normally would succeed the annuals. In these situations, herbaceous perennials appear to have lower competitive ability than annuals in the seedling stage, but greater persistence and stability associated with vegetative reproduction, and therefore have difficulty becoming established as seed. Once established, however, perennial species tend to replace annuals in the community.

Under the disturbed regime typical of agriculture, it is unnecessary for plant species to have different life history characteristics in order to replace earlier residents. Direct control of weeds is common on most farms and forest plantations, which provides an environment of continued disturbance. Thus, no difference in competitive ability needs to occur among weed species, since the earliest stage of succession is constantly being recycled. Replacement of weed species over time may occur at random or due to subtle year-to-year changes in meteorological conditions or management practices. However, the entire weed-crop community can respond to such management manipulations. These responses are usually short-term owing to the transitory nature of most cropping systems, but under some conditions long-term responses are possible. Once they have occurred, neither short- nor long-term responses are easily reversed, and both can have significant impacts on continued weed and crop management. These topics are discussed further in Chapters 3 and 4.

NICHE DIFFERENTIATION

Niche is a term used to describe a species' place within a community, including its place in the space, time, and function of that community. The concept of a niche denotes specialization. As Whittaker (1975) points out in his analogy of a niche to human society, an individual may gain from professional specialization to acquire the resources (income) needed to live. Two or more individuals may gain by following different specialties since they are not in direct competition, and society at large may gain if the specialization of one individual satisfies the needs of another. Thus, considerable evolutionary advantage must underlie the specializations of the plant species within any plant community. Through differential specialization, species avoid at least some degree of direct competition.

In order to understand the importance of niche separation in natural communities, and perhaps in managed ones, we must consider the logistic equation of Volterra (1926) and Lotka (1925). As described by Whittaker (1970), if environmental resources are not limiting, a population may increase geometrically, that is

$$dN/dt = rN \qquad \textit{(eq. 2.1)}$$

in which the rate of growth in numbers of individuals per unit time (dN/dt) equals the number of individuals (N) in the population at a given time, multiplied by r, the intrinsic rate of increase for that population in the absence of crowding or competition effects on growth. If environmental resources are limited, the growth rate of the population is continually lessened by competition as the number of individuals approaches the maximum number the environment can support. This maximum number is the carrying capacity of the environment, K. The logistic curve (Figure 2.6) generated from the following equation is a convenient first approximation for growth rate of a population to a ceiling level set by a limiting environment:

$$dN/dt = rN\,(K - N)/K \qquad \textit{(eq. 2.2)}$$

In the above equation, (K - N)/K specifies that population growth will be reduced as population number, N, approaches carrying capacity, K, and will be zero when N = K; the population is then stabilized at carrying capacity. The logistic equation now may be applied to two competing populations:

$$\frac{dN_1}{dt} = r_1N_1\,\frac{K_1 - N_1 - \alpha N_2}{K_1} \qquad \textit{(eq. 2.3)}$$

$$\frac{dN_2}{dt} = r_2N_2\,\frac{K_2 - N_2 - \beta N_1}{K_2} \qquad \textit{(eq. 2.4)}$$

In these equations, N_1 and N_2 are the populations of species 1 and 2 at a given time, r_1 and r_2 are their intrinsic rates of population increase, and K_1 and K_2 are the environmental resource limits (carrying capacities) for each species in the absence of the other. α and β are competition coefficients that express, through αN_2 and βN_1, the effects of the population level of one species on the population change of the other species. The equations imply that, for most values of α and β, one species increases while the other competitor declines, until at equilibrium the latter is extinct. This idea that two species cannot coexist permanently in the same niche is known as *Gause's competitive exclusion principle* (Gause, 1934).

Species that divide a shared resource among themselves are collectively called a *guild*. According to Gause's principle, if two species in a guild are direct competitors, one species should approach extinction. This suggests that the competitive relationships that nearly always develop between weeds and crop plants in crop production systems might be regulated to some extent by natural (competitive exclusion) processes. In the agricultural field where seeds or propagules are repeatedly introduced, the competitive exclusion principle would be manifest as extreme dominance or suppression of one species by another rather than local extinction. If, however, the species differ in their requirements or specializations,

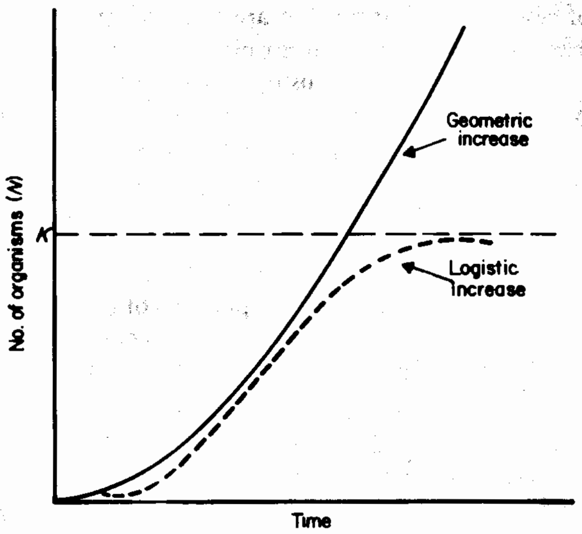


FIGURE 2.6 Geometric (solid line) versus logistic (dashed line) population growth over time. K is the carrying capacity of the environment for a population showing density-dependent logistic growth (dashed line). (From Barbour et al., 1987, by permission of the Benjamin Cummings Publishing Co., Inc., Menlo Park, CA.)

then it is possible for them to coexist. Because of niche separation, many natural systems are typified by a high degree of species diversity, coexistence, and uniform total productivity. In rangeland and forest systems, species diversity and uniform productivity are acceptable when coexistence of several species is the ultimate goal. In addition, because of the range of vegetation types often present in rangelands and forests, some spatial and temporal specializations are evident among particular weed and crop plants that would allow coexistence without significant reductions in productivity of desirable species. In contrast, when productivity of a single species is of concern, most of the environmental potential (resources) should be directed toward the crop; weed suppression, not coexistence, is the desired goal. Although some agricultural crops are superior competitiors compared to many weeds, it is not enough simply to allow them to compete with the hope of eventual weed suppression or even extinction since some loss in crop yield would inevitably occur over the time frame of a typical production season. Furthermore, the niche differences between weeds and agricultural crops usually are not great enough to allow maximum crop productivity to occur without some human intervention for weed control.

