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Modeling the Population Dynamics of Pacific Yew

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Abstract

A study of Pacific yew *(Taxus brevifolia* Nutt.) population dynamics in the mountains of western Oregon and Washington was based on a combination of long-term population data and computer modeling. Rates of growth and mortality were low in mature and old-growth forest stands. Diameter growth at breast height ranged from 0 to 3 centimeters per decade. The annual mortality rate for individuals >5 centimeters in diameter at breast height was about 1 percent of the population. A matrix population model was constructed by using these and other fundamental data on yew population dynamics. The model was designed to perform population viability analyses of yew under various harvest regimes. Model projections suggested a slow rate of recovery from major disturbance.

Keywords: Matrix population model, Pacific yew, *Taxus brevifolia,* population dynamics, population viability analysis.

Introduction

Pacific yew (*Taxus brevifolia* Nutt.) is a small, slow-growing tree of Northwestern coniferous forests (Bolsinger and Jaramillo 1990). With the recent discovery of taxol, an anticancer agent from the tissues of Pacific yew, the species has received much attention (USDA Forest Service 1992). Natural populations of the species have been harvested over large areas of the Pacific Northwest for taxol production. Although pressure on the species will probably decline as other sources of taxol are eventually developed, harvesting of wild populations may continue for some time, raising concerns about the effects this will have on the sustainability of Pacific yew populations in western North America.

In response to these concerns, interim management guidelines for the conservation of yew were recently developed (USDA Forest Service 1992). They require the establishment of genetic reserves for yew, replanting of yew after harvest, and retention of some live yew trees in harvesting areas. Before the recent interest in yew, it was cut during clearcut logging operations with no provision for regeneration or consideration of the effects on the population as a whole. Consequently, conservation of the species may be better ensured now that it has become a valuable product rather than being considered a worthless tree. Impacts on the population may have been particularly strong during the 1970s and 1980s when timber production in the Pacific Northwest was high. For conservation and management of the species to be successful, scientific information is needed on the ecology of Pacific yew and its population dynamics in response to human and natural disturbances.

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In this paper, we outline some of the characteristics of the ecology and population dynamics of Pacific yew based on recent studies. In addition, we present a modeling approach to assessing the potential impacts of harvesting on wild populations at stand and landscape levels.

Methods and Results

Growth and Mortality Data

Census data from long-term ecological research plots in forests of the central Oregon Cascade Range and Mount Rainier National Park in Washington were analyzed to determine rates of yew growth and mortality. In mature and old-growth stands, yew exhibited slow diameter growth and a low mortality rate. Annual diameter growth at breast height typically ranged from 0 to 0.3 centimeter when averaged over a period of about 10 years. The average diameter growth increment from a sample of 979 individuals greater than 5 centimeters in diameter at breast height (d.b.h.) was 0.082 ± 0.092 centimeter per year (mean and standard deviation). This was reasonably close to the estimate of 0.06 centimeter per year from independent data on yew beneath dense overstories (Bolsinger and Jaramillo 1990).

Mortality rates for yew populations in the reference stands were low. The annual mortality rate for all individuals greater than 5 centimeters d.b.h. was 0.0083 of the total. The maximum life span of yew has been determined to be at least 250 years (Liegel and Bailey 1993), making it a relatively long-lived tree species. The estimated annual mortality rate of 1 percent or less was similar to that of various long-lived tree species (Franklin and DeBell 1988, Harcombe 1987, Spies and others 1990).

Population Modeling

A stage-projection matrix model (Lefkovich 1965) was developed to simulate yew population dynamics in old-forest stands. This modeling study was limited to old stands simply because there are more data on Pacific yew from such stands for model parametrization. Seven stage classes, based on stem height or d.b.h., were chosen for the model (fig. 1). Simulations involved the movement of individuals from one stage class to another over a time step of 1 year. The possible exchanges among stages, indicated as transition pathways (fig. 1), were based on information concerning yew growth and reproduction. Annual transition probabilities of advancement from one stage to another were estimated from the permanent plot data on growth and mortality and estimates of stage duration (Caswell 1989). They are presented here in matrix format (table 1). Preliminary simulation of reproduction followed the approach of Huenneke and Marks (1987) where reproduction was assumed to be proportional to stem diameter. In the case of yew, it was further assumed that reproduction from live stems <1.5 meters tall was negligible. Further research is needed to evaluate the accuracy of the reproductive parameters used in this modeling exercise.

