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Population Diversity with Special Reference to Rangeland Plants

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Abstract

Population diversity is the second level in the diversity hierarchy immediately above genetic diversity and below species diversity. It is revealed through variation in characteristics among individuals that form the population. The modular structure of plants contrasts with the unitary structure of animals and leads to a need for a clear definition of the plant individuals. Developmental stages and age classes are common components of structural diversity that should vary in healthy plant populations. Data regarding these components are gathered with techniques that ensure that the fate and reproduction of each individual plant is maintained. Techniques such as population viability analysis use measures of the probability of individuals progressing from one stage or age to another stage or age. When these measures are obtained under differing management objectives they can be used to project the vulnerability of the population to management options. Examples are presented that demonstrate the risk of a population explosion of a cheatgrass population and the risk of extinction for bluebunch wheatgrass under two grazing systems.

INTRODUCTION

Population diversity is revealed through variation in characteristics among its individuals. We can subdivide or categorize individuals and determine the fates (alive or dead; reproductive or nonreproductive) of individuals by category. The categories may represent the changes in sizes, ages, or stages of development of the individuals or they may depict the heterogeneous environment in which the individuals must exist. By constructing these groups and by following fates, we can begin to predict long-term stability of a species on a site and to predict its susceptibility to changes in environmental factors or to changes in management.

Population diversity is the second level in the diversity hierarchy immediately above genetic diversity and below species diversity; therefore, one must recognize that genetic diversity is nested within population diversity and may contribute to the overall population diversity along with environmental components. Since genetic diversity has been treated in another paper,[1] I will limit my discussion of population diversity to the variation in traits, such as size, age, and reproduction, that arises from interactions among individuals and from interactions between individuals and their environment.

I will formulate a basic framework about populations that is common to plants and animals. I will provide descriptions of common methods used to collect data pertaining to plant population diversity. I will discuss how species and environmental interactions affect population size classes, age distributions, and stages of development using rangeland plant examples.

Populations are often impacted by unpredictable risks such as abnormal environmental conditions, disease outbreaks, or devastating events such as fires and floods. These risks may be rare occurrences, but they can devastate local populations. The size of a population and its distribution across the landscape may dictate its success in sustaining the species within the community. As an aid in predicting this sustainability, I will discuss how population viability analysis can be used by managers to forecast the impact of risks (events or interactions), both predictable and unpredictable, on a population's stability.

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[1] See McArthur and Tausch, this volume.

WHAT IS A POPULATION?

The general public is acquainted with the term *population* as it is used to describe numbers of humans in specific locations. They are familiar with some of the basic descriptions of human demography, the study of births, deaths, and movements of people in and out of a given location. The beginnings of population biology as a science are largely unknown, but the description by John Graunt of age structure and mortality in English communities during the plague epidemics of the early 1600s (Petty et al. 1964) is one of the earliest examples of population descriptions. Many recognize Malthus's publication of *An Essay on the Principle of Population* as the first to recognize that populations are restricted by limited resources (Malthus et al. 1992).

A population, as it pertains to both plants and animals, is the number of individuals of a species in a definable location at a moment in time. Demography is the study of the dynamics of a population and of the conditions that regulate population change over time. A description of population diversity will require knowledge of the types and numbers of individuals that form the population and will require a description of variation among the individuals.

The determination of an individual is simple for most animals because they are *unitary organisms;* organisms that cannot be subdivided into parts forming additional individuals. The definition of an individual for plants and some animals (e.g., sponges and coral) becomes less clear. These groups are classified as *modular organisms* with the unit of organization being the module. In plants, some commonly recognized examples of modules include branches from shrubs or herbs, grass tillers, and "root suckers" in trees like aspen (*Populus tremuloides* Michx.). A modular individual is often constructed of many connected modules that are capable of surviving independently if provided the appropriate environmental conditions (White 1979).

When determining population sizes for plants it is critical to define the type of individual being counted. When possible, counts should be made of genetically distinct individuals (genets). Each genet is an individual that arises from a single zygote or seed. For clonal plants, counting genets may be impractical, if not impossible, without killing the individual or without describing the genotypes of all individuals; therefore, modules with a high probability of surviving independently (ramets) are generally counted. Ramet-producing plants are commonly referred to as plants that reproduce vegetatively. Many common rangeland grasses fall into this category, such as western wheatgrass (*Pascopyron smithii* [Rhydb.] A. Löve) and blue gramma (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.).

Managing areas for population diversity requires a knowledge of the dynamics of the individuals that compose the population over time. A simple mathematical equation relates the four basic components that influence changes in population sizes during a time interval from time t to time t+1:

$$N_{t+1} = N_t + B_t + I_t - D_t - E_t$$

In other words, the number of individuals at the end of the interval (N_{t+1}) equals the number of individuals in the population at the beginning of the interval (N_t), plus the number of births or new propagules (B_t), plus the number of individuals immigrating into the population (I_t), minus the number of deaths (D_t), minus the number of individuals emigrating out of the population (E_t) during the interval.