PATTERNS OF EVOLUTIONARY DEVELOPMENT

It is generally recognized that organisms are capable of budgeting energy or resources in order to complete their life cycle successfully. This process is called *resource allocation*. Allocation is closely linked to species survival, and the patterns of resource allocation that are retained are generally viewed as adaptations that minimize extinction. In plants, the resources available to a species must be divided among various organs and activities in order to complete the life cycle successfully. The amount of photosynthetic energy allocated to root, shoot, leaf, and reproductive portions and the amount of time (implied resources) spent in dormancy, growth, and maintenance are important attributes that govern plant species success. Figure 1.3a illustrates those major activities performed by annual plants that require resource allocation. Figure 1.3b illustrates those activities necessary for a perennial species. Several points of view are possible concerning the patterns of resource allocation that exist among species; however, these theories all recognize the importance of resource allocation for species survival and plant community development.

r and K Selection

The most widely held theory dealing with patterns of evolutionary development is that of r and K selection. This idea was derived from the logistic equation of population growth (Lotka, 1925; Voltera 1926, see page 56). As shown in Figure 2.6, population growth in an ideal (limitless) environment would be expected to increase geometrically, whereas in real (limited) environments growth declines as the population approaches K, or carrying capacity.

The theory of r and K selection, first proposed by MacArthur (1962) and later Pianka (1970, 1994), is that organisms lie on a continuum between two extremes of resource allocation that represent two strategies for survival. In the extreme cases, species may be r-selected or K-selected. Table 2.3 lists various traits associated with each strategy. Extreme K-selected species tend to be long lived, have a prolonged vegetative stage, allocate a small portion of biomass to reproduction, and occupy late stages of succession. The population size is near carrying capacity and is regulated by biotic factors. Extreme r-selection leads to a short-lived plant that occurs in open habitats and early stages of succession. A large portion of biomass is allocated to reproduction, and the population is regulated by physical factors. It should be noted that few plant species, if any, are entirely r-selected or K-selected. Most species represent a compromise between the two strategies. Weeds associated with agricultural lands and highly disturbed sites in forests and rangelands seem to fit most closely the characteristics of r-selection noted in Table 2.3.

C, R, and S Selection

Another theory concerning plant resource allocation and evolutionary pattern was proposed by Grime (1979), although this view may be regarded as an extension of the more widely acknowledged r and K continuum. Grime proposed that there are two basic external factors that limit the amount of plant material in an environment: stress and disturbance. He defined *stress* as

TABLE 2.3 Traits of r and K Selection

Trait	*r Selection*	*K Selection*
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic; density-independent	Density-dependent
Survivorship	Mortality at early age	Continuous mortality through life span or more as age increases
Population size	Variable in time; not in equilibrium; usually well below carrying capacity of the habitat; recolonization each year	Fairly constant in time; in equilibrium; at or near carrying capacity of the habitat; no recolonization necessary
Intraspecific and interspecific competition	Variable; often lax	Usually keen
Life span	Short, usually less than one year	Long, usually more than one year
Selection favors	Rapid development; early reproduction; small body size; single reproduction period in life span	Slower development; greater competitive ability; delayed reproduction; larger body size; repeated reproduction periods in life span
Overall result	Productivity	Efficiency

Source: Pianka, 1994.

external factors that limit production, such as reduced or limiting light intensity, water availability, nutrients, or suboptimal temperature. *Disturbance* is the partial or total disruption of plant biomass, for example, by mowing, tillage, grazing, or fire. As with the r and K continuum, the spectrum of these two factors can vary widely, but if only the extremes of high and low stress and disturbance are considered, four possible combinations occur (see Table 1.5). Of these four combinations, only three possible evolutionary strategies are apparent: *ruderals, stress tolerators*, and *competitors*. The fourth possible combination, high stress and high disturbance (Table 1.5), creates an environment unsuitable for plant survival. Plants that fall into each of these strategies can be classified according to their common adaptations (Table 2.4, Figure 1.6).

Grime prefers to arrange the three evolutionary strategies into a triangular model (Figure 2.7) to describe the various equilibria between stress (I_s), disturbance (I_d), and competition (I_c). In this model C, R, and S represent the three extremes of specialization. Since few species have all the characteristics listed in

TABLE 2.4 **Some Characteristics of Competitive, Stress-tolerant, and Ruderal Plants**

	Competitive	*Stress-tolerant*	*Ruderal*
Morphology			
1. Life forms	Herbs, shrubs, and trees	Lichens, herbs, shrubs, and trees	Herbs
2. Morphology of shoot	High dense canopy of leaves; extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
3. Leaf forms	Robust, often mesomorphic	Often small or leathery, or needlelike	Various, often mesomorphic
Life History			
4. Longevity of established phase	Long or relatively short	Long to very long	Very short
5. Longevity of leaves and roots	Relatively short	Long	Short
6. Leaf phenology	Well-defined peaks of leaf production coinciding with period(s) of maximum potential productivity	Evergreens, with various patterns of leaf production	Short phase of leaf production in period of high potential productivity
7. Phenology of flowering	Flowers produced after (or more rarely, before) periods of maximum potential productivity	No general relationship between time of flowering and season	Flowers produced early in the life history
8. Frequency of flowering	Established plants usually flower each year	Intermittent flowering over a long life history	High frequency of flowering
9. Proportion of annual production devoted to seeds	Small	Small	Large
10. Perennation	Dormant buds and seeds	Stress-tolerant leaves and roots	Dormant seeds
11. Regenerative strategies*	V,S,W,B_s	V,B_r	S,W,B_s

TABLE 2.4 Continued

	Competitive	*Stress-tolerant*	*Ruderal*
Physiology			
12. Maximum potential relative growth rate	Rapid	Slow	Rapid
13. Response to stress	Rapid morphogenetic responses (root-shoot ratio, leaf area, root surface area) maximizing vegetative growth	Morphogenetic responses slow and small in magnitude	Rapid curtailment of vegetative growth, diversion of resources into flowering
14. Photosynthesis and uptake of mineral nutrients	Strongly seasonal, coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth
15. Acclimatization of photosynthesis, mineral nutrition and tissue hardiness to seasonal change in temperature, light, and moisture supply	Weakly developed	Strongly developed	Weakly developed
16. Storage of photosynthate and mineral nutrients	Most are rapidly incorporated into vegetative structure with some storage for growth the following season	Storage systems in leaves, stems and/or roots	Confined to seeds

Source: Grime, 1979.