The model was implemented with RAMAS-stage software[1] (Applied Biomathematics, Setauket, NY; Ferson 1990) on an IBM PC compatible computer. A dominant eigenvalue slightly greater than 1.0 (1.02) was calculated from the transition probability means, thereby indicating a growing population. This attribute of the model seemed reasonable for yew in old stands. Indeed, field observations suggest that this shade-tolerant species gradually increases in abundance as forest stands age (Busing and others 1995). Further information on the model is presented in the appendix.

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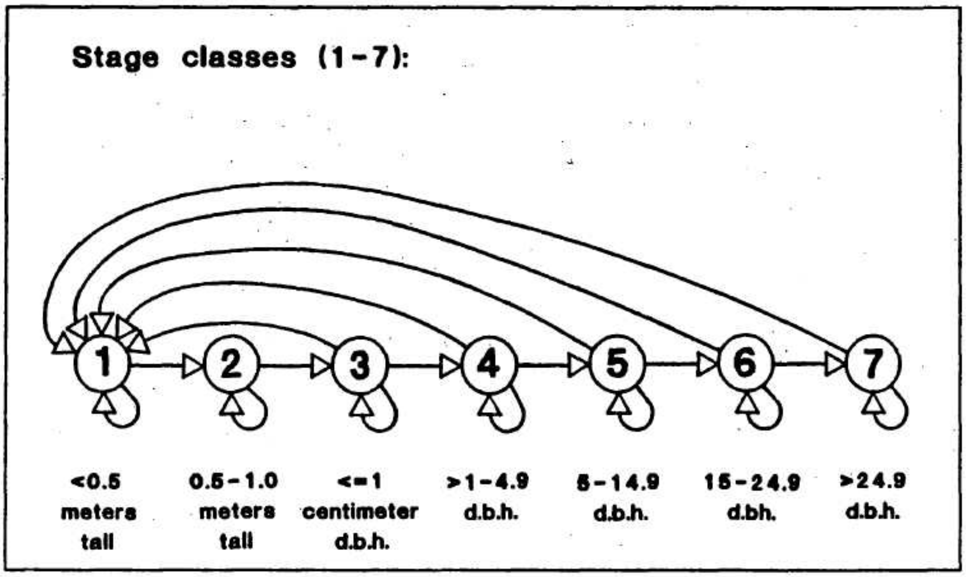

Figure 1—Preliminary stage-projection matrix model for Pacific yew populations in old-growth stands. Seven stages are based on tree size (height or d.b.h. classes). Transition pathways indicating the advancement or production of individuals from one stage to another over time are shown with arrows.

Table 1—Stage-projection matrix for Pacific yew populations in old forests

	Donor stage class						
Recipient class	1	2	3	4	5	6	7
1	0.88	0	0	0.12	0.16	0.2	0.24
2	.09	.88	0	0	0	0	0
3	0	.08	.89	0	0	0	0
4	0	0	.07	.97	0	0	0
5	0	0	0	.025	.99	0	0
6	0	0	0	0	.005	.99	0
7	0	0	0	0	0	.009	.993

Preliminary simulations of Pacific yew population dynamics in old-forest stands indicated a population with steady but slow growth. A localized population simulation of changes in total size over 200 years reflected an effectively sound population. The simulation was based on 50 replications with normally distributed variation (variance/mean = 0.01) in all transition parameters. Mean population size increased gradually from about 300 to 500 individuals per hectare over the period (fig. 2). The mean population size of individuals >5 centimeters d.b.h., referred to here as "the harvestable population," showed an initial decline followed by a gradual increase (fig. 3). The mean size of this population ranged from about 40 to 60 individuals per hectare.

Population recovery after simulated harvest of individuals >5 centimeters d.b.h. is slow. Although total mean population size rises slowly and continuously after harvest, it does not reach levels characteristic of old natural populations even after two centuries of recovery (fig. 4). Similarly, mean population size of individuals >5 centimeters d.b.h. (the harvestable population) recovers slowly (fig. 5). The most rapid increase occurs in the first half century of recovery. It is followed by a relatively gradual increase in the number of harvestable individuals, but even after two centuries, the mean level remains low in comparison with natural old populations.