Just as the definition of an individual is easier to define for animals than for plants, so is the definition of births easier to define for animals than for plants. Birth for plants may refer to several different stages in development including viable seeds, germinated seeds, and clonal growth (vegetative reproduction). The preferred phase of a plant's life cycle that equates to births is the production of viable seeds because they are the product of genetic recombination producing a new genetic individual, a genet (cf. Harper 1977). Yet for many species, seed viability is difficult to determine without chemical tests such as a standard tetrazolium chloride test (see Bewley and Black 1982). Unfortunately, even these tests may provide overestimates of viability (Roberts 1972). An alternative is to use total seed number regardless of the viability status; however, total seed number is an overestimate of the potentially viable seeds since it is the upper limit if all seeds are viable. For taxa (e.g., the grasses) where visual inspection can determine many nonviable seeds (e.g., unfilled caryopses), such inspections should be completed before estimating seed numbers. Equating germination to birth should be done cautiously, recognizing that the seed phase of the life cycle is ignored, thus ignoring the impacts of seed predation, microbial pathogens, deep burial in the soil, and dormancy on the total number that germinate. Clonal growth produces a new individual, a ramet (cf. Harper 1977), in the population, but it does not increase the genetic diversity of the population since it is genetically identical to the parent plant.

Plant death is normally defined as occurring when no photosynthetic portions of the plant are active during normal seasons of activity. Simply, green plant parts have turned brown. For seeds, death is more difficult to define without viability tests.

Immigration and emigration in animals is common due to their mobility, but most plants are immobile after germination; therefore only the seed phase is capable of dispersal into and out of a population. Most seeds disperse only short distances from their parents. Dispersal distance is enhanced by adaptations for seed transport such as barbs and hooks for external transport or such as the development of fleshy fruits for internal animal transport.

In stable populations, emigration and immigration tend to cancel each other since the probability of successfully leaving the population is likely equal to the probability of a seed from another population successfully dispersing to this population. In the simple model, E_t equals I_t, resulting in population changes being driven by changes in births and deaths.

An exception can be found where populations remain stable along the fringes of their range of existence due to harsh environmental conditions. These populations may rarely produce viable seeds; therefore they rely on immigration from nearby populations to periodically replenish their numbers. This may be the situation when managing rangelands for the maintenance of peripheral species that are rare within a location, yet more common elsewhere. Management to maintain these peripheral populations may require cooperation among managers in adjoining jurisdictions (i.e., states or landowners) so that dispersal is maintained.

STRUCTURAL DIVERSITY IN POPULATIONS

Diversity at the population level is largely a description of the variation in the structural composition of the population. Population structure can be divided several ways, for example: (1) sex ratios; (2) age classes; (3) developmental stages; or (4) size classes. Sex ratios are generally more important for animal than for plant populations since most plants contain both sexes on the same individual (monoecious, hermaphroditic). Some rangeland ecosystems, however, provide exceptions. In arid ecosystems such as the salt-desert shrub of the Great Basin, U.S.A., a large proportion of woody species are dioecious, including the dominant species shadscale (*Atriplex confertifolia* [Torr. and Frem.] Wat.) and four-winged saltbush (*A. canescens* [Pursh] Nutt.). In addition, some species are capable of changing their sex ratios under different environmental conditions (Freeman et al. 1981). Insights into changes in population diversity of these species might require knowledge of sex ratios and their changes through time.

Although age class is commonly used to describe animal populations, evidence suggests that for most animals and plants size may be a better predictor of survival and reproduction than age (see references in Caswell 1989, p. 31). Age class distributions are commonly used to describe the stability of tree populations in forested stands (Daubenmire 1968). Graphically, a stable age structure is represented by a reverse J-shaped age distribution (Figure 1a). In general, the population is growing or stable when the greatest number of individuals are in the youngest age classes and progressively fewer individuals are in older age classes. Distributions with similar numbers of individuals in all age classes typically indicate a reduction in population growth and if continued may lead to reductions in populations after several generations (Figure 1b). Caution must be taken, however, when using age class distributions to predict the stability of species that reproduce or establish episodically since age distributions represent only a single moment in time.

In harsh environments, such as arid ecosystems, perennial plants have adapted their life-history strategies to cope with an unpredictable environment by relying on episodic establishment of new individuals. The production of adequate numbers of viable seeds may occur only in years with sufficient moisture during flower and seed production. For example, bluebunch wheatgrass *(Pseudoroegnaria spicata)* seed production and flowering culm production vary widely from year to year (Mueggler 1975).

Age class distributions alone do not provide all the necessary information to forecast adequately population trends. Knowledge of the age-specific birth and death rates and of the regularity of seed production and germination is required. If the reproduction occurs regularly and at nearly the same levels per individual each year and if survival is age dependent, then age class distributions may strongly reflect population trends. Otherwise populations are described better by classifying the individuals into size classes or developmental stages. Generally, size class or stage of development is a better predictor of an individual's fate than its age (e.g., Werner 1975, Sarukhán et al. 1984).

Some perennial plants with plastic growth can switch from being reproductive in one year to nonreproductive in the next. Thus, stages like seed, seedling, sapling, clonally reproducing, sexually reproducing, and both clonally and