* Key to regenerative strategies (11): V, Vegetative expansion; S, seasonal regeneration in vegetation gaps; W, numerous small wind-dispersed seeds or spores; B, persistent seed (s) or seedling (r) bank.

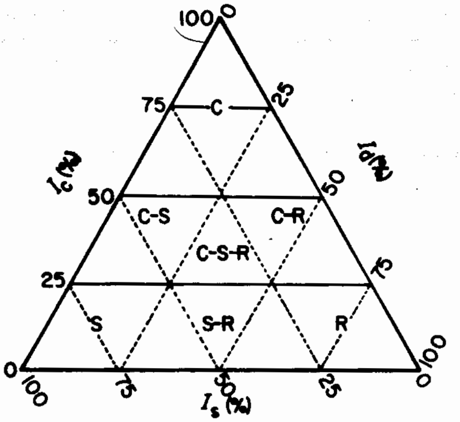


FIGURE 2.7 Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strateges. I_c, relative importance of competition; I_s, relative importance of stress; I_d, relative importance of disturbance. C, competitive strategy; S, stress-tolerant strategy; R, ruderal strategy; secondary (combination) strategies are discussed in the text. (From Grime, 1977, *American Naturalist* 111: 1169–1194. Copyright 1977 by University of Chicago.)

Table 2.4, Grime "maps" the species according to certain traits using triangular ordination. Although the indices for stress, disturbance, and competition are difficult to establish quantitatively, this procedure provides a tool to categorize plants according to life history and successional stage.

In terms of evolutionary strategy, many weeds possess characteristics common to both competitors and ruderals (Table 2.4). From Figures 2.7 and 1.7, it appears that many herbaceous annuals, biennials and certain herbaceous perennials follow a pattern of *competitive-ruderals.* Trees and shrubs, however, most closely follow the pattern of *stress-tolerant competitors* (see Chapter 1). Although Grime describes many other patterns of vegetation in relation to both life form and evolutionary strategy, it seems that these two classes warrant further investigation in order to characterize the nature of weediness. This aspect of weed evolution will be explored later in Chapter 3.

PLANT DEMOGRAPHY AND POPULATION DYNAMICS

Stages in the life history of plants provide the opportunity to assess how changes in population size or structure occur over time. These basic changes in plant life history are shown in Figure 2.8. Beginning with seeds, the population of seeds in the soil is generally referred to as a *seed bank*, or reservoir. Some seeds in this population germinate, graduate to the next stage and become *seedlings*, while others remain dormant in the reservoir or die. Seedlings that germinate at nearly the same time are a *cohort*, although agriculturists often refer to the phenomena as "flushes" of germination. *Recruitment* is the transi-

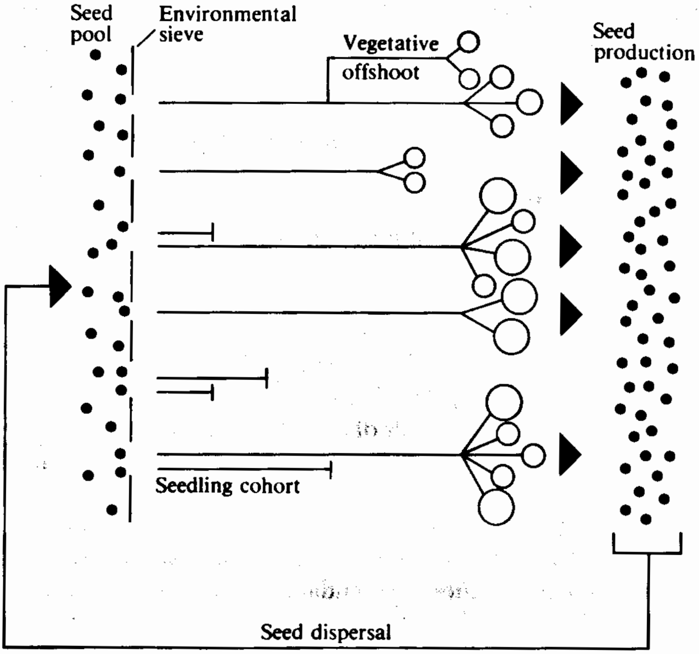


FIGURE 2.8 An idealized plant life history. (Adapted from Harper and White, 1971, in Silvertown, 1987).

tion from juvenile stages, seeds and seedlings, to adult form, in which independent existence and reproduction are possible. Seeds are a primary method of recruitment but vegetative reproduction also occurs in many plants. These vegetative offshoots, called *ramets* or *clones*, may remain attached to the "mother" plant or be separated from it. *Genets*, in contrast, are genetically distinct individuals that arise from a seed.

Plant demography is the statistical study of population changes and their causes throughout the life cycle (e.g., Figures 1.3 and 2.8). There are four basic demographic processes that determine how a population of plants changes over time:

- birth (B)
- death (D)
- immigration (I)
- emigration (E)

Population ecologists describe how these processes change the size of a plant population (N) between one time interval (t) and another (t + 1) by using the following difference equation:

$$N_{t+1} = N_t + B - D + I - E \quad \textit{(eq. 2.5)}$$

All experiments or analyses about the population dynamics of plants, weeds, crops, or natural systems ultimately come back to the above simple equation (Chapter 4).

Selection

Significant evolutionary change in a population occurs when three criteria are met: (a) there is phenotypic variation, (b) some of this variation is heritable, and (c) selection acts differentially upon the range of genotypes (Silvertown and Lovett Doust, 1993). This potential for evolutionary change is easily demonstrated in the grocery store or plant nursery. The wide array of cole crops (crops in the mustard family, Brassicaceae)—cabbage, broccoli, cauliflower, brussel sprouts, kohlrabi—is a result of artificial selection of the same ancestral species of wild plant, wild mustard, *Brassica campestris* (Silvertown and Lovett Doust, 1993). Similarly, all of the strains and varieties of roses originated from a common wild plant. Natural selection can produce results just as dramatic as artificial selection; the process is just not as rapid. Natural selection occurs when one phenotype leaves more descendants than others because of its superior ability to survive or produce offspring in a particular environment. When it is possible to analyze the demography (B, D, I, and E) of individual phenotypes, it becomes possible to determine which phenotypes are likely to leave the most offspring, and thus to determine the direction of natural selection.

Fitness

Because survival and reproduction are both demographic processes, natural selection is also a demographic process. *Fitness* is a single value of relative evolutionary success that combines both survival and reproduction. It is not fixed. Rather, fitness is determined within a particular environment or suite of ecological conditions and is relative to the success of other phenotypes that also exist in the same population. Fitness is an important factor in determining the ecological success of many, if not most, weed species.