Preliminary population viability analyses were conducted with the model. Viability analysis with matrix models involves running multiple simulations and varying transition probabilities among simulations so that each one is unique. In this case, transition probabilities differ randomly in a normal distribution with a variance of 1 percent of the mean. The resulting trajectories of population size over time are then examined. The fraction of simulations in which population size falls below a critical threshold (predetermined by the investigator) provides an estimate of population vulnerability to local extinction. The greater the fraction of simulations falling below the critical size, the greater the risk of local extinction. Conversely, one also can examine the propensity for population explosions (population size rises above a specified threshold) with this approach. Sample outputs from extinction and explosion analyses are described below.

Population size (reported in stems per hectare) did not fall below 100 in any of the 50 replicate simulations of population dynamics in old forests. Minimum population sizes attained throughout the duration of each simulation replication are known as "interval quasiextinction levels." They ranged predominantly from 100 to 300 individuals (fig. 6). Thus, the simulations suggested a low propensity for declines in natural populations. Maximum population sizes attained throughout the duration of each simulation replication are called "interval quasiexplosion levels." They generally ranged from 350 to 800 individuals (fig. 7). Population size exceeded 800 in about 10 percent of the replications, thereby suggesting occasional population growth to very high levels.

Viability analyses for populations subjected to harvest of all individuals >5 centimeters d.b.h. indicate that such populations may be at greater risk of decline. For example, total population size falls below 100 in almost 20 percent of the replicate simulations (fig. 8). Although this may not be detrimental to population viability, it does show a greater propensity for decline of harvested populations. Minimum population sizes generally ranged from 80 to 200 individuals, well below those of the simulations for undisturbed populations.

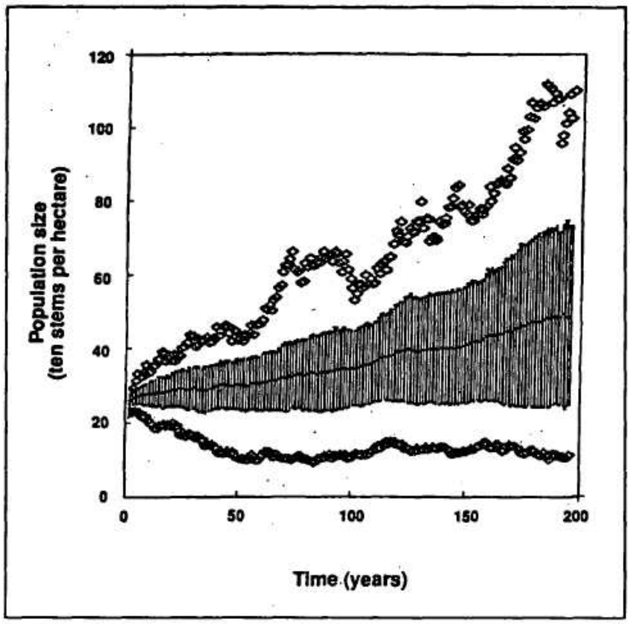

Figure 2—Simulations of total population size vs. time for an undisturbed population of Pacific yew in old forests. The trajectory of total population size vs. time is summarized for 50 replications. Mean population sizes and standard deviations are represented by lines and vertical bars, respectively. Minima and maxima of population size are indicated by diamonds.

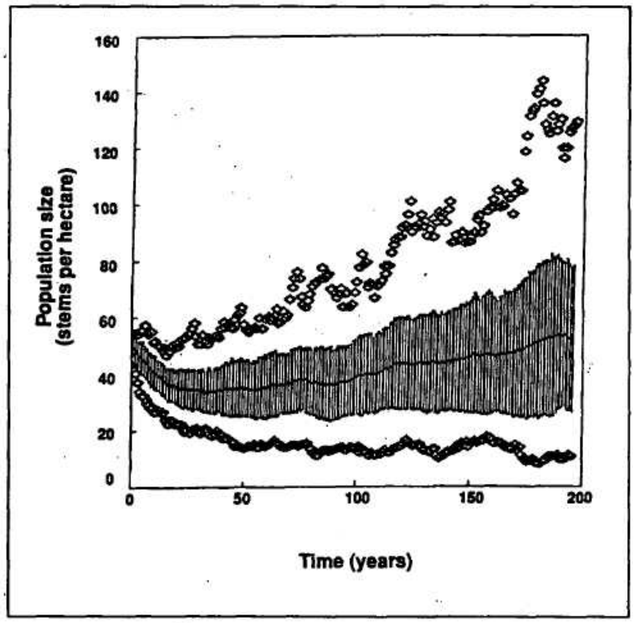

Figure 3—Simulations of tree (>5 centimeters d.b.h.) population size vs. time for an undisturbed population of Pacific yew in old forest. See figure 2 for interpretation.