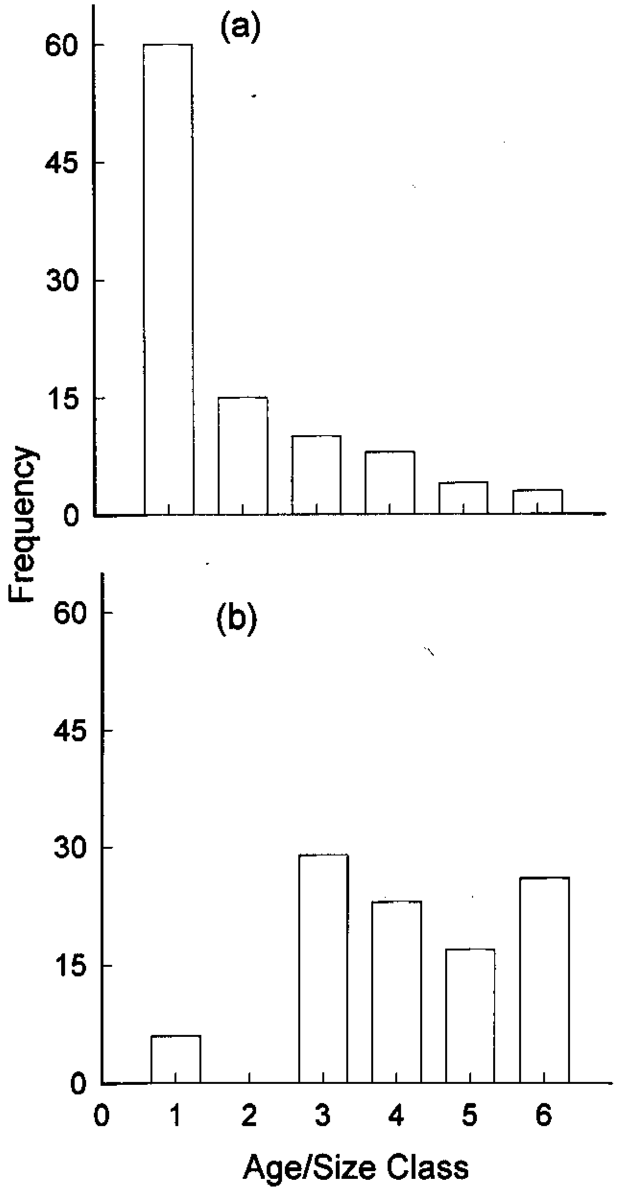


Figure 1. A hypothetical age or size class distribution demonstrating (a) a stable or growing population and (b) a slowing or declining population.

sexually reproducing individuals, provide several structural classes among which individuals may shift in either direction, in contrast to age classes that by definition are unidirectional.

Annual censuses of populations allow counts of individuals in each structural class. If fates of the same individuals are monitored each year, then probabilities of an individual successfully making a transition from one structural class to the next can be estimated. These transitional probabilities (P) are calculated as a ratio of the number of individuals in a class that change to another class. For example, the proportion ($P_{n\to r}$) of nonreproductive adults at time t ($N_{n,t}$) that become reproductive adults at time t+1 ($N_{n\to r,t+1}$) is calculated as follows:

$$P_{n\to r} = \frac{N_{n\to r,\ t+1}}{N_{n,\ t}} .$$

One method of describing the structural diversity of a population is to develop a diagrammatic life table (Figure 2) that combines the relative numbers of individuals in each category with their transitional probabilities. Simple diagrams can convey the potential for dynamism in age- or size-dependent populations. Complex diagrams demonstrate the multiple paths available to individuals in some classes in the next generation.

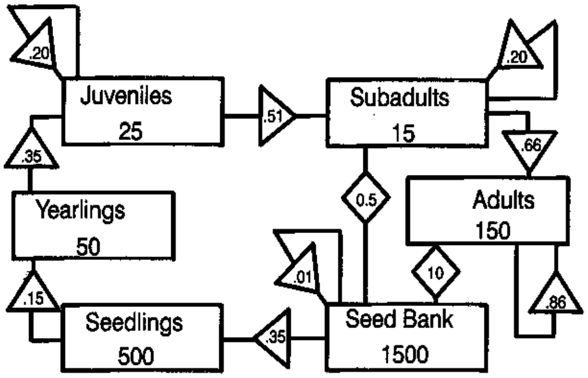


Figure 2. Diagrammatic life table for bluebunch wheatgrass. Rectangles represent the numbers of individuals in that stage of development, triangles represent the transitional probabilities between each stage, and diamonds represent the number of viable seeds per individual.

Transitional probabilities in life tables are often viewed as static values, but the displayed probabilities normally represent the mean or median of several proportions. When data for multiple years are available, both the mean probability and the variation around that mean should be presented. The variation is used in developing models that project the likelihood that populations will increase, decrease, or remain constant.

TECHNIQUES FOR SAMPLING POPULATION DIVERSITY

Techniques used to collect estimates of demographic parameters vary depending on the plant and on its stage of development. In all cases, density (numbers of individuals per unit area) must be accurately determined at different times (t_i and t_{i+1}) and there must be a method to identify that the same individuals are being tracked through time. Methods for tracking individuals include using markers such as toothpicks, colored wire collars, and numbered tags. However, markers associated with the plants are vulnerable to removal or destruction; therefore censuses using data collected with markers may be biased.

Alternative methods that do not rely on the presence of markers use coordinate systems to map the position of individuals and to verify their continued existence. Many types of coordinate systems have been used to monitor rangeland plant populations. Pantographs aid in drawing scaled maps of plant locations and plant basal area in permanent plots (Wright and Van Dyne 1976, West et al. 1979). Mapping tables use a sighting scope to mark the plant position on an acetate map placed on a table directly above the plot (Chambers and Brown 1988, Pyke 1990). Mapping tables are more accurate than pantographs for relocating individuals in dense populations. Photographs may provide maps of plant positions in sparse communities where canopies do not overlap (Owens et al. 1985). Using scanners and digital processing, large mature and juvenile plants may be detected and analyzed over multiple censuses within a geographic information system. Measured coordinates can use an angle-distance technique (Muir and McCune 1992, Hutchings1986) or an x,y-coordinate technique (Cullen et al. 1978) to measure the position of the plant within the plot.