SUMMARY

Plant ecology is the study of interrelationships between vegetation and its environment. It is through such study that new information about weeds and associated plants, crops, is generated. Furthermore, it is through application of plant ecological principles that land managers can begin to understand the nature of weediness and develop less costly, environmentally sound suppression tactics. Some general principles of ecology that are relevant to weed biology are environment, scale and hierarchical structure, community and niche differentiation, succession, evolutionary development, and plant demography. Environment is the summation of all living and nonliving factors that can affect the development or distribution of plants. The concept of scale, derived from hierarchy theory, explains how organisms are grouped or ordered in nature. A common ecological hierarchy is biome, ecosystem, community, species, population, and organism. Human social systems also can be ordered in a hierarchical manner, such as country, region, community, neighborhood, family, and individual. Ecological and human systems often interact in agroecosystems and it is these interactions that often determine relevant researchable questions in weed science. Plant communities can be both horizontally and vertically differentiated through space. Communities also change over time through the process of succession. Niche is a term used to describe a species' place in space, time, and function in a plant community. It is generally held that species, through differential specialization, avoid direct competition with one another, at least to some degree. The r and K continuum is a generally accepted theory regarding evolutionary development of most plant and animal species. The C, R, and S strategies are part of an alternate theory which is an extension of the r and K continuum. Within this structure, weed species may follow a combined strategy of either stress-tolerant competitors or competitive ruderals. Plant demography is the study of how plant populations change in size and structure during various stages of their life cycle. It is possible, using demographic principles, to assess how weed populations might change through time or respond to perturbations in their habitat or environment.

Chapter

4

Weed Demography and Population Dynamics

Population ecology is the branch of ecology that deals with the impact of the environment on a population, or group of individuals of a particular species occurring within a defined geographical area. In the case of weeds, populations are often selected by the tools or tactics designed to suppress them (Harper, 1956). Demography is the study of the numerical changes in a population through various stages of development. Analysis of these numbers can suggest reasons for changes in population size or species composition over time. The consequences of various management practices on a weed flora also can be determined through demographic study.

PRINCIPLES OF PLANT DEMOGRAPHICS

The life cycle is the fundamental descriptive unit of an organism. Specifically, an individual plant is the result of a series of processes that started at fertilization and continued through embryonic growth, seed germination, seedling establishment, development into adulthood, and finally senescence and death (Figures 1.3 and 2.8). Each of these processes occurs at a measurable, requisite rate. These *vital rates*, which form the basis of plant demography, describe a plant's development through its life cycle. The response of vital rates to the environment determines population dynamics in ecological time and evolution of life histories in evolutionary time.

By focusing on the vital rates of the life cycle, demography addresses both the dynamics and the structure of plant populations. The potential for exponential growth of groups of individuals is one fundamental fact of population dynamics (Figure 2.6). Another is that populations do not continue unrestricted growth for long (Figure 2.6), because the eventual resource limitation and biotic interactions curtail population growth until an equilibrium between birth rate and death rate is attained (Caswell, 1989).

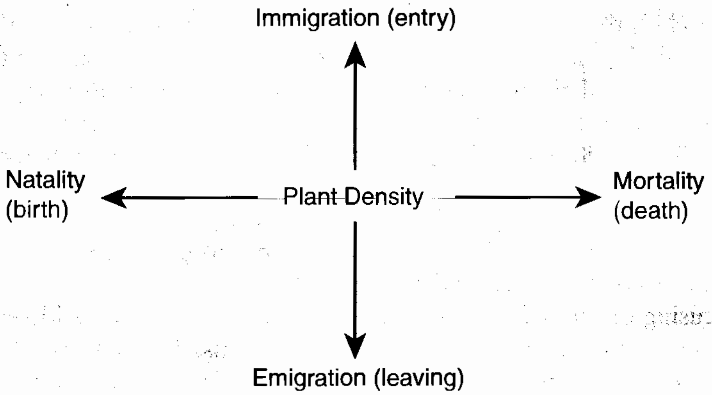
Natality, Mortality, Immigration, and Emigration

Plants differ substantially among species in life form and timing of stages of development, but certain basic population processes are common to all (Chapter 2). For example, a large number of plants inhabiting a field would not remain static over time. If the number of plants increases, either there has been an influx of individuals from somewhere else, new plants have been created (born), or both events have occurred. These are two of the most basic processes that affect plant population size: *immigration* and *birth*. Alternatively, if the number of plants in the hypothetical field declines, some of them must have died since it is difficult to explain how plants could simply leave a field. The processes that reduce plant numbers are *death* and *emigration*. Dispersal is an example of how plants emigrate. All four of the basic processes can occur simultaneously in a population (see below). If the population declines, then death and emigration together outweighed birth and immigration, and vice versa, if the population increases.

In Chapter 2, birth, death, immigration, and emigration were combined in a simple algebraic equation to describe the change in numbers of a population between two points in time.

$$N_{t+1} = N_t + \mathrm{B} - \mathrm{D} + \mathrm{I} - \mathrm{E} \qquad (eq.\ 2.5)$$

However, if the population is so large that absolute numbers cannot be used, then the equation is constructed in terms of density, so N_t becomes, for example, the number of plants per square meter at time *t*. Equation 2.5 demonstrates



that understanding demography requires measurement of the four basic processes and accounting for their values. Unfortunately, this task is rarely simple or straightforward because every plant species passes through a series of stages in its life cycle (seed, seedling, adult plant, and so on) and each stage must be identified individually. Therefore, equation 2.5 represents a general, ideal model upon which more realistic descriptions are built.

The complexities of weed populations are best described using diagrammatic life table models (to be discussed later). This demographic approach to the study of weed population dynamics was first introduced by Sagar and Mortimer (1976) and has been used widely by weed ecologists for the past twenty years. Complete reviews are found in Mortimer (1983), Cussans (1987), and Cousens and Mortimer (1995).

Life Tables

In order to study the demography of any plant, its life cycle must be divided into fractions or components. For example, the plant's life cycle could be divided into an active fraction (growing plant) and a passive one (dormant seed and vegetative plant parts such as stolons, bulbs, and rhizomes). It might also be divided into the sporophyte (plants as we see them) and the gametophyte (a phase that is very reduced in higher plants and includes reproductive structures in the flower). The number of fractions included in a study and the level of detail necessary largely depend on the purpose of the project or study. The aims of some projects may only require simple and general descriptions in which a few components are considered in terms of a similar level of detail. In other cases, when deeper understanding is required, more fractions would be included and those determined to be critical would be studied in great detail. An approach followed by many plant demographers is to start with a simple general model to find critical components to be studied later in greater detail.

