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ALTERNATIVE SILVICULTURAL REGIMES IN THE PACIFIC NORTHWEST: SIMULATIONS OF ECOLOGICAL AND ECONOMIC EFFECTS[1]

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Abstract. New silvicultural strategies to sustain both ecological and human communities are being developed and implemented on federal forest lands in the Pacific Northwest (PNW) United States. Two important stand-level components of the new silviculture regimes are rotation age and retention level of live trees in harvest units. Ecologists have suggested that canopy tree retention and longer rotations will create patterns of stand structure in managed forest that are similar to those in natural forests, and promote long-term ecological productivity and biodiversity. Forest economists, however, are concerned that canopy tree retention and long rotations may reduce wood production, although the high value of large logs produced by these new silvicultural regimes may compensate for reduced growth rates.

We used the forest model ZELIG to perform a factorial simulation experiment on long-term responses of ecological and economic variables to nine retention levels and four rotation lengths. ZELIG output on forest structure and composition was input to a forest economics model that calculated net value of wood products in 1989 dollars. The simulated stand data were also linked with regression equations to predict the densities of 17 bird species as a function of tree size class distribution. Five replicates of each treatment were run for the 240-yr simulation period.

Results indicated that stand structure under each of the canopy tree retention levels was more similar to the pre-treatment natural forest than following clear-cutting. Variation in tree size under intermediate levels of retention, however, did not reach the level of the natural forest during the simulation period. Tree species composition was strongly related to retention level and rotation age. Shade-intolerant Douglas-fir (*Pseudotsuga menziesii*) lost dominance to shade-tolerant species under intermediate retention levels and longer rotations. Wood production decreased significantly with increasing retention level and rotation age, with a notable threshold between retention levels of 0 and 5 trees per hectare. Net wood products value did not decrease as rapidly with retention level, and did not differ much among rotation ages, because of the high value of large logs. Bird species responded individualistically to retention level and rotation age. Some had peak densities under short-rotation clear-cutting, but most were associated with structurally complex, closed-canopy forest. Consequently, bird species richness increased significantly with retention level and rotation age.

Within the assumptions and limitations of our models, this application provided knowledge on trends and thresholds that can help land managers to choose silvicultural regimes that best balance their management objectives. We concluded that retention level and rotation age strongly influence ecological and economic responses in PNW forests; efforts are needed to reduce uncertainty about these effects.

Key words: adaptive management; biodiversity; conservation; ecosystem management; forest economics; natural forests; Pacific Northwest; silviculture; simulation models; trade-off analyses; wood production.

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INTRODUCTION

A new paradigm is emerging in ecology that views humans as integral parts of ecological systems (Costanza et al. 1993). Strong feedbacks are seen to closely couple human well-being with the state of ecological systems. Accordingly, society is demanding that natural resource policy be based on analyses of interactions among socioeconomic and ecological factors across multiple temporal scales (Ervin and Berrens 1993). Such analyses are central to the current debate over forest management on Federal lands in the Pacific Northwest (PNW) United States. The goal on many of these lands is now to sustain both ecological processes and human communities. New stand- and landscape-level silvicultural strategies have been devised and implemented to achieve this goal (Franklin 1992). The long-term economic and ecological consequences of these strategies are not well known.

Two stand-level components of silviculture under close scrutiny in the PNW are rotation age and retention level of live trees in harvest units (Gillis 1990). Traditionally, National Forest lands in the region were clear-cut on a 60–100 yr rotation to favor commercial tree species, maximize wood production, and provide habitat for game species. Recently, ecologists have advocated retaining some live trees in harvest units (rather than clear-cutting) and lengthening the rotation to maintain structural complexity in forest stands and to provide more late seral habitats (Franklin 1988, 1992, Swanson and Franklin 1992, Verner et al. 1992).

The rationale for canopy tree retention and longer rotations is based on patterns of disturbance and succession in natural PNW forests. Disturbances resulting in stand replacement recurred on scales of 150–500 yr in presettlement times on mesic sites on the western slopes of the Cascades (Morrison and Swanson 1990). Mature and old-growth stands covered 40–60% of the landscape through time, providing the structurally complex habitats required by many organisms (Harris 1984, Forest Ecosystem Management Assessment Team 1993). Even young natural forests were highly variable in tree size and canopy layering because of the "legacies" of structures that commonly survived disturbance in the region (Spies et al. 1988). Thus, high levels of structural complexity are characteristic of all ages of natural forest in the PNW (Hansen et al. 1991). This structural complexity is associated with several ecological properties, including ecological productivity and biodiversity (Franklin et al. 1989, Hansen et al. 1991).

Ecologists have suggested retaining canopy trees and lengthening rotations in managed forests to produce larger trees, greater variability in tree size, multistoried canopies, and recruitment of large woody debris. The hypothesized benefits of this structural complexity include maintenance of: tight nutrient cycles; refugia and inocula for nonvagile mycorrhizae and nitrogen-fixing bacteria; beneficial predator–prey relationships among forest invertebrates; habitats for vascular plants and vertebrates that require either structural complexity and/or late-seral stands; and dispersal opportunities for species that avoid forest openings (Franklin 1992, Swanson and Franklin 1992). Studies designed to test many of these hypotheses are now underway in the PNW.

Initial results for breeding birds indicate that both level of canopy retention and forest age are strongly correlated with abundance of many bird species. Vega (1993), Hansen and Hounihan (1995), and Hansen et al. (1995) examined bird distributions across a range of stand structures and ages in the western Oregon Cascades. They found that bird species responded individualistically to canopy tree density and forest age. Some species were primarily associated with each of the following stand types: open-canopy without overstory; open-canopy with overstory; structurally simple closed-canopy; and structurally complex closed-canopy. Many bird species showed nonlinear relationships with canopy tree density, suggesting thresholds in tree density where habitat quality changes abruptly. At least three ecological factors may link canopy tree density and bird communities: pathways of net primary productivity, habitat niche diversity, and nest predation rates (Hansen et al. 1994).

Canopy tree density and rotation length also may have consequences for wood production and economics. Overstory retention may be more costly than clear-cutting in terms of layout and logging costs (Kellogg et al. 1991, Weigand and Burditt 1992), but the greatest concern is over wood production and value. Shade cast by overstory trees may reduce the growth rates of regenerating Douglas-fir (*Pseudotsuga menziesii*) (Birch and Johnson 1992), a shade-intolerant species of high commercial value in the region. Moreover, long rotations require that capital be held for longer time periods, and economists argue that temporal increase in forest value must exceed a "discount rate" to allow longer rotations to be profitable (Birch and Johnson 1992). Such reductions in wood production and discount effects may be offset in part, however, by the higher value of large-dimension, high-quality trees produced by canopy retention and long rotations (Weigand 1994).