Methods for monitoring seed fates are more difficult. Mark and recapture techniques have been used successfully for several species in differing habitats. The marking method is normally a paint or dye applied to the seed surface (Watkinson 1978). Recapture of the seeds is dependent on the seed being seen by the observer. Techniques using radionuclide markers on seeds allow the observer to detect the seed even if it is hidden from view (Primack and Levy 1988). The fates of individual seeds have been followed by gluing thin nylon fishing line to seeds and connecting the line to a stake, thus allowing secondary dispersal of the seed once it comes into contact with the soil (Schupp 1990).

Analysis of mark and recapture data for plants or seeds requires techniques similar to those used to analyze animal mark and recapture data. Recapture and survival probabilities may independently depend on time. Only when the probability of recapture is 100 percent is it possible to directly measure the survival probability. When recapture probability is less than 100 percent, researchers must estimate both the survival and recapture probabilities; otherwise survival estimates will underestimate actual survival probabilities. For example, a survival probability for an organism may increase over time while recapture probability decreases over time. Techniques are available to treat independently survival and recapture probabilities (Lebreton et al. 1992), although these techniques are not commonly used for plant populations.

In lieu of marking individual seeds, a common technique identifies a known quantity of seeds and introduces those seeds in a location so that the surviving seeds can be collected at some later time. For seed bank longevity experiments, seeds are placed in bags that allow moisture and microorganisms to move through the fabric (e.g., Hopkins and Graham 1987). Alternatively, seeds can be mixed with soil and buried with an inert material, such as sand or glass beads, placed above and below the soil-seed mixture, reducing some of the bias associated with a container holding the seeds (Vázquez-Yanes and Smith 1982). The layers of inert material mark the location of the seeds so remaining seeds can be extracted later. Tests of the germinability and viability at varying times can provide estimates of dormancy, seed survival, and seed bank persistence. Dormancy estimates based only on germinability will require germination tests under differing environmental conditions. Techniques using ranges of temperature treatments have been widely applied to rangeland plants (Palmquist et al. 1987).

For measurements of sexual reproduction, the number of viable seeds must be estimated independently for each individual in a defined area so that estimates of both the central tendency for seed production and of variation in seed production can be made for the population of individuals. Combinations of bulk harvests of seeds from all plants (S) and of counts of individuals (N) in the same area can provide only estimates of the mean seed production per individual (S/N). These estimates assume a normal distribution of seed production among individuals, but distributions are typically skewed to the right; few individuals produce large numbers of seeds while most individuals produce few or none (Levin and Wilson 1978, Mack and Pyke 1983). The skewed distribution of seed production per individual generally makes the median a preferred measure of central tendency over the mean.

Competition among plants can differentially influence the vital rates of plants in different size or developmental stages. Density-dependent effects normally reduce the survival of the younger age classes or smaller stages of development. These effects can be roughly measured using experiments where competitors are removed. These experiments may overestimate the effect of competition because of confounding effects of the decomposition of the roots of the removed plants increasing nutrient availability for the remaining plants.

An alternative method is to grow plants under varying densities of competitors to develop the relationship between the density of competitors and the vital rates of the target species. For perennial plants, these experiments need to be conducted over several years to determine the effect of density on plants of different ages, sizes, and structural stages. Additive-series experiments provide an excellent method for developing these relationships (Silvertown 1987) since they incorporate changes in plant densities and in proportions of the competing species. Francis (1993) has demonstrated this approach for determining the density-dependent effect of cheatgrass on the seedling biomass of crested wheatgrasses (Figures 3a,b). Similar experiments need to be conducted for multiple years to explore the range of density-dependent effects on seed production and survival for rangeland plants.

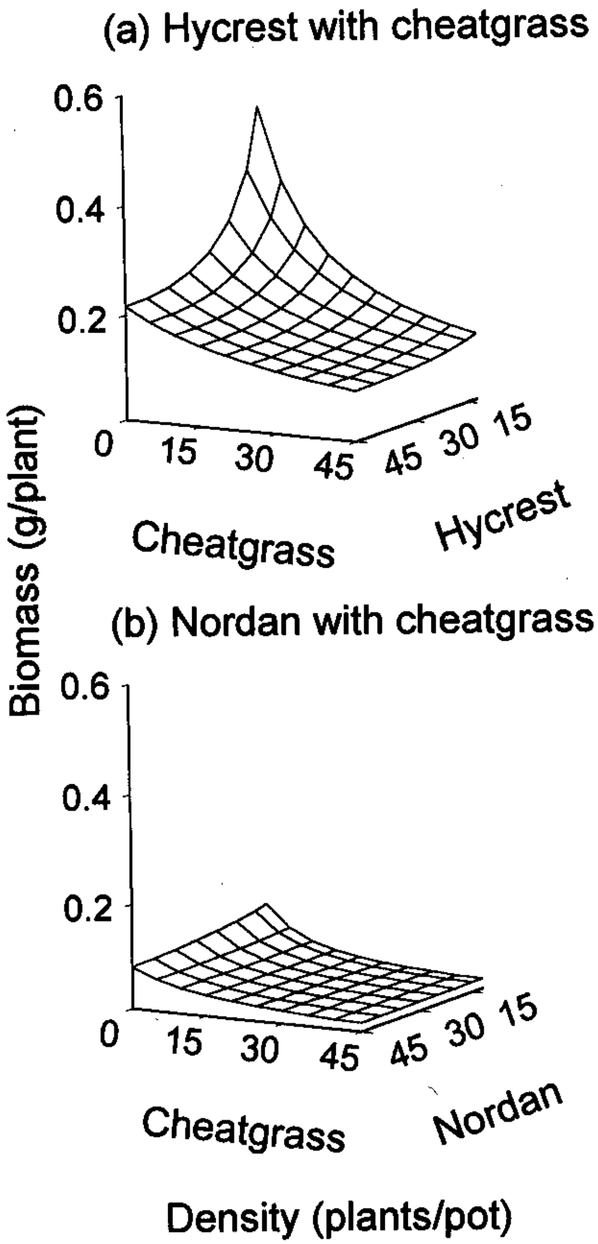


Figure 3. Median biomass per individual for seedlings of (a) "Hycrest" and (b) "Nordan" crested wheatgrass when competing with cheatgrass in two-species mixtures of varying densities in pots with dimensions of 33 cm upper diameter, 30 cm lower diameter, and 36 cm deep (from Francis 1993).