A simple diagrammatic life table of an idealized higher plant is shown in Figure 4.1. The number of individuals (N) at the start of each developmental stage (seed, seedlings, adults) is given inside the rectangular boxes. The N_{t+1} adults alive at time $t + 1$ (i.e., the next generation) come from two sources: (1) survivors of the N_t adults alive at time t and (2) those coming from birth, which in Figure 4.1 is a multi-stage process involving seed production, germination, and the survival and growth of seedlings. In the first source, the probability of survival (the proportion of them that survive) is placed inside the triangle and noted by p in Figure 4.1. For instance, if $N_t = 100$ plants and p, the survival rate, is 0.9, then there are 100 × 0.9 or 90 survivors contributing to N_{t+1} at time $t + 1$ (10 individuals have died; the morality rate, $1 - p$, between t and $t + 1$ is 0.1).

For the other source of plants in Figure 4.1, birth, the average number of seed produced per adult (the average fecundity of the plant population) is noted by F in Figure 4.1 and placed in a diamond. The total number of seed produced

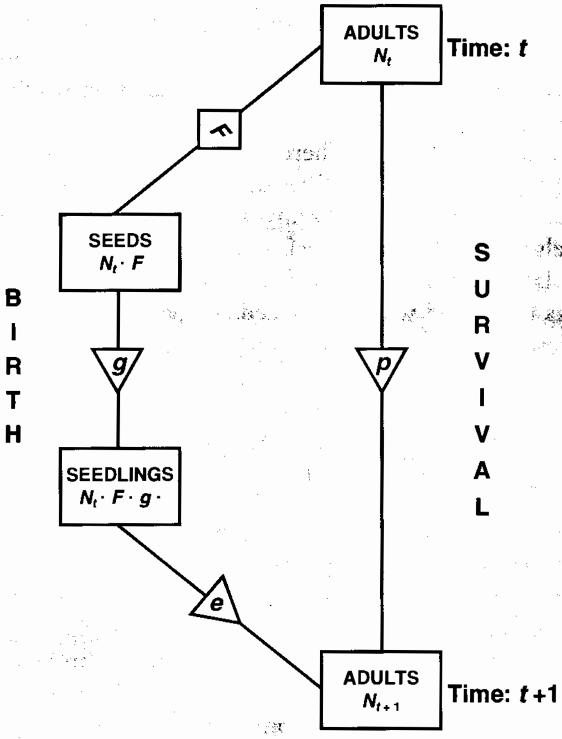


FIGURE 4.1 A diagrammatic life table for an idealized higher plant. *F:* number of seed per plant; *g:* chance of a seed germinating ($0 \leq g \leq 1$); *e:* chance of a seedling establishing itself as an adult ($0 \leq e \leq 1$); *p:* chance of an adult surviving ($0 \leq p \leq 1$). (From Begon and Mortimer, 1986.)

is, therefore, $N_t \times F$. The proportion of these seed that germinate is denoted by g. Multiplying $N_t \times F$ by g gives the number of seed that germinated successfully. The final step of the process is the establishment of seedlings, as independently photosynthesizing adults. The probability of surviving this stage of plant development is denoted by e in Figure 4.1 and the total number of births is, therefore, $N_t \times F \times g \times e$. The number of the population at time t + 1 is the sum of this calculation and $N_t \times p$.

It is now possible to substitute the terms of the life table (Figure 4.1) into equation 2.5, giving a basic equation for population growth of this hypothetical species:

$$N_{t+1} = \overbrace{N_t \underbrace{- N_t\ (1-p)}_{\text{death}}}^{\text{survival}} + \underbrace{N_t \times F \times g \times e}_{\text{birth}} \qquad \textit{(eq. 4.1)}$$

In this example, immigration and emigration were ignored, thus this description of how a plant population may change over time is incomplete. Moreover, death was calculated as the product of N_t and the mortality rate $1 - p$, because survival and mortality are opposite processes whose sum is one.

Modular Growth

A major distinction between species of the plant and animal kingdoms is how they grow and develop, which provides a pattern to the organization and differentiation of tissues. Most animals grow in a unitary and linear manner, while the growth of plants is modular (Harper and Bell, 1979; Harper, 1981). In animals, development from the zygote to the adult involves an irreversible process of tissue differentiation leading to organ development. In contrast, growth and differentiation in plants are usually initiated in *meristems* at the apices of shoots and roots (Esau, 1965). Cell division occurs in these meristems, which results in root and shoot elongation and the creation of more meristems. Thus, growth from meristems leads to a repetitive modular structure in the plant body, a *phytomer*. Botanically, a module is an axis with an apical meristem at its distal end. The axis is subdivided by nodes at which leaves, axillary meristems, and vegetative outgrowths may occur. A meristem may further differentiate into a terminal flower, at which time extension growth of the axis ceases.

Three demographic consequences arise from the modular construction of higher terrestrial plants. First, the addition of modules generates a colony of repeating units arranged in a branched structural form. The exact architecture of the plant depends on (1) whether modules vary in form, (2) their rate of production, and (3) their position relative to one another. The way the modules are structured influences the size and shape of the organ and, therefore, interactions among static individuals, which has demographic implications (Horn, 1971). Second, phytomers are relatively autonomous; therefore, herbivory or other physical damage may harm the plant but rarely kill it. The relatively autonomous meristem system also allows reiteration of many parts of the individual. In most plants, removal of vegetative branches will often lead to the replacement of the branch, but in unitary organisms, even though tissue regeneration does occur, removal of a whole organ can cause death. The third consequence of modularity is the opportunity for natural cloning of plants (Harper, 1984), which is only possible when the meristems at the nodes retain the ability to produce new shoots and roots. Fragmentation of an individual into independent clones may arise through physical agents, such as tillage, trampling, and grazing of herbivores, or it may be determined genetically. Cloning is an important characteristic for the persistence and dispersal of many perennial weeds (Holzner and Numata, 1982).

Harper (1977) indicates that the fundamental equation of population biology (eq. 2.5) applies not only to genets (the plant as a whole), but also at the lower level of ramets (i.e., modular units of the clone, Figure 1.4). Demographic approaches to modular dynamics can use the same techniques as for populations of unitary organisms (Harper and Bell, 1979).