Clearly, trade-off analyses are needed on the relative costs and benefits of alternative silvicultural strategies for biodiversity, economics, and other factors (Liu et al. 1994). Analysis of the likely consequences of different management scenarios is a key component of adaptive ecosystem management (Walters 1986, Everett et al. 1993, Hansen et al. 1993). Such analyses allow forest managers to make rational decisions, even when response variables cannot be quantified by one currency (Ervin and Berrens 1993). Computer simulation models are useful for performing such analyses for forest ecosystems, where the temporal dynamics are too slow to be amenable to short-term experiments (Shugart 1984).

The goal of this study was to determine the likely long-term responses of ecological and economic variables under a range of retention levels and rotation lengths. The key response variables were stand structure and composition, breeding bird densities and richness, wood production, and value of wood products. The study was done as a factorial simulation experiment with nine levels of retention and four rotation ages. We were particularly interested in quantifying the trends in the response variables across the treatments, and in identifying thresholds where changes in response are abrupt. Knowledge of these thresholds can help managers choose silvicultural strategies that best balance competing objectives.

Study area

Data for calibrating the simulation models were derived from forests in the Western Cascades Province (Franklin and Dyrness 1973) in western Oregon. This topographically complex landscape was created by volcanic activity during the Oligocene and Miocene epochs. The present climate is wet (precipitation 1500–3000 mm/yr) and mild (mean annual temperature 8°–9°C), with most precipitation during winter and spring. The Province is within the *Tsuga heterophylla* Vegetation Zone, with dominant tree species including western hemlock (*Tsuga heterophylla*), Douglas-fir, and western redcedar (*Thuja plicata*).

Most of the lands in this area are managed by the Willamette National Forest and private timber companies. Forest productivity is high in the region and the forest products industry is important in many local communities. Natural forests in the Willamette National Forest have been highly fragmented by clear-cutting under a staggered-setting harvest design (Ripple et al. 1991). These landscape patterns have jeopardized the viability of various animal species, including the Northern Spotted Owl (*Strix occidentalis*) (Thomas et al. 1990, Forest Ecosystem Management Assessment Team 1993). In recent years, new silvicultural designs have been implemented in the Willamette National Forest to retain various levels of canopy trees, snags, and coarse woody debris within harvest units. Most of the private lands have been converted to short-rotation plantations using an aggregated-clearcut harvest system (Ripple et al. 1991).

METHODS

Our general approach was to simulate alternative silvicultural scenarios with a forest succession model, an economics model for stumpage and wood products, and statistical habitat functions for birds. Each of the models was calibrated with local data. We simulated stand dynamics for a 240-yr period under the different silvicultural regimes using the gap model, ZELIG (Urban 1990). The stand data were then input into the economic model to calculate volume and value of stumpage and wood products. The stand data also were linked with regression equations to predict bird density as a function of tree size class distribution.

Forest model ZELIG

ZELIG.PNW.2.0 (Urban 1992) is a version of the mechanistic gap model ZELIG (Urban 1990), modified for application in forests of western Oregon and Washington. ZELIG descends from the FORET model of Shugart and West (1977). These models simulate the annual establishment, diameter growth, and mortality of individual stems on a small model plot (0.06 ha) corresponding to the zone of influence of a canopy-dominant tree. The basic approach used to model growth and establishment is to begin with maximum potential behavior (i.e., maximum growth and inseeding rates), and subsequently constrain this potential based on available light, soil fertility and moisture, and ambient temperature. Mortality is modeled as a probabilistic function of maximum age and number of years of suppressed growth. Input parameters include a list of potential tree species and species-specific values for: maximum age and diameter; relative tolerances to shading, moisture, and nutrient stress; maximum growth rate; seedling establishment rate; and minimum and maximum temperatures of the current geographical range. Additionally, monthly temperature and precipitation means and variances for the elevation of a simulation run are required to simulate ambient weather conditions.

ZELIG.PNW.2.0 (Urban 1992) differs from the original version of ZELIG (Urban 1990) in using a new tree height per diameter function, in considering more explicitly the effect of leaf area on tree growth, and in considering soil moisture in more detail. ZELIG.PNW.2.0 can be run either in independent-plot mode or in grid-mode, where simulated plots are arrayed over a grid and interact relative to shading. The ability to design and implement silvicultural prescriptions was also added to the model (Garman et al. 1992).

Tree species parameters for our study area were derived from literature reports and detailed field studies (Garman et al. 1992, Garman et al., *in press*). Regression equations were used to estimate local and regional temperature and precipitation values (Urban et al. 1993). Calibration and testing of the ZELIG.PNW.2.0 under current climatic conditions have been performed using extensive field data sets from the western Oregon Cascades (Garman et al. 1992). Initial tests of model performance at 1000 m elevation have indicated good agreement between observed and predicted dynamics of unmanaged stands over a 500-yr period (Fig. 1). ZELIG.PNW has been used to simulate effects of climate change (Urban et al. 1993) and alternative silviculture (Garman et al. 1992, Hansen et al. 1992, 1993).

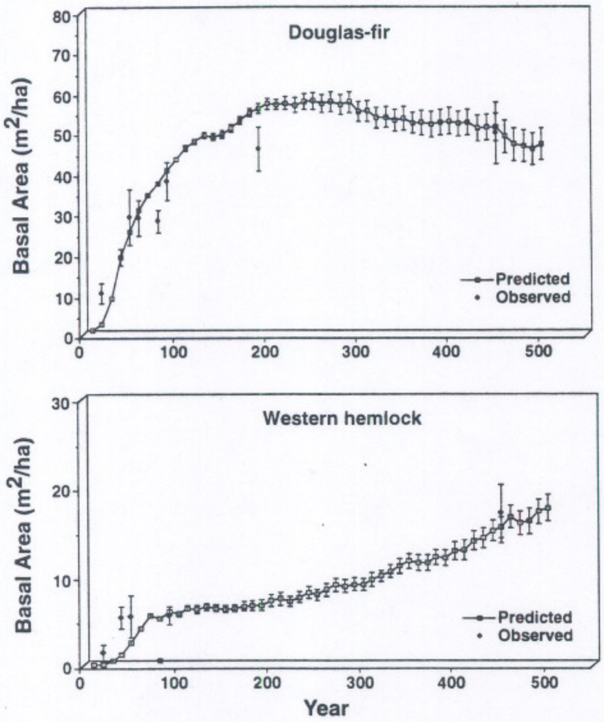

FIG. 1. Observed and simulated basal area (mean ± SE) for the two dominant tree species at 1000-m elevation in the western Oregon Cascades. Simulated data are based on 36 model plots (0.06 ha each), using the grid version of ZELIG.PNW.2.0. Sample sizes of observed data varied from 3 to 20 plots per age class.