PROJECTING FUTURE POPULATIONS

Land managers and conservation biologists over the last ten years have recognized a need for quantitative methods to predict the risks of extinction for species existing in small populations. On the opposite end of the spectrum, managers and biologists are concerned with the potential for population explosions of recently introduced exotic species. Both of these concerns can be addressed using a population modeling technique known as Population Viability (Vulnerability) Analysis (PVA). PVA is similar to techniques that determine Minimum Viable Populations (MVP), a population level that a population must remain above to sustain itself. Defining a single MVP level is difficult and has become controversial (Soulé 1987). For the purpose of this paper, PVA will be presented since it incorporates the processes and the variability that influence the level of the MVP as well as estimates of the risk to the population of management alternatives.

Two types of quantitative measures are possible in a PVA: (1) deterministic measures are those based on single values that predict the fate of a population; and (2) stochastic measures are those based on a probability of a fate for a population. These two types of measures have resulted in two schools of thought concerning population projections. The deterministic school relies heavily on the estimate of the population's finite rate of increase known as λ. Populations with $\lambda=1$ are stable whereas values above 1 and below 1 indicate a trend for a population to increase or decrease, respectively, over time. The usefulness of λ as a predictor of population stability for small populations has come under scrutiny. Values of λ are estimated when populations are assumed to have a stable age or stage distribution; however, small populations may never satisfy this assumption and thus invalidate the estimate of λ.

Stochastic measures incorporate estimates of the natural variability under which each population exists. Instead of providing a single measure for comparison against a goal (MVP), stochastic measures recognize that extinction, stability, or explosions for any given population are probabilistic expressions. They measure the chance of extinction or the chance of the population exceeding some upper or lower level during a time period.

The three major types of PVA are distinguished by the underlying models used to project future populations. The simplest forms are unstructured models that treat all individuals equally; that is, survival and reproduction rates do not differ among age or stage classes. These models use difference equations, such as exponential growth, logistic growth, or Ricker equations to predict population size at the next census as a function of the population size at the current census. An example of a series of unstructured models for PVA is found in the program DRAMA (Crow et al. 1992).

The complexity of models increases when internally structured population models are used to predict the numbers of individuals in each age or stage of development. Internally structured models are matrix models that allow stage-specific fates. These fates equal the transitional probabilities between stages discussed earlier in this paper. The simplest forms are the Leslie matrix for an age-classified population (Leslie 1945) and the Lefkovitch matrix for a stage-classified population (Lefkovitch 1965). Examples of three internally structured PVA programs are RAMAS/AGE (Ferson and Akçakaya 1990), RAMAS/STAGE (Ferson 1990), and RAMAS/SPACE (Akçakaya and Ferson 1992) for analyzing age-structured, stage-structured, and spatially structured populations, respectively.

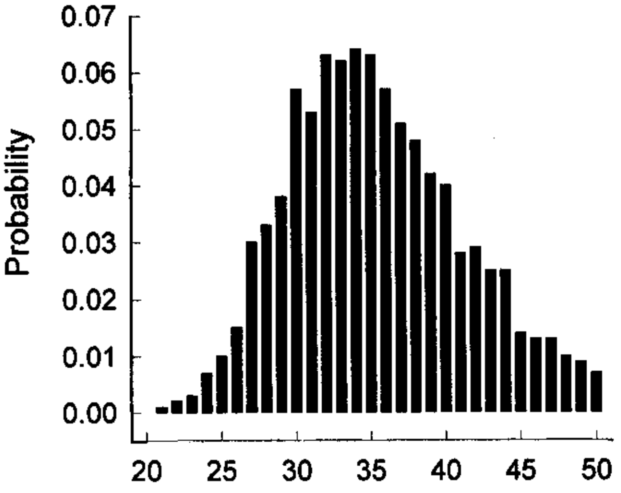
The most complex forms of PVA are the individual-based models. These models examine the reproduction and survival of different genotypes in the population. Individual-based models predict the genetic structure of the population and predict changes in allele frequencies in a population. Three individual-based programs for PVA are VORTEX (Lacy and Kreeger 1992), ALEX (Possingham et al. 1992), and GAPPS II (Downer et al. 1992).

An effective PVA involves three steps. First is a combination of field demography and statistical analyses to estimate reproduction, germination, and survival probabilities for a population under different growing conditions (e.g., grazed vs. ungrazed or with and without competitors). If field data are available for multiple years, then estimates of the annual variability in these vital rates can be calculated. Second is a risk analysis to predict the impact of alternative actions upon the species persistence. Third is the implementation of the chosen management action followed by additional long-term monitoring of demographic data. At this stage, the manager cycles back to step one where the process begins again, making this process an integral part of adaptive resource management (Holling 1978, Walters 1986).