Models of Plant Population Dynamics

Models of how a population behaves are needed to understand how the fundamental demographic processes of birth, death, immigration, and emigration influence the stability or change in population size. We have already seen the simplest form of a demographic model (eq. 2.5), which Silvertown and Lovett Doust (1993) suggest may approach being an algebraic truism. However, much more complex equations for population change arise from attempts to account for the way in which birth rates, death rates, and migration rates change along with population density and age structure and with the effects of competitors, predators, pathogens, and mutualists (Silvertown and Lovett Doust, 1993). Although detailed mathematical treatment is not possible in this text, some of these modeling approaches are described below.

MODELS BASED ON DIFFERENCE EQUATIONS

Two life cycle models are needed to examine the population dynamics of any higher plant species: (1) for species in which vegetative multiplication does not occur (Figure 4.2), such as most annual and biennial plants; and (2) for species in which vegetative multiplication does occur (Figure 4.3), as in perennial plant species.

When vegetative reproduction does not occur. Two routes are shown in Figure 4.2 by which a population of individuals of size A_1 in generation G_t may occur in the succeeding generation G_{t+1}. The population A_2 in generation G_{t+1} may come from genet reproduction (Kays and Harper, 1974), and sometimes from survivors of the previous generation. Route I (Figure 4.2) represents genet reproduction and plant establishment from seed which is divided into six intermediate phases. B is the total number of viable seed produced by the population A_1; C is the total number of viable seed falling onto the soil surface, to which are added any seed arriving by invasion (G); D_1 is the total number of viable seed that are present in the surface seed bank. This seed bank may lose individuals to the buried seed bank (D_2), which includes the "carry over" seed from previous generations. [There also may be inputs to the surface seed bank from invading seed or to the buried seed bank by sowing crop seed contaminated with weed propagules]. E is the number of seedlings germinated from either seed bank and F is the number of plants established.

Seven interphases are also recognized in Figure 4.2, including *a* through *g*, where, for example, *d* is the probability of a seed giving rise to a seedling within the time span of a generation. The invasion interphase *g* is further subdivided to distinguish contributions to the seed rain g_1, to the surface seed bank g_2, and to the buried seed bank g_3.

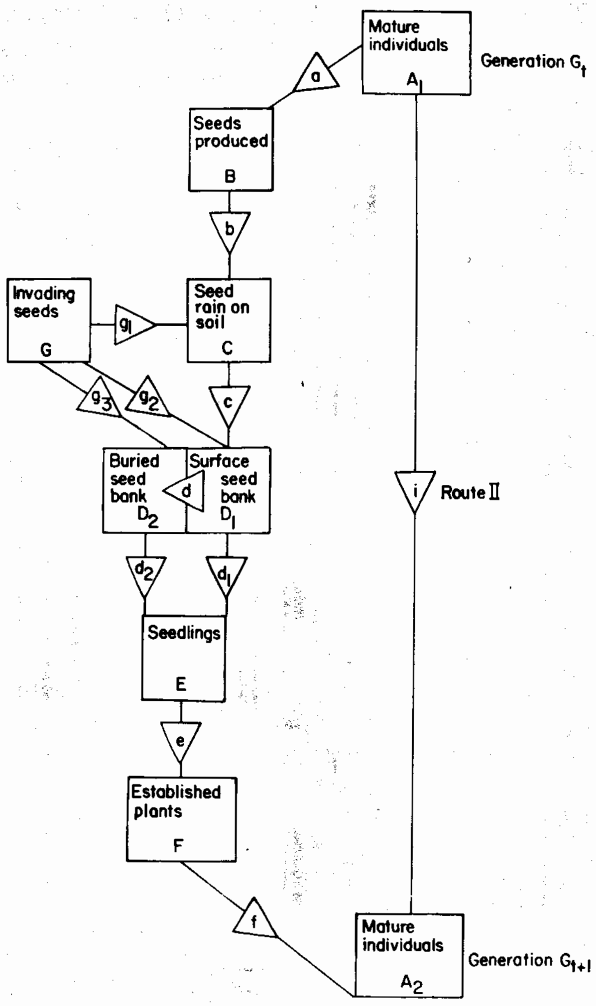


FIGURE 4.2 The generalized life table for a higher plant species that does not have ramet production. Symbols are described in the text. (From Sagar and Mortimer, 1976.)

Route II (Figure 4.2) is found in all species except ephemerals and annuals. This route indicates an interphase probability for the fraction of the population A_1 that survives to generation G_{t+1}. For a biennial species, the interphase (i) may theoretically carry a value of 0.5, for half the plants in the population A_1 would flower and die and half would remain vegetative and survive into population A_2. However, Figure 4.2 requires some slight modification for biennial species because of the overlap of generations and is inappropriate for species that have mixed populations of genets and ramets (Kays and Harper, 1974).