Bird habitat functions

The methods used to develop statistical models of bird habitat relationships are described in Hansen et al. (1995) and are summarized here. Data were derived from five bird habitat studies in the west-central Cascades of Oregon: Gilbert and Allwine (1991), Vega (1993), Hansen and Hounihan (1995), and W. C. McComb et al. (*unpublished data*). The 68 forest stands examined in these studies included eight clearcuts, 22 harvest units with canopy retention (range of canopy tree densities: 1.3–56 trees/ha), 16 young plantations, four mature stands that were commercially thinned, three young natural stands, seven mature natural stands, and nine old-growth stands. Stand ages were: 2–6 yr for clearcuts and retention units; 30–60 yr for young stands; 80–190 yr for mature stands; and 200–450 yr for old growth. These stands ranged in elevation from 366 to 1189 m and were 9 to >20 ha in area.

Birds were sampled during the breeding season using the Variable Circular-Plot method (Reynolds et al. 1980). Five to six plots were sampled in each stand, except for the OGWHS study, where 12 plots per stand were censused. Each plot was censused four to six times during May and June of the years studied. Only birds registered within 50 m of plot centers were included in the analyses. Graphs of detection distance indicated that the songs of all species could be reliably detected within this radius (Vega 1993); thus we calculated the relative abundance of each species as the number of individuals registered within the 50-m radius plot surrounding the plot center. Only species detected in ≥15 stands were included in the analyses. Under this study design, stands (and not census plots) were the independent units of analysis. Hence, the results for each bird species were averaged over plots within a stand and across censuses, and were analyzed as mean number of registrations per hectare per census.

We were able to derive four key habitat variables from the studies. These were densities of trees in each of four diameter at breast height (dbh) classes: TOT2 (10–30 cm), TOT3 (30–50 cm), TOT4 (50–90 cm), and TOT5 (>90 cm). Tree density by dbh class was averaged among plots within a stand and was expressed as trees per hectare. Some of the density classes were aggregated for the analysis into: TOT2_5, which combines all four classes; TOT345 = TOT3 + TOT4 + TOT5; and TOT45 = TOT4 + TOT5.

Linear and nonlinear regression were used to quantify relationships between bird abundance and each of the habitat variables. To meet the assumptions of these tests, log conversions (natural log(variable + 1)) of the bird abundance and/or the habitat variables were used to correct deviations from normality and constant variance. An "L" at the end of a variable name denotes a log conversion (i.e., TOT2L).

To determine the best model relating bird abundance to habitat, we first plotted the relative abundance of each species of bird against each individual habitat variable. Where the plots were generally linear, stepwise linear regression (P to stay = 0.05) was used to evaluate which variables contributed to significant models. Where the plots of bird abundance on habitat appeared nonlinear, the results of various polynomial and nonlinear functions were compared. These functions included second and third degree polynomial, Gaussian, Logistic, Lorentzian, and Extreme Value equations (TableCurve 1991). We selected "best" models and variable sets based on highest R^2 values (adjusted for degrees of freedom) and on the extent to which the models made sense ecologically for the bird species in question. For a few species, the best models predicted nonsensical bird abundances (i.e., negative bird density) at extreme habitat values. For these species, we carefully defined the domain over which the function is realistic.

Significant functions were developed for 17 of the 23 species that were recorded sufficiently for analysis. Hairy Woodpecker, one of these 17 species, was not included in this analysis because its abundance is probably influenced by snag availability, a habitat factor not considered in this study. The remaining functions explained 9–67% of the variance in bird density. Common and scientific names for the bird species included in this analysis are in Table 1, and the resulting habitat functions are in Table 2.

TABLE 1. Species included in this study of bird densities in relation to tree size class distribution.

Species code	Common name	Scientific name
AMRO	American Robin	*Turdus migratorius*
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*
BRCR	Brown Creeper	*Certhia americana*
CBCH	Chestnut-backed Chickadee	*Parus rufescens*
DEJU	Dark-eyed Junco	*Junco hyemalis*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
HAFL	Hammond's Flycatcher	*Empidonax hammondii*
HETH	Hermit Thrush	*Catharus guttatus*
HTWA	Hermit/Townsend's Warbler*	*Dendroica occidentalis/ D. townsendi*
MGWA	MacGillivray's Warbler	*Oporornis tolmiei*
PSFL	Pacific-slope Flycatcher	*Empidonax difficilis*
SWTH	Swainson's Thrush	*Catharus ustulatus*
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*
WEBL	Western Bluebird	*Sialia mexicana*
WETA	Western Tanager	*Piranga ludoviciana*
WIWR	Winter Wren	*Troglodytes troglodytes*

* These two species overlap and hybridize in the study area and are difficult to distinguish by song. Consequently, they were lumped in this study.

Merging results of the five bird habitat studies produced the most complete data set of this type available for our study area. An unknown amount of variation exists in the data set, however, because of differences among studies in observers, geographic location of study sites, sampling effort (either number of plots within a stand or number of censuses per plot), habitat sampling methods, and survey years. Another limitation of these data relevant to this application is that one important stand type, young stands (30–79 yr) with residual large trees, was not included in the study. Finally, independent data were not available for validating these functions.

Economic model

The computer program NEOTROP, written in BASIC, was used to compute net merchantable stumpage volume and value, lumber volume, and net wood products value (lumber + chips + sawdust) for each ZELIG output file. Seven tree species were considered: Pacific silver fir (*Abies amabilis*), noble fir (*A. procera*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), Douglas-fir, western redcedar, and western hemlock. Because information on growth and economic use of bigleaf maple is scanty, this species was treated as red alder.