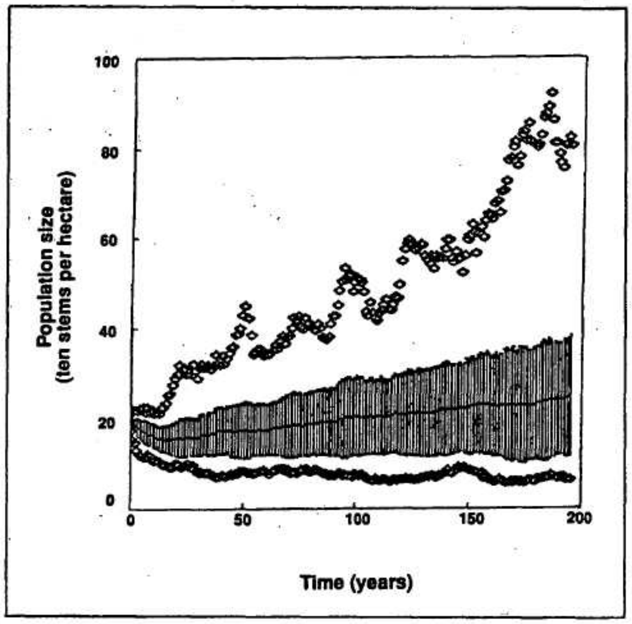

Figure *4*—Simulations of total population size vs. time for harvested population of Pacific yew in old forest. Stems >5 centimeters d.b.h. are absent at time zero.

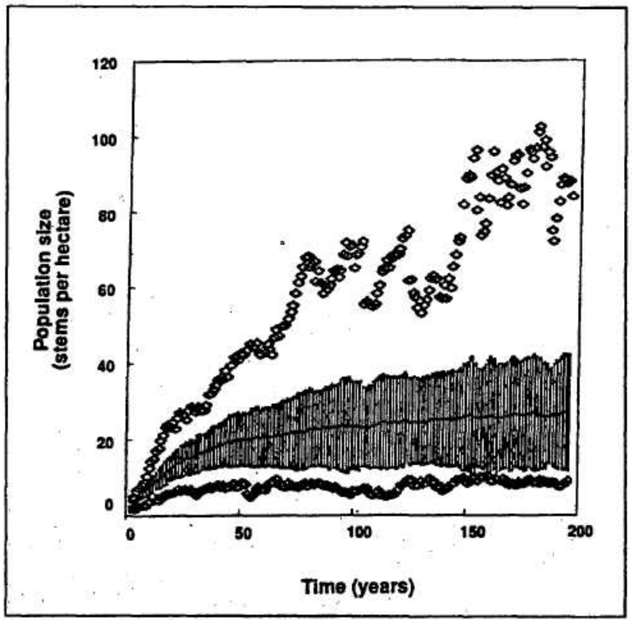

Figure 5—Simulations of tree (>5 centimeters d.b.h.) population size. vs. time for harvested population of Pacific yew in old forest. Stems >5 centimeters d.b.h. are absent at time zero.