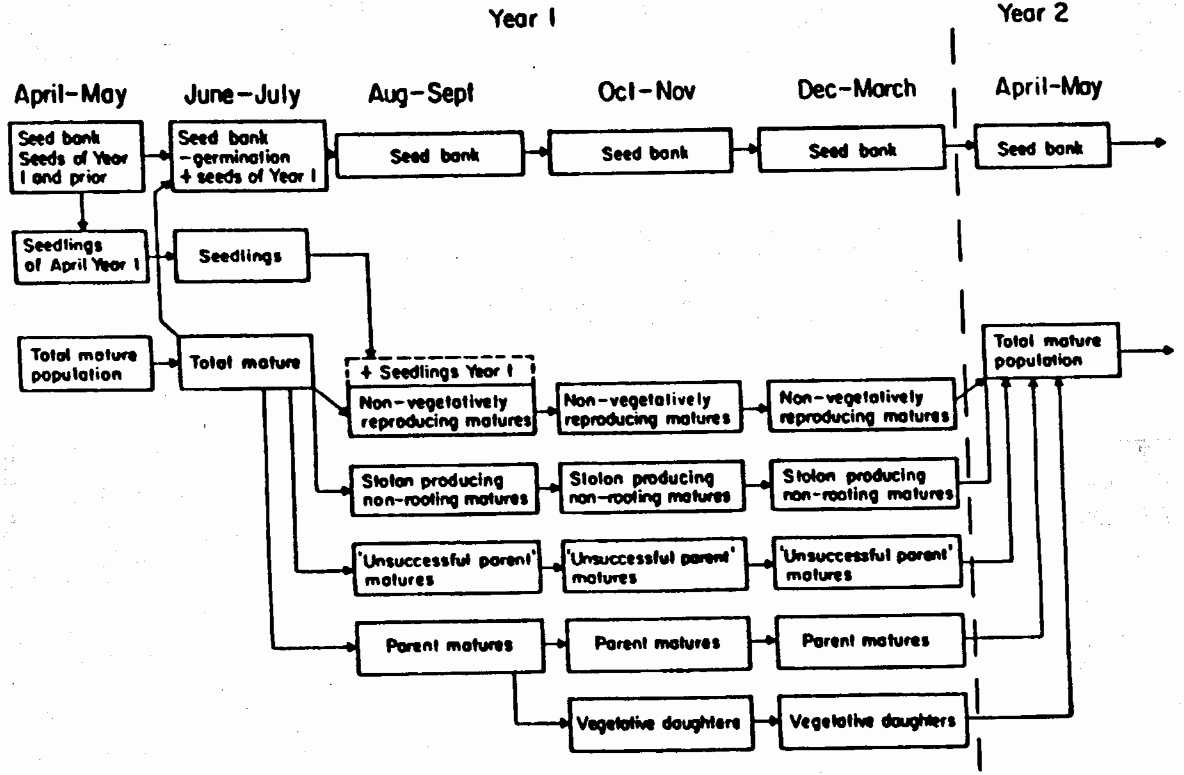


FIGURE 4.3 The transitions occurring throughout the year in a buttercup population (*Ranunculus repens*), as envisioned by Sarukhan and Gadgil, 1974.

When vegetative reproduction occurs. Sarukhan and Gadgil (1974) used transitions depicted in Figure 4.3 to describe the population dynamics *of Ranunculus repens* in Great Britain. This species reproduces sexually by seed and asexually by vegetative propagation, though recruitment by these means occurs at different times during the year. Seed germinate in late spring and early summer while new "daughter" plants become established in late summer as separate adult plants from shoots borne at nodes along creeping stolons. In essence, this complex flow diagram (Figure 4.3) is an age-state classification in which the fluxes from one stage to another are precisely defined chronologically. This approach makes an additional distinction in that asexually produced vegetative daughters are classified separately from sexually produced seedlings, at least during the first year of life. This demographic approach has also been used to describe the dynamics of many other perennial weed species (Sagar and Mortimer, 1976).

Age specific models. Mortality and fecundity are often age specific. In order to solve complex age and stage problems that may arise when describing plant populations, it is necessary to increase the complexity of the general model (e.g., Figure 4.1) into a diagrammatic life table like Figure 4.4. Here the population is divided into four age groups: a_0, a_1, a_2, and a_3; a_0 represents the youngest adults and a_3 the oldest. In a single time-step, t_1 to t_2, individuals from group a_0, a_1, and a_2 pass to the next respective age group; each age group contributes new individuals to a_0 (through birth); and the individuals in a_3 die. This model clearly rests on the assumption that the population consists of discrete age groupings and has discrete survivorship and birth statistics, in contrast to the reality of a continuously aging population.

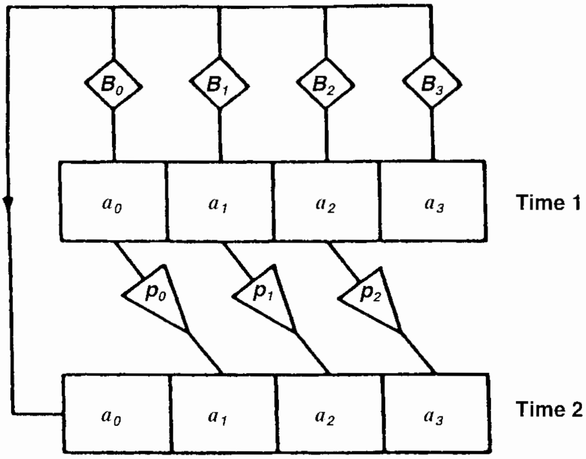


FIGURE 4.4 The diagrammatic life table for a population with overlapping generations: *a* = numbers in different age groups, *B* = age specific fecundities, and *p* = age specific survivorships. (From Begon and Mortimer, 1986.)

It is now possible to write a series of algebraic equations to express the changes that might occur in Figure 4.4:

$$t_2a_0 = (t_1a_0 \times B_0) + (t_1a_1 \times B_1) + (t_1a_2 \times B_2) + (t_1a_3 \times B_3) \qquad \textit{(eq. 4.2)}$$
$$t_2a_1 = (t_1a_0 \times p_0) \qquad \textit{(eq. 4.3)}$$
$$t_2a_2 = (t_1a_1 \times p_1) \qquad \textit{(eq. 4.4)}$$
$$t_2a_3 = (t_1a_2 \times p_2) \qquad \textit{(eq. 4.5)}$$

where the numbers in the age groups are subscripted t_1 or t_2 to identify the time period to which they refer. There are four equations in this model because there are four age groups, and they specifically state how the numbers in age groups are determined over the time step t_1 to t_2. An example of how to use this type of life table is given in Appendix 1.

TRANSITION MATRICES

Another way to describe the behavior of populations with overlapping generations that have individuals that fall into different age or size classes, that is, have different rates of reproduction and death depending upon age or size, is with *matrix models*. These models are generally simpler to use and more realistic than those using difference equations.

The matrix model was introduced to population biology by P.H. Leslie in 1943 and is often called the Leslie model. In general form, for n age groups, it is written as:

$$\begin{bmatrix} B_0 & B_1 & B_2 \ldots\ldots B_{n-1} & B_n \\ p_0 & 0 & 0 \ldots\ldots 0 & 0 \\ 0 & p_1 & 0 \ldots\ldots 0 & 0 \\ 0 & 0 & p_2 \ldots\ldots 0 & 0 \\ \cdot & \cdot & \cdot \quad \cdot & \cdot \\ \cdot & \cdot & \cdot \quad \cdot & \cdot \\ 0 & 0 & 0 \ldots\ldots p_{n-1} & 0 \end{bmatrix} \times \begin{bmatrix} t_1a_0 \\ t_1a_1 \\ t_1a_2 \\ t_1a_3 \\ \cdot \\ \cdot \\ t_1a_n \end{bmatrix} = \begin{bmatrix} t_2a_0 \\ t_2a_1 \\ t_2a_2 \\ t_2a_3 \\ \cdot \\ \cdot \\ t_2a_n \end{bmatrix}$$

which may alternatively be written as: $\mathbf{T} \times t_1\mathbf{A} = t_2\mathbf{A}$. **T** is called a ***transition matrix***, which when multiplied by the vector of ages (**A**) at t_1 gives the age distribution at t_2. For further information, references include Searle (1966) and Caswell (1989). An example of this approach is given in Appendix 2

Simulation of leafy spurge population growth and effects of management. Maxwell et al. (1988) used a matrix modeling approach to simulate population changes of leafy spruge (*Euphorbia esula*) and determine the consequences of several management tactics used on that species. Leafy spurge is a herbaceous perennial weed of range and pasture lands in the northern Great Plains of the United States and southern Provinces of Canada. The species grows under a wide range of habitats, most commonly open grasslands. There are no herbicides, applied as a one-time treatment, or biological controls that provide effective, acceptable, long-term control of the species. Maxwell et al. (1988), following Watson (1985), divided the life history of leafy spurge into five stages: seeds, buds, seedlings, vegetative shoots, and flowering shoots. By identifying these stages (state variables), the processes of population development were determined (Figure 4.5).