Variables input from ZELIG included tree density by dbh class (5-cm dbh intervals) and tree species for each simulated harvest. Tree heights were estimated from dbh for each species using regression coefficients from Garman et al. (*in press*). Equations from Czaplewski et al. (1989: Tables 1 and 2) provided merchantable stem volumes (without defect) for Pacific silver fir, Douglas-fir, and western hemlock. Total tree volume was computed from stump height (0.15 m) to merchantable top height (diameter > 10 cm). Some ZELIG output exceeded tree sizes in the Czaplewski et al. data set. Thus, extrapolations from the Czaplewski et al. equations were used for simulated Douglas-fir trees with dbh > 196 cm and western hemlock with dbh > 145 cm. Volumes for noble fir were estimated using equations for California red fir (*Abies magnifica*) from the same study. Volumes for red alder were estimated from Curtis et al. (1968), and those for western redcedar were estimated from Garman et al. (*in press*).

Stem volume was reduced to account for defect (unmerchantable rot and checking in otherwise merchantable timber). This is particularly important for large trees. The volume deducted varied by species and dbh, using region-wide regressions from M. E. Harmon et al. (*unpublished manuscript*). Defect was estimated only for the three major species (Douglas-fir, western hemlock, and western redcedar), because the true fir and hardwood species did not attain sufficient size to incur much defect. Deduction for defect was assumed to be: $D_f = D_{max}/(1 + B_9 \cdot e^{-B_{10} \cdot \mathrm{dbh}})$, where D_f is percent deduction for defect; D_{max} is percent maximum possible defect, B_9 and B_{10} are regression coefficients; and dbh is tree diameter at breast height. For Douglas-fir, $D_{max} = 12.9$, $B_9 = 19\,774$, and $B_{10} = 0.093$; for western redcedar, $D_{max} = 95.9$, $B_9 = 89$, and $B_{10} = 0.051$; and for western hemlock, $D_{max} = 57.6$, $B_9 = 39$, and $B_{10} = 0.031$.

Merchantable stumpage volume was derived from bucking models we developed as LOTUS 1–2–3 (version 3.0) spreadsheets. These calculations used the aforementioned bole volume equations from a 0.15 m stump height to a 10 cm stem width. A 0.30-m length of the tree bole was assumed to be lost to saw kerf and damage between each long log created in the bucking model. Trees of all species except red alder were cut into logs 9.75 m (32 feet) long or into 2.44 m (8 feet) logs for the highest part of the stem unable to accommodate a full 9.75 m log. Red alder tree boles were cut into 4.88 m (16 feet) or 2.44 m (8 feet) lengths.

Lumber volume from the merchantable stumpage

TABLE 2. Habitat functions for the 16 species of birds showing significant habitat associations among the 67 stands sampled. For all species, if $\mathrm{LOG}(Y) < 0$ then $\mathrm{LOG}(Y) = 0$. LOG denotes natural log, and conversions were done as LOG(response variable + 1). Species abbreviations as in Table 1.

Species	Function	R^2	F	P	Notes
AMRO	$\mathrm{LOG}(Y) = 9.932/(1 + 105.720 \cdot \mathrm{EXP}(0.220 \cdot \mathrm{TOT2\_5LL}))$	0.09	9.5	0.001	If $\mathrm{TOT2\_5L} > 6.1$ then $\mathrm{LOG}(Y) = 0$
BHGR	$\mathrm{LOG}(Y) = 0.0061 + 0.00013 \cdot \mathrm{TOT2}$	0.19	15.0	0.0002	
BRCR	$\mathrm{LOG}(Y) = 0.0309 + 0.00055 \cdot \mathrm{TOT4} + 0.0024 \cdot \mathrm{TOT5}$	0.35	17.4	0.0001	If $\mathrm{LOG}(Y) < 0.031$ then $\mathrm{LOG}(Y) = 0$
CBCH	$\mathrm{LOG}(Y) = -0.0499 + 0.0672 \cdot \mathrm{TOT3L} + 0.0510 \cdot \mathrm{TOT4L} + 0.0760 \cdot \mathrm{TOT5L}$	0.58	28.7	0.0001	
DEJU	$\mathrm{LOG}(Y) = 0.5651 - 0.0654 \cdot \mathrm{TOT2\_5L}$	0.36	36.5	0.0001	
GCKI	$\mathrm{LOG}(Y) = 0.047 + 0.0014 \cdot \mathrm{TOT3} - 0.0012 - \mathrm{TOT4} - 0.0011 \cdot \mathrm{TOT5}$	0.63	35	0.0001	
HAFL	$\mathrm{LOG}(Y) = 0.0395 - 0.2445 \cdot \mathrm{TOT2\_5L} + 0.1374 \cdot \mathrm{TOT2\_5L}^2 - 0.0152 \cdot \mathrm{TOT2\_5L}^3$	0.45	17.4	0.0001	If $\mathrm{TOT2\_5L} < 1$ then $\mathrm{LOG}(Y) = 0$
HETH	$\mathrm{LOG}(Y) = -0.0046 + 0.00085 \cdot \mathrm{TOT3} - 0.00054 \cdot \mathrm{TOT4}$	0.65	59.1	0.0001	
HTWA	$\mathrm{LOG}(Y) = 0.1306 + 0.0022 \cdot \mathrm{TOT3} + 0.0034 \cdot \mathrm{TOT4} + 0.0032 \cdot \mathrm{TOT5}$	0.54	24.4	0.0001	If $\mathrm{TOT2\_5} = 0$ then $\mathrm{LOG}(Y) = 0$
MGWA	$\mathrm{LOG}(Y) = 0.0149 + 0.3142 \cdot \mathrm{EXP}(-0.5 \cdot ((\mathrm{TOT2\_5L} - 2.4253)/-0.9752)^2)$	0.35	15.3	0.001	If $\mathrm{TOT2\_5L} > 5$ then $\mathrm{LOG}(Y) = 0$
PSFL	$\mathrm{LOG}(Y) = 0.0030 + 0.0003 \cdot \mathrm{TOT2} + 0.0005 \cdot \mathrm{TOT3} + 0.0007 \cdot \mathrm{TOT4} + 0.0037 \cdot \mathrm{TOT5}$	0.67	31.7	0.0001	If $\mathrm{TOT2\_5} < 25$ then $\mathrm{LOG}(Y) = 0$
SWTH	$\mathrm{LOG}(Y) = 0.0120 + 0.0003 \cdot \mathrm{TOT2} + 0.0005 \cdot \mathrm{TOT3} - 0.0007 \cdot \mathrm{TOT4}$	0.58	29.4	0.0001	
WCSP	$\mathrm{LOG}(Y) = 0.0142/(1 - 0.9486 \cdot \mathrm{EXP}(-0.1430 \cdot \mathrm{TOT2\_5L}))$	0.24	15.0	0.001	If $\mathrm{TOT2\_5L} > 3.4$ then $\mathrm{LOG}(Y) = 0$
WEBL	$\mathrm{LOG}(Y) = 0.0102 + 0.1442 \cdot \mathrm{EXP}(-0.5 \cdot ((\mathrm{TOT2\_5L} - 1.7630)/0.5240)^2)$	0.26	9.2	0.001	If $\mathrm{TOT2\_5L} > 4.2$ then $\mathrm{LOG}(Y) = 0$
WETA	$\mathrm{LOG}(Y) = 0.0068 + 0.0680 \cdot \mathrm{TOT2\_5L} - 0.0213 \cdot \mathrm{TOT2\_5}^2 + 0.0017 \cdot \mathrm{TOT2\_5L}^3$	0.18	4.7	0.02	If $\mathrm{TOT2\_5} = 0$ then $\mathrm{LOG}(Y) = 0$; If $\mathrm{TOT2\_5L} > 6$ then $\mathrm{LOG}(Y) = 0$
WIWR	$\mathrm{LOG}(Y) = 0.0574/(1 + 333.86 \cdot \mathrm{EXP}(-1.549 \cdot \mathrm{TOT345L}))$	0.61	80.0	0.001	If $\mathrm{TOT2\_5} < 3.3$ then $\mathrm{LOG}(Y) = 0$