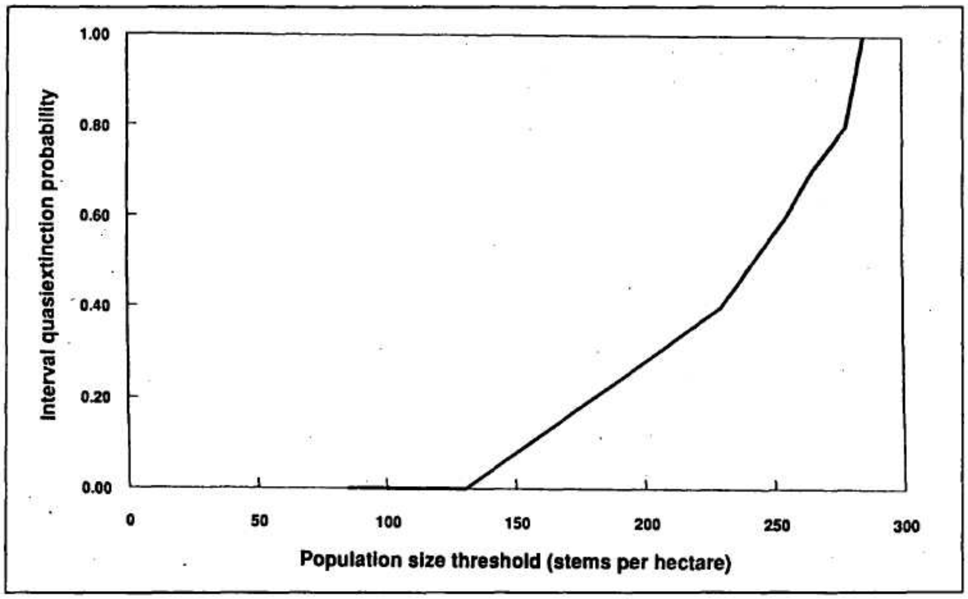

Figure 6—Extinction probability diagram for an undisturbed population. Population size minima from 50 replications over the 200-year simulation interval are interpreted as quasiextinction probabilities. The probability that the total population will fall below a given size is plotted for a range of minimum population size thresholds. Given a specific minimum viable population size, one can determine the extinction probability for the population from this diagram.

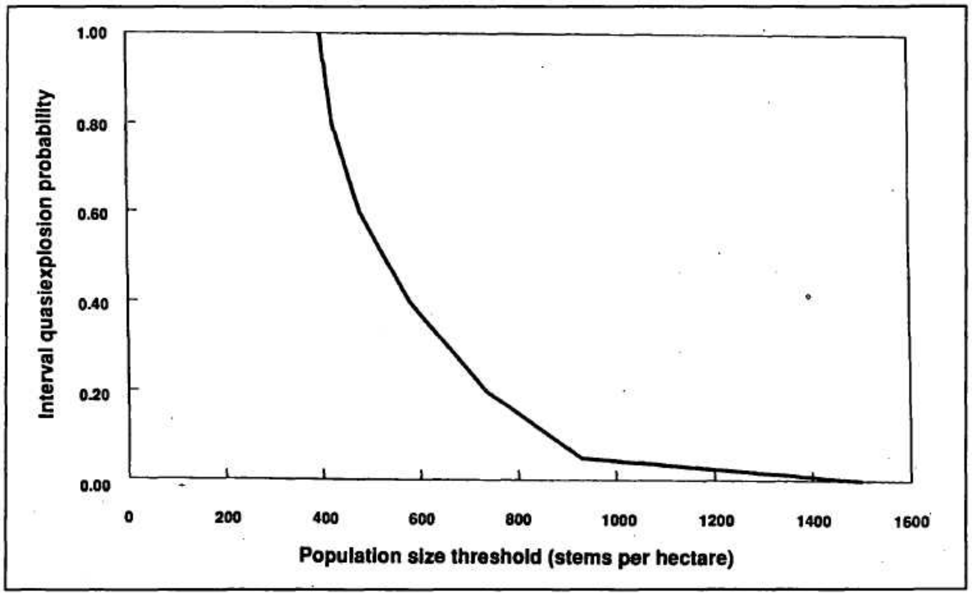

Figure 7—Explosion probability diagram for an undisturbed population. Population size maxima from 50 replications over the 200-year simulation interval are interpreted as quasiexplosion probabilities. The probability that the population will rise above a given size is plotted for a range of maximum population size thresholds.