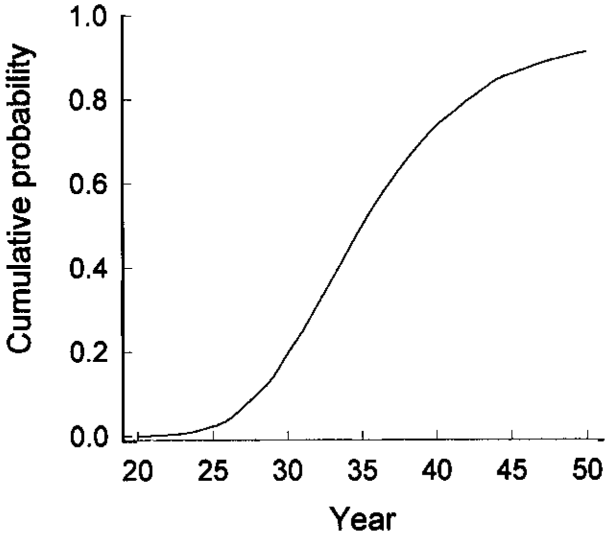
In the risk analysis phase, demographic data are run through a series of computer simulations (e.g., 1,000 simulations consisting of 50 generations per simulation) based on the initial numbers of individuals in each age or stage and based on the probabilities of individuals shifting to various stages. The process of shifting from one stage to another is often variable and unpredictable; thus some transition probabilities may have a degree of uncertainty associated with them that needs to be included in the model (Shaffer 1987). Four classes of uncertainty are generally recognized (Shaffer 1981). *Demographic uncertainty* is the unpredictable survival or reproduction not related to environmental conditions. *Environmental uncertainty* is the unpredictable survival or reproduction due to weather or changes in resource availability. *Natural catastrophes* are events like fire, floods, wind storms, etc., that rarely occur but have major impacts on the population. *Genetic uncertainty* is random change in the genetic composition of the population that has a range of beneficial to detrimental effects on the vital rates of the population.

Once the analysis is initialized with the population sizes for each stage, and their associated vital rates, then simulations can begin to evaluate the risk of extinction for rare species or of explosion for invasive species. The model estimates the risk of extinction by first determining when a simulated population became extinct, if ever. The model then repeats the process for the fixed number of simulations with the same initial data. A frequency distribution of extinction times or of probabilities of extinction can be developed (Figure 4a). However, a histogram of extinction times does not provide a useful picture of the probability of extinction since the probability of extinction at time t_x is not represented by the frequency of extinction in that single year, but is the summation of the probabilities in year x and all previous years. An improved method of displaying the probability of extinction is with a cumulative probability of extinction (Figure 4b).

Managers may find it more useful to know the probability of a population dropping below some specified threshold size rather than the probability of extinction. This threshold level is known as the quasi-extinction abundance (Ginzburg et al. 1982). Choosing a reasonable threshold level may eliminate criticisms of inherent difficulties in modeling low population sizes, such as the potential for finding a mate, the probability



(a) Extinction times



(b) Time to extinction

Figure 4. (a) A hypothetical distribution of the frequency of different time to extinction from 1,000 simulations and (b) a cumulative probability of extinction developed from the same data.

of successful pollination, or the consequences of inbreeding depression that may influence the population more at low population sizes (Gilpin and Soulé 1986). The calculation of the quasi-extinction risk is the same as the extinction risk, but the frequency distributions are based on the time when populations dropped below the threshold, rather than to zero.

These same techniques determine probabilities of population explosion for weedy species or of population recovery for rare species. These approaches could be useful when deciding on which species to concentrate limited labor and money. Those weedy species that are likely to explode in the shortest period of time need immediate action. For rare species, information on the impact of different management options can provide insight into the likelihood of recovery.

The reliability of any PVA, however, is dependent on the accuracy of the empirical data (mean and variance) and on the assumptions used for unknown attributes. For matrix models, additional analyses can be performed to detect which portions of the species' life stages are likely to affect the population. These are called sensitivity and elasticity analyses (de Kroon et al. 1986, Caswell 1989). If critical stages of the life cycle are dependent on assumptions or scientific guesses, then the results of the PVA are strongly suspect. This does not mean that the PVA is useless, because it has identified areas of study for future data collection that will strengthen the PVA.

TWO EXAMPLES OF POPULATION VIABILITY ANALYSIS

The following PVA examples provide two different techniques for addressing management decisions on rangelands. The first projects the impacts of autumn vs. spring grazing regimes on a bluebunch wheatgrass population. The factor of interest is the probability of bluebunch wheatgrass becoming extinct in the next 50 years. The second example evaluates the potential for cheatgrass populations to explode on a site. Both examples are largely based on data from the literature with some parameters estimated when data were not available. An appendix provides the equations used to calculate these projections.