volume of long logs was based on best available information from mill utilization studies conducted by the Production of Goods and Services unit at the Pacific Northwest Research Station in Portland, Oregon, USA. Utilization of Douglas-fir was modeled on long-log equations for unmanaged stands developed by Willits and Fahey (1988). We based utilization of western hemlock and true fir species on regressions developed by S. Willits (*personal communication*) from a composite of western Oregon and Washington mill studies for western hemlock and true fir logs. Marlon Plank provided long-log utilization for red alder based on Plank et al. (1990).

Determination of lumber utilization for western redcedar is based on unpublished data from northern Idaho for lumber grade (T. Fahey, *personal communication*) and for utilization efficiency (lumber recovery) from mill studies for Ponderosa pine (*Pinus ponderosa*) in eastern Oregon (D. Parry, *personal communication*). Because many of the trees generated by ZELIG exceed dimensions covered in existing Forest Service mill studies, Douglas-fir and western hemlock logs with small-end diameters >99 cm were considered to have the same percentages of yield by grade as logs with small-end diameters of 99 cm. Western redcedar logs with small-end diameters >89 cm were likewise estimated to have the same percentages of product yield by grade as are logs with small-end diameters of 89 cm.

Values for lumber and stumpage were given for 1989 price levels and expressed in 1989 real dollars. Haynes and Fight (1992) provided lumber prices for Douglas-fir, western hemlock, and true fir species for the lumber grades used in this study. Red alder lumber prices were derived from mid-1989 issues of the *Weekly Hardwood Review*, and western redcedar lumber prices were from Western Wood Products Association (1990). Estimations of stumpage prices were calculated by subtracting 1985 logging and hauling costs (Haynes 1990) in thousand board feet (westside Scribner scale), expressed in real 1989 dollars and adjusted for log dbh and cubic volume using conversion factors established by Cahill (1984). These estimations are extrapolations for all species except Douglas-fir because Cahill's sample for western Oregon and Washington included only Douglas-fir. Logging and hauling costs are site specific; the regional averages used here (Haynes 1990: Table 81) may diverge significantly from local averages for the study area. These costs are derived largely from clearcuts, and probably underestimate costs for retention cuts (Kellogg et al. 1991). Estimates of the stumpage values are likely to be the least realistic estimations.

Data for net merchantable stumpage volume and value, lumber volume, and net wood products value (lumber + chips + sawdust) were computed for each ZELIG output file. Variables were expressed in thousand cubic meters per hectare for volume and in dollars per hectare for monetary values. A total for each variable is given for the entire 240-yr time frame and for the residual stand (at 241 yr). Only net wood products value is reported here. Wood value was not discounted in this study.

Simulation experiment

We performed a factorial experiment using ZELIG.PNW.2.0 to simulate nine levels of canopy tree retention and four rotation ages. ZELIG was parameterized for site conditions at 1000-m elevation in the H. J. Andrews Experimental Forest in the west-central Oregon Cascades. The model was run in grid mode and simulated a 10 × 10 grid of 0.06 ha plots, for a total simulated stand area of 6 ha. This plot size of 0.06 ha was selected because it corresponds to the area shaded by a canopy tree, and thus the scale of gap regeneration in these forests. Shading from adjacent plots is considered in this grid version of ZELIG, allowing a more realistic treatment of the light regime following larger scale disturbances such as clear-cutting. A simulated stand size of 6 ha was selected to correspond both to the spatial scale at which the birds we studied probably select habitat (e.g., a breeding territory size or larger), and to the scale at which the bird habitat functions were developed. Another consideration was that the simulated stands not require an infeasible amount of computer time to process.

Initial forest conditions were generated by simulating establishment from bare ground and forest growth for a 500-yr period. Five replicates of each scenario were simulated. Characteristics of this initial forest were typical of old-growth stands in the area. The simulated harvest systems included clear-cutting and retention cuts. Half of the specified number of trees retained were drawn from the 20–50 cm dbh class and the remainder from trees >50 cm in diameter at breast height (dbh). If the specified retention level could not be reached within the larger dbh class, more trees were retained in the smaller size class. The trees retained were selected randomly with regard to tree species. The retention levels simulated were 0, 5, 10, 15, 20, 30, 50, and 150 trees/ha (hereafter referred to as RET = 0, RET = 5, etc.). The latter level required the harvest of relatively few trees, and approximated the 500-yr old forest continuing to undergo natural succession. Simulated rotation lengths were: 40, 80, 120, and 240 yr (hereafter referred to as ROT = 40, ROT = 80, etc.). Each scenario was run for a 240-yr time period. Following each harvest, the simulated stands were replanted with 988 Douglas-fir seedlings (diameter 2.5 ± 0.25 cm, mean ± 1 SD) per hectare. Regenerating stands were thinned to 543 trees/ha 15 and 30 yr following planting. Thinning was random with respect to tree species. For the economic analyses, we assumed a tree planting cost of $361 per hectare in 1989 dollars (Weigand and Burditt 1992). Thinning costs were calculated using projections from Haynes (1990: Table 81), and thinned trees were included in the wood products volume and value calculations. Possible damage to retained trees during harvest events was not considered because calibration data were not available.