It was found that three important transition parameters—basal buds to vegetative shoot (G2), the number of basal buds that flowering shoots produced (V5), and the number of basal buds that vegetative shoots produced (V4)—were sensitive to their own density. When the three density-dependent functions were included in the model simultaneously, initial exponential growth resulted, followed by growth decline and eventual stabilization of the simulated population (Figure 4.6). Maxwell et al. (1988) then subjected the simulated populations to several management tactics: a single application of picloram (Figure 4.6, top) and a foliage-feeding herbivore that removes 40, 50, and 60 percent of the stems (Figure 4.6, bottom). These simulations were compared to effects of actual picloram or sheep grazing treatments on leafy spurge. The accuracy of the simulation was striking in predicting the outcome of the management treatments. The model also indicated what stages in the life cycle of this weed species were most sensitive to manipulation.

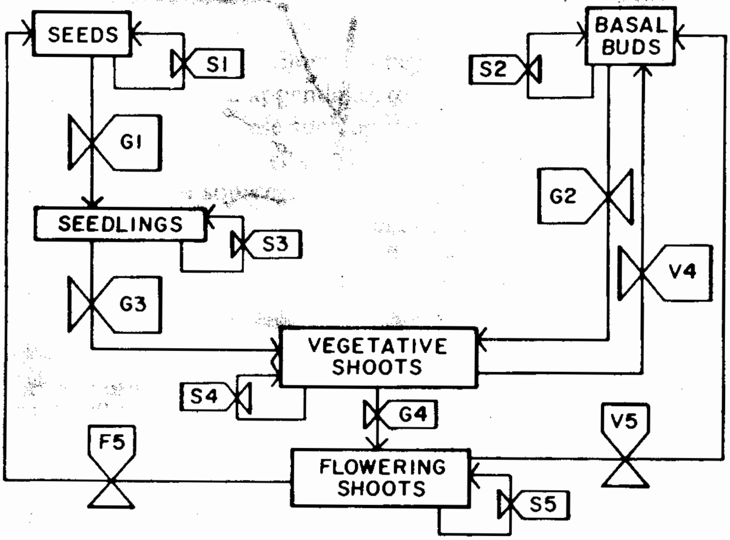


FIGURE 4.5 Diagrammatic model of a leafy spurge population: the boxes represent stages in the lifecycle, arrows indicate processes, valve symbols represent the rate at which a process occurs over a specified iteration time. (From Maxwell et. al, 1988.)

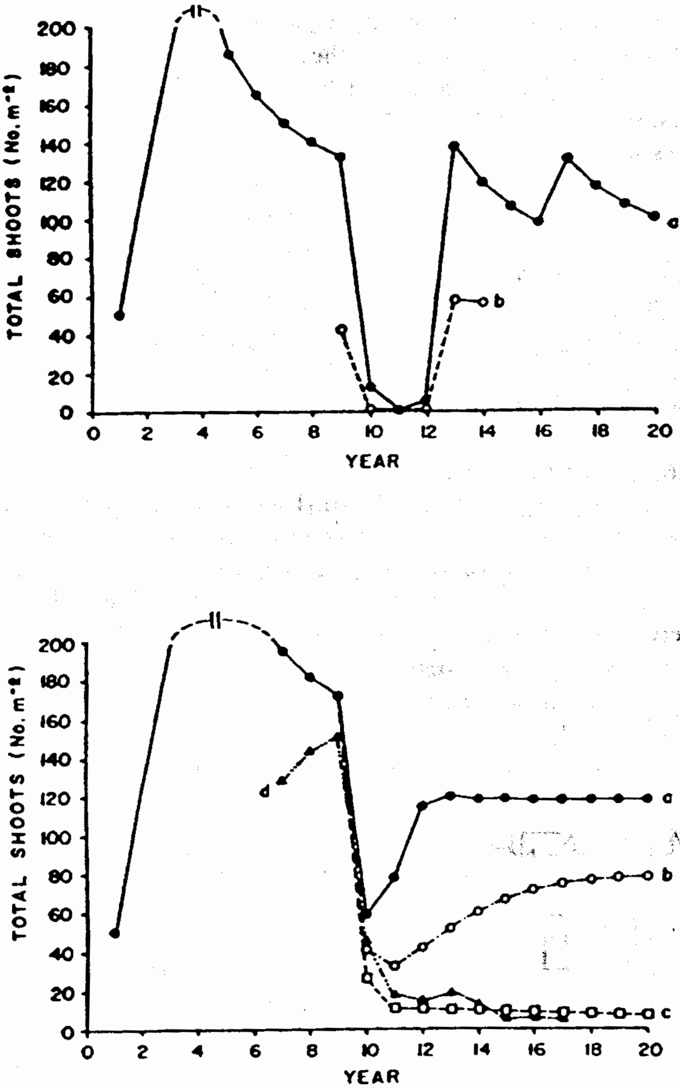


FIGURE 4.6 *Top:* Leafy spurge population simulation with density-dependent functions and a single application of picloram simulated at year 10 (a), and (b) observed effects of picloram application. *Bottom:* Leafy spurge population simulation with density-dependent functions simulating the introduction of a foliage-feeding herbivore at year 10 that removes (a) 40, (b) 50, and (c) 60 percent of the stems. Also shown are (d) observed effects from sheep feeding on leafy spurge. (From Maxwell et al., 1988.)

WEED SEED DYNAMICS

It is sometimes convenient to consider separately the two demographic processes related to plant movement, immigration and emigration, although both processes can be combined under the general term, *dispersal.* Most propagules of weeds are