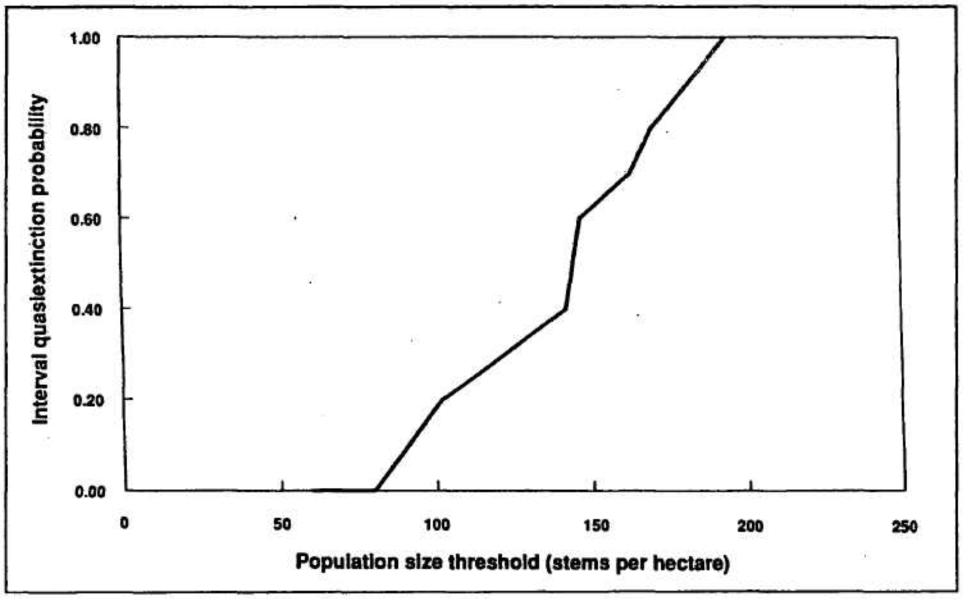

Figure 8—Extinction probability diagram for a harvested population. Population size minima from 50 replications over the 200-year simulation interval are interpreted as quasiextinction probabilities. The probability that the total population will fall below a given size is plotted for a range of minimum population size thresholds. Given a specific minimum viable population size, one can determine the extinction probability for the population from this diagram.

Discussion

These preliminary simulations corroborate empirical findings that the dynamics of yew populations are relatively slow (Busing and others 1995, Franklin and DeBell 1988, Halpern 1989). Undisturbed populations show little change in size and structure over periods of several decades, and disturbed populations may require centuries to recover the population size and structure characteristic of old-forest stands.

The fact that yew is a slow-growing species requiring several decades or more to recover from disturbance makes careful management planning essential. Quantitative projections of long-term population trajectories under various management regimes are potentially useful in the planning process. These projections must be based on realistic models, however. To project the effects of harvesting on yew populations, it is necessary to understand the autecology of Pacific yew. We have quantitative information on yew growth and mortality in older, closed-canopy forests; it would be ideal to have comparable information for yew in other habitats, including young forests recovering from disturbance. More information on yew regeneration also would be helpful. Factors related to sexual reproduction, including reproductive maturity, pollen production and dispersal, seed production and dispersal, seed viability, seed germination, and seedling survival, are poorly understood, yet they may be critical to population dynamics. Similarly, factors related to vegetative reproduction are poorly understood (Minore and Weatherly 1994) but potentially important. For landscape-level analyses, quantitative information on dispersal capabilities is heeded. Genetic analyses of yew distributed across a landscape may indicate levels of gene. flow, and provide clues on the importance of sexual reproduction in natural populations.

For management purposes, information is needed on conditions that do not favor yew regeneration. Even if the mechanisms of regeneration are poorly understood, simply considering the factors that limit regeneration may be sufficient to produce useful model projections. Studies by Crawford (1983) and Halpern (1989) suggest that intense burning retards yew recovery, and fire should not be implemented in preparation of sites where yew regeneration is desired.

The fact that yew is often most abundant in old-growth forests must be considered in management for population viability. Some proposed management alternatives call for the protection of yew in habitat conservation areas set aside primarily for conservation of the northern spotted owl. If yew harvest is disallowed in these old-growth and mature forest dominated landscapes, then large numbers of yew will remain in their natural state, and populations are likely to persist in these areas without further management. How such populations might affect the recovery of harvested populations in surrounding areas is unknown. It is likely, however, that unless yew seed dispersal is widespread and abundant, yew populations in the conservation areas would have little short-term effect on the recovery of harvested populations. Instead, their primary benefit would be as genetically diverse reserves of yew that could have implications for population maintenance over the long term. For these reasons, the management decisions related to yew in habitat conservation areas may strongly affect the long-term dynamics of the yew population as a whole.

The Pacific Northwest landscape is becoming an increasingly fragmented patchwork of forest stands of contrasting ages and disturbance histories (Spies and others 1994). For this reason, a single stand-level approach to modeling population viability is not ideal. This is particularly true for Pacific yew because it seems to be scattered over the landscape rather than concentrated in a few localized populations. Because yew establishment, growth and survival patterns may be strongly related to canopy cover, several different population projection models may be needed to characterize its population dynamics in a heterogeneous landscape. Where yew has been eliminated from a watershed or a landscape unit by extensive clearcut logging or wildfire, it is desirable to know how long it might take seeds to reach the area and populations to recover to levels observed in older forests. Only recently have landscape-level models been used in studies of population viability (Gilpin 1987), and there is room for improvement and refinement of these approaches. Landscape models require more information than localized population models, but if adequate information is available for the parametrization of such models, their projections are likely to be more useful in management planning.