To assess the statistical significance of the results, the five runs of each silvicultural scenario were assumed to be independent samples. This assumption is justified given the stochastic structure of ZELIG relative to weather, inseeding, and tree mortality. The units of analysis used in this study are means and variances of the response variables for the stand (comprised by the 100 interacting model plots) simulated under each scenario and replicates. The variables reported include (1) stand structure: mean dbh (DBHMEAN), standard deviation in dbh (DBHSD), and mean density (trees per hectare) (DENSITY); (2) stand species composition: percent of total basal area comprised by Douglas-fir (PCTPSME); (3) wood volume and value: cumulative basal area at year 240 (CUMBA), cumulative net wood products value (1989 real dollars) (VALUE); and (4) bird diversity: relative abundance of selected bird species, bird species richness). Means of cumulative variables are depicted graphically and variances are reported in tables. Figures for variables depicted over time indicate statistical significance of differences among treatments at each time step, but not the variance associated with each treatment.

The variables involving wood production, tree species composition, and mean bird richness met the assumptions of normal distribution and constant variance. These data were analyzed using ANOVA to determine the individual and interactive effects of each factor (rotation and retention). Where models were significant, multiple range tests (least significant difference test, SAS 1982) were used to determine the pairs of treatments that differed significantly. The Kruskal-Wallis test was used for time traces of stand structure and bird density and richness to determine differences at each time step among levels of retention for particular rotation lengths, and among rotation lengths for particular retention levels. Differences were considered significant at $P = 0.05$.

RESULTS

Forest structure

The initial 500-yr-old stand had 324 trees/ha, with DBHMEAN = 36 cm and DBHSD = 47 cm. Trees <20 cm dbh were primarily cut under RET = 150, causing density to drop initially and DBHMEAN and DBHSD to rise (Figs. 2–4). These variables returned

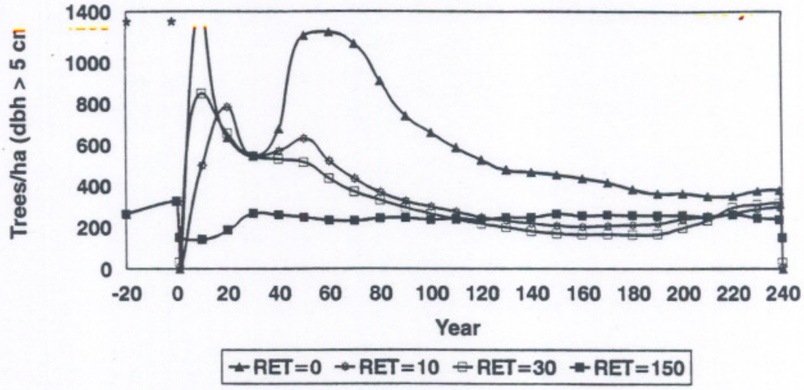

FIG. 2. Mean density of trees for four levels of canopy tree retention (RET, in trees per hectare) over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

to preharvest levels by year 30, and remained little changed over the 240-yr rotation. Clear-cutting caused DENSITY to drop to 0, increase rapidly under planting and inseeding, then decrease over the rotation under the influence of prescribed thinning and self-thinning. Tree density under clear-cutting exceeded that under other retention levels over the 240-yr simulation period. DBHSD under clear-cutting remained below that of other retention levels, but DBHMEAN exceeded RET = 150 by year 120. This is caused by relatively rapid increase in diameter increment for the initial cohort. Intermediate levels of retention (e.g., RET = 10 and RET = 30), showed trends in stand structure similar to clear-cutting, except that overstory shading resulted in reduced seedling establishment and DENSITY. Also, DBHMEAN and DBHSD under intermediate retention exceeded that under clear-cutting over most of the 240-yr rotation. Interestingly, DBHMEAN under intermediate retention exceeded that of the initial forest, caused both by retention of large trees and by relatively large sizes attained by the initial regenerating cohort. Thus, canopy retention increased stand complexity (as indicated by DBHMEAN and DBHSD) over that produced by clear-cutting.

The range of standard errors among replicates within treatments was: DENSITY (0–148); DBHMEAN (0–5.3); and DBHSTD (0–3.0). This variance among replicates was generally small relative to differences among treatments, resulting in statistically significant differences among treatments at most time steps (Figs. 2–4).

Forest composition

Tree species composition was significantly related to retention level and, to a lesser extent, rotation length (Table 3). Differences established during the first few decades remained through the end of the simulation period. For simplicity, PCTPSME at year 240 (prior to final harvest) is presented in Fig. 5 (means) and Table 4 (means and variance). Douglas-fir and western hemlock comprised most of the basal area in the initial stands. Clear-cutting and planting produced virtual Douglas-fir monocultures. Retention of 5 to 30 trees/ha, however, resulted in dominance by western hem-

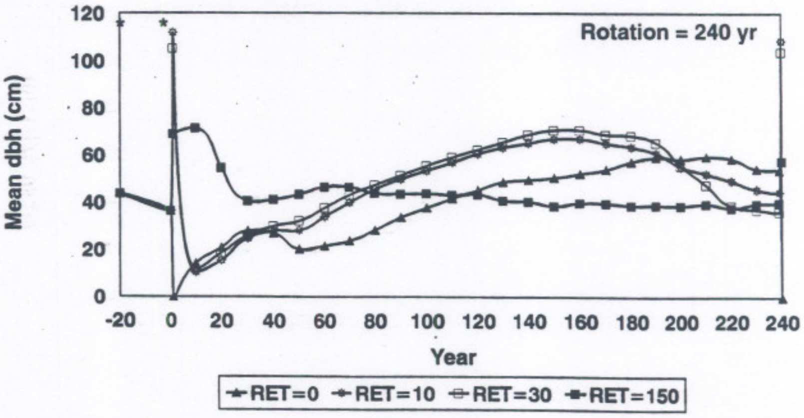

FIG. 3. Mean tree dbh for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

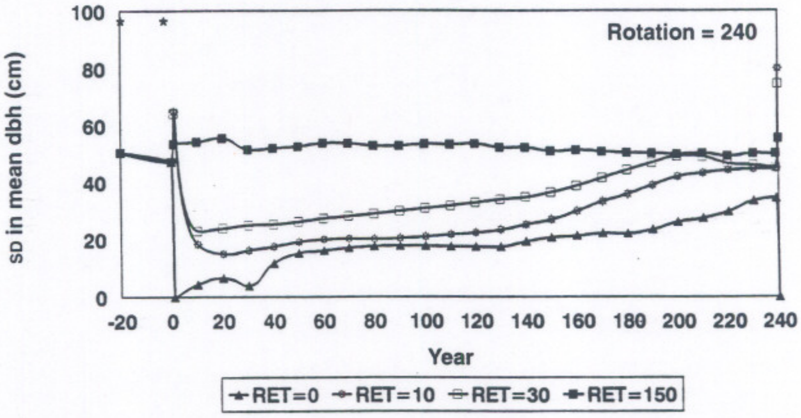

FIG. 4. Standard deviation in mean tree dbh for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