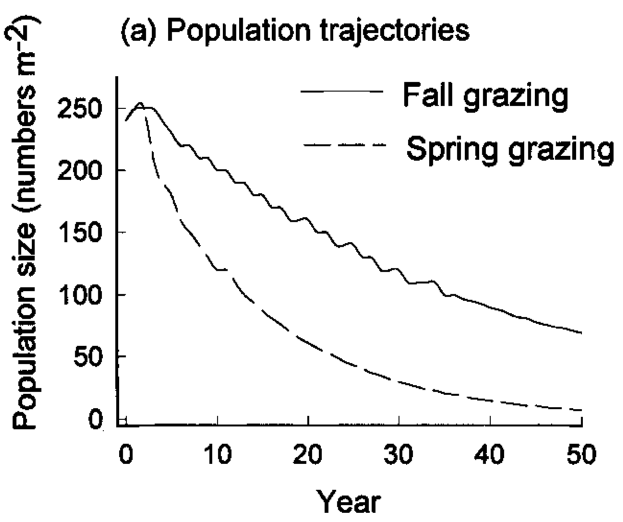
BLUEBUNCH WHEATGRASS

Bluebunch wheatgrass is a dominant native perennial bunchgrass in many communities in the Intermountain West, U.S.A. The population is divided into six age-stage classes (Figure 2): (1) a small persistent seed bank; (2) germinated seeds remain as seedlings for one year; (3) yearlings have survived one summer dormant season, but are too small to reproduce; (4) juveniles are older and larger plants than yearlings, but have not reached reproductive size; (5) subadults are small reproductive plants, but contribute very little seed to the seed bank; and (6) adults are large enough to reproduce consistently. Germination and survival rates for seeds in the seed bank, seedlings, and yearlings are based on data from Pyke (1990), while rates for juveniles, subadults, and adults are estimated from West et al. (1979). Reproduction per individual is not available, but is estimated from the seed production per unit area in Pyke (1990). The only difference between the two grazing treatments is that the fall treatment is given the full reproductive rate (10 and 0.5 seeds per adult and subadult), whereas the late-spring treatment produces half the number of seeds per stage. The estimates of reproduction rate were based on a 50 percent proper-use value for bluebunch wheatgrass. Grazing during the growing season in late spring will reduce the number of reproductive culms produced by each plant. Fall grazing maintains the level of grazing above the level of the apical meristems, thus ensuring that reproduction will not be affected by grazing. This is an area where further empirical data is necessary to improve the model.

Precipitation can significantly affect the survival of seedlings and affect the reproduction of this species. The amount of precipitation in a year is randomly selected from a normal distribution with a mean of 30 cm and a variance of

11.4 square cm. Seed production and seedling survival are assumed not to occur in years when precipitation is less than 20 cm, whereas they double when precipitation is above 36 cm. Precipitation between 20 and 36 cm is assumed to yield multiplicative survival and seed production factors between zero and two in a linear relationship with the precipitation (Appendix).

Autumn grazing of bluebunch wheatgrass led to a slight but continuous decline in the population over the projected 50 years, whereas late-spring grazing caused a more precipitous decline (Figure 5a). A manager can use this output to determine the probability of a population dropping below a minimal density. By selecting the threshold density to be 0.5 plants m^{-2}, the fall-grazed population has a 40 percent probability of dropping below the threshold in 50 years, whereas the late-spring-grazed population always drops below the threshold during the same time (Figure 5b).


(a) Population trajectories

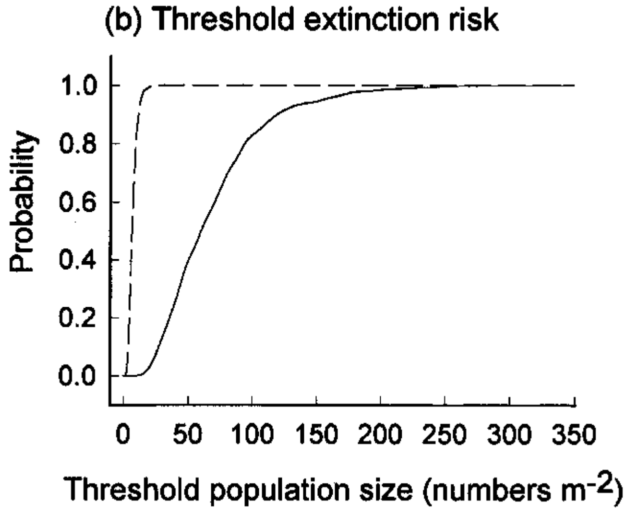
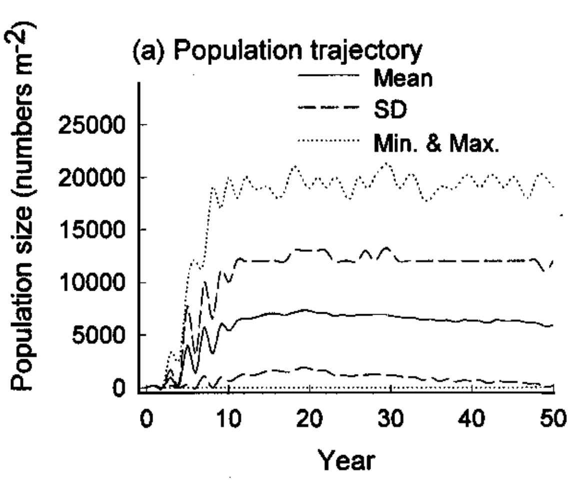

(b) Threshold extinction risk

Figure 5. A comparison of fall and late-spring grazing on populations of bluebunch wheatgrass where (a) is the mean population size for 1,000 simulations over 50 years and where (b) is the probability of the population becoming extinct for each of 50 years based on the number of simulations where the population reached zero.