The use of matrix models in population viability analyses is somewhat controversial. The basic argument against their use is the lack of data to fully parameterize and test the models (Mann and Plummer 1990). Temporal variation in transition probabilities is a key element of this approach to assessing population viability. Data on such variation generally is lacking as well (Menges 1992). Both of these arguments apply to current efforts to model population viability in Pacific yew. Although the projections of the model presented here seem reasonable, the reliability of viability analyses performed with such a model can be evaluated only with substantial long-term data on the demography of Pacific yew.

After further testing and refinement of the localized population model, it can be applied to test the effects of various harvest regimes on yew population dynamics. Impacts on population size, local extinction probabilities, and population recovery can be explored. Ultimately, models of this form can be employed as elements in a landscape-level simulation of many interacting populations. Simulations at this scale may be particularly useful in the management of yew.

Acknowledgments

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Appendix

Additional information on the stage-classified matrix model is provided below (tables 2-3 and figs. 9-12). Interpretation of this information may be aided by reference to Caswell (1989) or other literature on matrix population models.

Table 2—Sensitivity matrix corresponding to the stage-class model[a]

	Donor stage class						
Recipient class	1	2	3	4	5	6	7
1	0.111	0.070	0.043	0.057	0.044	0.007	0.002
2	.176	.111	.067	.090	.070	.011	.003
3	.313	.198	.120	.161	.125	.019	.005
4	.591	.374	.226	.303	.235	.037	.011
5	.700	.443	.268	.359	.279	.043	.013
6	.946	.599	.362	.486	.377	.058	.018
7	.914	.579	.350	.469	.364	.056	.017

[a] Sensitivity values indicate how strongly population growth is affected by changes in any given transition matrix element.

Table 3—Elasticity matrix corresponding to the stage-class model[a]

	Donor stage class						
Recipient class	1	2	3	4	5	6	7
1	0.096	0	0	0.007	0.007	0.001	0.000
2	.015	.096	0	0	0	0	0
3	0	.015	.104	0	0	0	0
4	0	0	.015	.288	0	0	0
5	0	0	0	.009	.270	0	0
6	0	0	0	0	.002	.057	0
7	0	0	0	0	0	.001	.016

[a] Elasticity values indicate the sensitivity of population growth to proportional changes in a given transition matrix element.

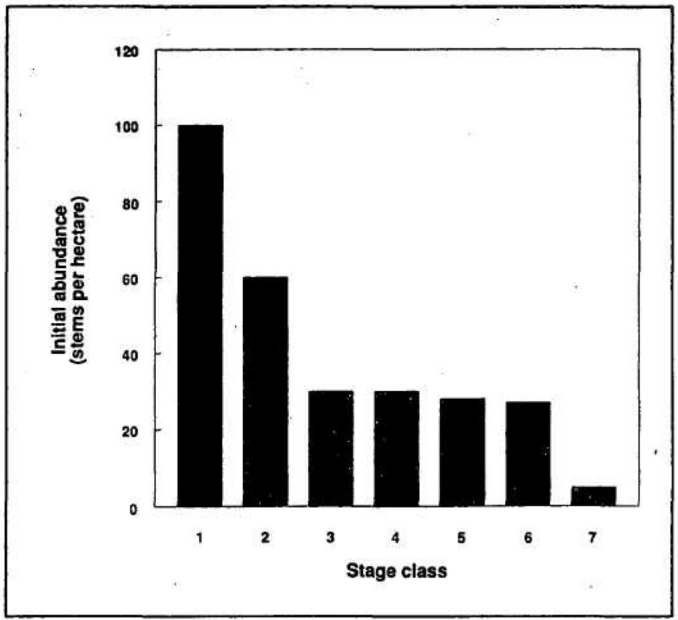

Figure 9—Initial abundances for simulations of population dynamics . by stage class. Initial abundances for harvested populations were similar except values for stages 5-7 were set to zero.