lock and western redcedar. This was because these species were able to establish and grow more rapidly than Douglas-fir under an overstory. Under higher levels of retention, the initial dominance by Douglas-fir remained throughout the simulation period. Douglas-fir also was favored by shorter rotations, especially when retention was ≤50 trees/ha. Important thresholds in PCTPMSE are evident in Fig. 5, especially between RET = 0 and RET = 5, and between ROT = 80 and ROT = 120. Of the pairwise comparisons among treatments shown in Table 4, 81% differed significantly.

Forest productivity and economics

Cumulative basal area over the 240-yr simulation was highest under clear-cutting and 40-yr rotation, and decreased with increasing retention level and rotation age (Fig. 6, Table 5). Retention, rotation, and the interaction all contributed significantly to the ANOVA model (Table 3). CUMBA under RET = 5 was 75–82% of that under clear-cutting, depending on rotation length. The reduction in CUMBA with retention level was more gradual through RET = 30, where CUMBA was 60–67% of that under RET = 0. CUMBA dropped somewhat linearly with rotation age under clear-cutting: ROT = 80, 120, and 240 were 81%, 68%, and 49%, respectively, of that for ROT = 40. The differences between ROT = 40 and the other rotation levels were even greater for RET = 5–30. Retention level has a relatively minor effect on CUMBA for RET = 100 and RET = 150. The majority of the pairwise comparisons among treatments differed significantly (Table 5), except that this was less pronounced in treatments where >50 trees/ha were retained.

The reduction in CUMBA with retention was caused by decreased growth rates of trees regenerating in the shade cast by an overstory. Growth rates also decreased after trees reached 60–80 yr of age. This explains the reduction in growth rates with longer rotations.

Cumulative value of wood products also was significantly related to retention level, but the effect of rotation length was substantially less than for CUMBA (Table 3). Value at RET = 5 was 81–83% of that under RET = 0. VALUE continued to decline with retention, reaching at RET = 30 only 60–65% of that under clear-cutting (Fig. 7, Table 6). At lower levels of retention, VALUE peaked at ROT = 80, but differences across rotation level were generally not significant. The reduced effect of the treatments on VALUE compared with CUMBA was largely caused by the higher value of the larger trees produced under longer rotations and higher levels of retention.

Bird community

Bird species responded individualistically to the treatments, generally falling into four habitat use guilds. Dark-eyed Junco was most abundant just after harvest and in stands with no or few canopy trees. Consequently, it was best represented under clear-cutting and short rotations (Figs. 8 and 9). American Robin and White-crowned Sparrow showed similar patterns.

TABLE 3. Results of ANOVA for four of the response variables examined in this study. Variables are defined in *Methods*. RET refers to retention level and ROT refers to rotation age.

		Factor *F*-value			Model		
Variable	df	RET	ROT	RET·ROT	R^2	*F*	*P*
PCTPSME	179	80	7	NS	0.827	20	0.0001
CUMBA	179	4001	4566	180	0.970	1430	0.0001
VALUE	179	1870	53	3	0.990	434	0.0001
RICHNESS	179	1073	217	46	0.990	295	0.0001

TABLE 4. Means (with standard error in parentheses) of percentage of total basal area comprised by Douglas-fir at year 240. Data are presented for nine retention levels and four rotation ages. The significance of the difference among means cannot be displayed graphically because of low values in the middle columns and rows.

Retention level	Rotation age 240 yr	120 yr	80 yr	40 yr
0 trees/ha	90.5 (0.4)	84.6 (0.8)	83.8 (0.8)	96.4 (0.9)
5 trees/ha	40.7 (5.1)	36.3 (5.6)	52.8 (7.7)	57.7 (7.0)
10 trees/ha	38.8 (4.9)	36.4 (5.4)	51.3 (6.8)	48.6 (5.6)
15 trees/ha	39.2 (3.6)	36.5 (4.0)	45.5 (4.5)	42.7 (5.3)
20 trees/ha	35.5 (4.0)	31.8 (1.4)	28.3 (1.4)	37.5 (3.4)
30 trees/ha	32.8 (2.7)	31.4 (0.7)	35.5 (1.5)	36.8 (1.8)
50 trees/ha	44.2 (4.3)	40.1 (2.2)	44.7 (1.4)	47.9 (5.8)
100 trees/ha	52.0 (2.0)	51.5 (1.1)	52.6 (1.4)	53.8 (1.5)
150 trees/ha	51.1 (0.9)	52.1 (0.9)	49.8 (1.0)	52.7 (1.2)

TABLE 5. Means (standard error in parentheses) of cumulative basal area (square metres per hectare) at year 240. Nine retention levels are compared across four rotation levels. All means are significantly different ($P < 0.05$), except those with similar superscripts. Superscripts represented by letters apply across rows. Superscripts represented by symbols apply along columns.

Retention level	Rotation age 240 yr	120 yr	80 yr	40 yr
0 trees/ha	226.5 (1.2)	317.8 (1.2)	376.3 (1.4)	463.3 (2.4)
5 trees/ha	184.7 (2.7)	244.2 (1.8)	283.2 (1.8)	355.5* (4.9)
10 trees/ha	176.9 (1.5)	235.8 (2.2)	273.9 (1.8)	352.8* (5.3)
15 trees/ha	167.8* (1.9)	224.0 (2.7)	261.6 (2.5)	342.6 (4.4)
20 trees/ha	161.7* (0.8)	215.6 (3.8)	254.3 (1.8)	333.6 (3.9)
30 trees/ha	151.2 (1.7)	195.2 (2.4)	227.4 (0.9)	306.4 (3.5)
50 trees/ha	133.1 (1.8)	159.7 (2.1)	175.7 (3.1)	238.8 (4.6)
100 trees/ha	$102.6^{\dagger\mathrm{a}}$ (1.37)	$102.7^{*\mathrm{ab}}$ (0.8)	108.3^{bc} (0.8)	113.2^{c} (1.0)
150 trees/ha	$98.9^{\dagger\mathrm{a}}$ (1.2)	$99.8^{*\mathrm{a}}$ (1.1)	100.9^{a} (1.40)	102.8^{a} (0.8)

Three species, MacGillivray's Warbler, Western Bluebird, and Western Tanager, were associated with open-canopy stands with intermediate densities of overstory trees. For example, MacGillivray's Warbler was only abundant immediately after harvest with retention levels of 10–30 canopy trees per hectare (Fig. 10).