(a) Population trajectory

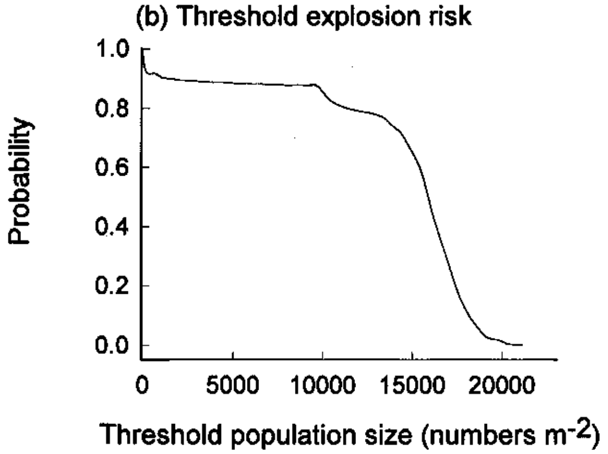

(b) Threshold explosion risk

Figure 6. Beginning with an initial population of 10 reproductive cheatgrass individuals, (a) represents the mean, standard deviation (SD), minimum (Min.), and maximum (Max.) population size simulated 1,000 times over 50 years and (b) represents the probability of the population achieving or exceeding a population threshold sometime during 50 years.

CHEATGRASS

The same principles used to determine the chance of a population dropping below a critical density can also be used to determine the chance of a population increasing above a certain level. This is particularly important for highly competitive weedy species. Cheatgrass is a highly competitive annual plant that was introduced into the Intermountain West from Eurasia in the late 1800s and expanded to its current range in about 30 years. The demographic parameters that describe cheatgrass population dynamics are highly plastic both annually and over several locations (Mack and Pyke 1983).

The cheatgrass model incorporates the variability in all stages of a simple annual life cycle. The data used to estimate survival and reproductive rates were compiled from several studies (Mack and Pyke 1983, 1984, Pyke 1986, Reichenberger and Pyke 1990). Seed production in the model is regulated by a nonlinear density-dependent function (see Appendix). Random variation in seed-bank persistence, seed germination, and plant survival was calculated using means and variances extracted from the above studies and was assumed to be normally distributed. The model was initiated with 10 reproductive plants m^{-2} and was run for 50 years.

Within 10 years the population stabilizes with a mean population size near 6,000 plants m^{-2} (Figure 6a), a realistic density in areas dominated by cheatgrass (Young et al. 1969, Upadhyaya et al. 1986). The plasticity in cheatgrass is seen in the high standard deviation. The potential for cheatgrass populations to explode is demonstrated by the high probability (0.88 to 0.92) of populations achieving sizes between 1,000 and 10,000 individuals m^{-2} at least sometime during a 50-year period (Figure 6b).

CONCLUSION

Managers have many tools available to them to monitor diversity at many levels. At the level of the population, population viability analysis is one tool for assisting managers in projecting the sustainability of species in a area. The accuracy of the projection will depend critically on a thorough understanding of the diversity and importance of life stages of the species and on accurate estimates of the rates of transition between these stages. Annual variation in these rates requires repeated measurements on the same individuals over a series of years. Knowing the effect that changes in management may have on each stage of a species will provide an additional tool in the decision-making process.

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APPENDIX

The following equations and distributions (Tables 1 and 2) were used in the simulations presented for bluebunch wheatgrass and for cheatgrass. Variables (x) selected at random from a normal distribution (N) with a mean of $\overline{x}$ and a variance of s^2 will be represented by the equation $x = N[\overline{x}, s^2]$.

$\overline{x}$

$N[\overline{x}, s^2]$

TABLE 1. EQUATIONS USED TO DETERMINE SIMULATED POPULATION LEVELS OF BLUEBUNCH WHEATGRASS UNDER FALL AND LATE-SPRING GRAZING PRESENTED IN FIGURE 5.

Description	Grazing Time	Equation
Randomly selected rainfall	Both	$x = N[12, 4.5]$
Linear relationship between rainfall and plant growth	Both	$f1 = -2 + 0.25x$
Seedling survival and reproduction driver	Both	$f2 = \begin{cases} \text{if } f1 < 8, \text{ then } f2 = 0, \\ \text{if } f1 > 14, \text{ then } f2 = 2, \\ \text{otherwise } f2 = f1 \end{cases}$
Number of seeds contributed to the seed bank at time i+1	Fall	$B_{i+1} = (f1 * 10 * A_i) + (f1 * 0.5 * S_i) + (0.01 * B_i)$
	Spring	$B_{i+1} = (f1 * 5 * A_i) + (f1 * 0.25 * S_i) + (0.01 * B_i)$
Number of seedlings at time i+1	Both	$D_{i+1} = f1 * 0.35 * B_i$
Number of yearlings at time i+1	Both	$Y_{i+1} = 0.15 * D_i$
Number of juveniles at time i+1	Both	$J_{i+1} = (0.35 * Y_i) + (0.20 * J_i)$
Number of subadults at time i+1	Both	$S_{i+1} = (0.51 * J_i) + (0.20 * S_i)$
Number of adults at time i+1	Both	$A_{i+1} = (0.66 * S_i) + (0.86 * A_i)$

TABLE 2. EQUATIONS USED TO DETERMINE SIMULATED POPULATION LEVELS OF CHEATGRASS REPRESENTED IN FIGURE 6.

Description	Equation
Seed bank persistence stochasticity	$b = N[0.015, 0.0026],$ $where\ 0 \leq b \leq 1$
Germination stochasticity	$g = N[0.30, 0.062],$ $where\ 0 \leq g \leq 1$
Seedling survival stochasticity	$s = N[0.82, 0.027],$ $where\ 0 \leq s \leq 1$
Density-dependent seed production	$f1_i = A_i * \left(\frac{77.9 * A_i}{1 + A_i^{1.36}} \right),$ $where\ 0 \leq f1_i \leq 10{,}000$
Number of seeds contributed to the seed bank at time i+1	$B_{i+1} = b * B_i + f1_i$
Number of reproductive plants at time i+1	$A_{i+1} = g * s * B_i$