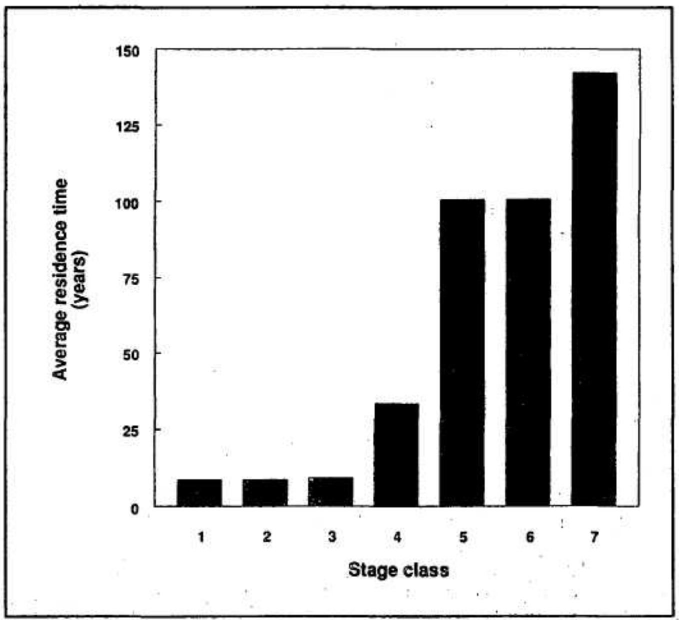

Figure 10—Average residence times by stage class.

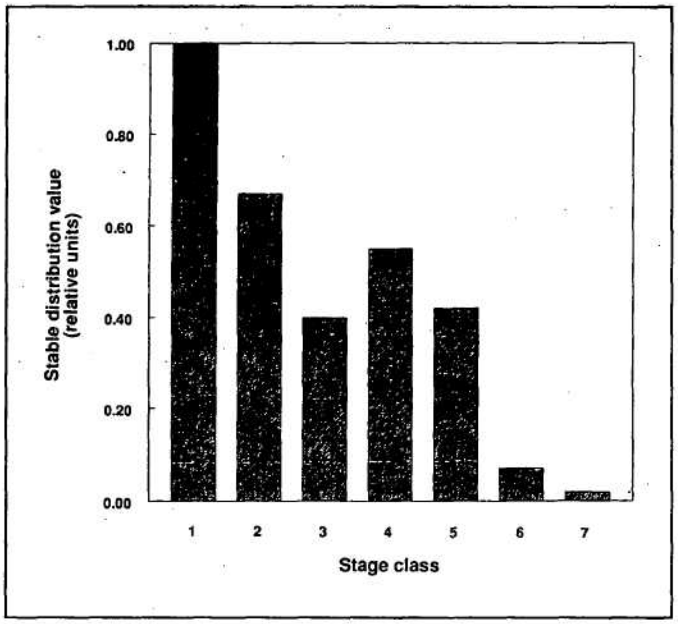

Figure 11—Stable population distribution showing the proportion of individuals by stage class.

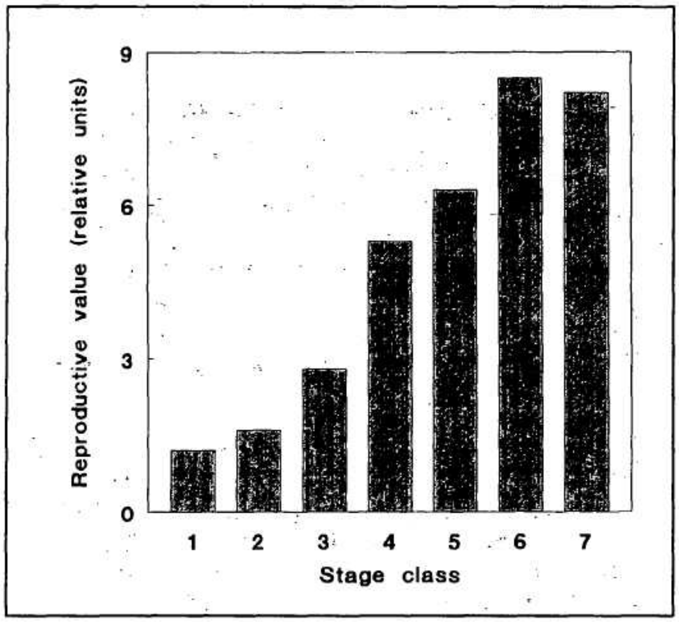

Figure 12—Reproductive values by stage class. These indicate the contribution of individuals in each stage to total population abundance.

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