Brown Creeper and five other species were most abundant in structurally complex closed-canopy stands. They were absent from recently clear-cut stands, had intermediate densities in open-canopy stands with retention, and reached peak abundance in closed-canopy stands >100 yr old (Fig. 11). Suitable habitats for Brown Creeper never developed when stands were clear-cut every 40 yr (Fig. 12). Unexpectedly, stands arising as clearcuts supported higher densities of Brown Creeper than stands originating with retention cuts during years 100 to 180 (Fig. 11). This is because the fast growth rates under clear-cutting produced a larger number of trees with large boles (required by this species) than did the retention cuts. This group of birds represented the well-known mature and old-growth forest associates that do best under long rotations and higher levels of retention.

The final guild was associated with closed-canopy, structurally simple habitats and comprised Black-headed Grosbeak, Golden-crowned Kinglet, Hermit Thrush, and Swainson's Thrush. Swainson's Thrush, for ex-

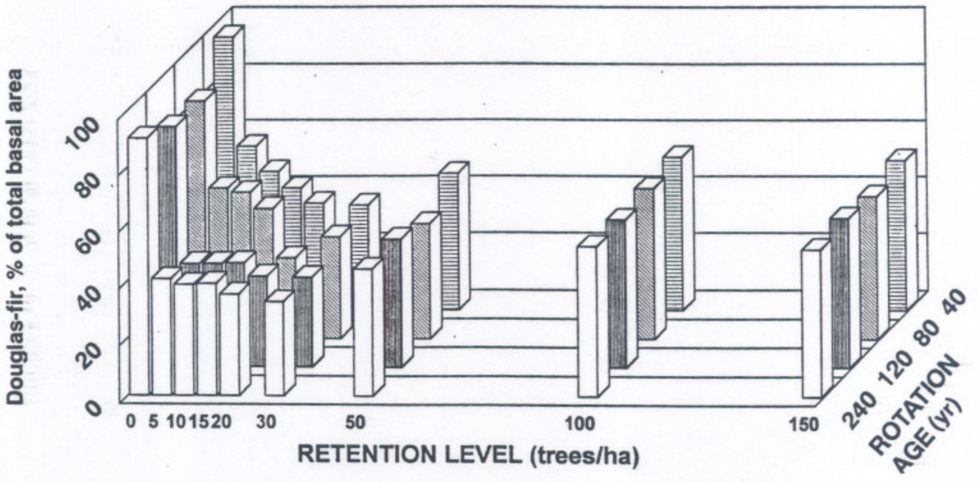

FIG. 5. Mean contribution of Douglas-fir to total basal area at year 240 (prior to final harvest) across nine levels of canopy tree retention and four rotation ages.

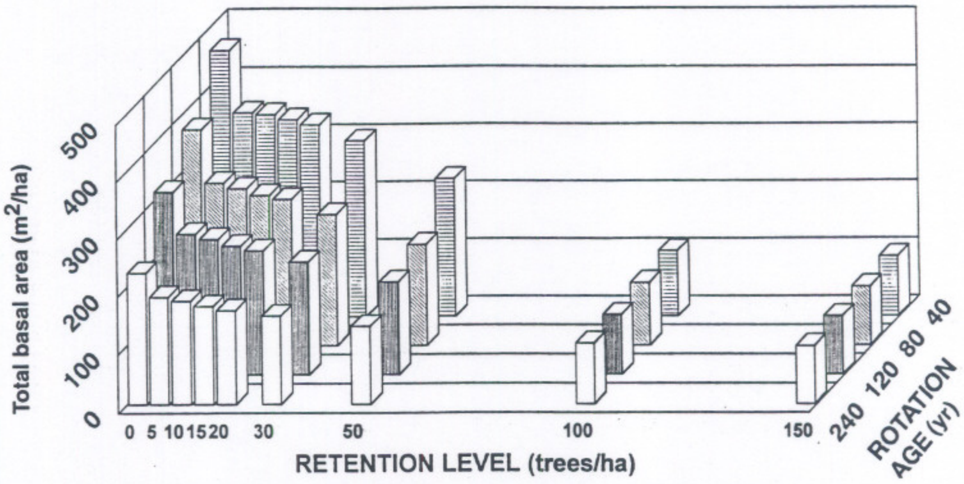

FIG. 6. Mean cumulative wood production per hectare (basal area of harvested trees plus trees standing at the end of the simulation period) over the 240-yr simulation across nine levels of canopy tree retention and four rotation ages.

ample, was most dense during the first 100 yr after clear-cutting (Fig. 13). It was also favored by short rotations (Fig. 14).

Bird species richness was lowest under clear-cutting for the first 140 yr, and thereafter exceeded RET = 10 and RET = 150 (Fig. 15). Richness peaked under intermediate levels of retention just after harvest, as habitats were provided for 16 of 18 species, decreased during years 20–40 as canopy closure occurred and open-canopy bird species dropped out, then returned to levels near that of RET = 150 thereafter. Bird species richness also increased dramatically with rotation length (Fig. 16).

Mean bird richness over the 240-yr simulation was significantly related to the treatments (Table 3). Mean richness was lowest under clear-cutting with short rotations (Fig. 17, Table 7). The largest increase with retention level was between RET = 0 and RET = 5. Mean richness also increased significantly with rotation age for retention levels <50 trees/ha.

DISCUSSION

Model performance and error propagation

Until long-term field experiments are done, simulation experiments are one of the few means to assess the consequences of alternative silvicultural strategies over multiple rotations. Inherent in simulation experiments is difficulty in determining whether or not predicted differences among treatments are due to chance. Our forest model is stochastic in representing weather, inseeding, and tree mortality. This allowed us to replicate the simulated treatments and to estimate the distribution of differences among treatments. It is difficult to assess how well the stochasticity in ZELIG matches the variability in real forests. Variance in model output

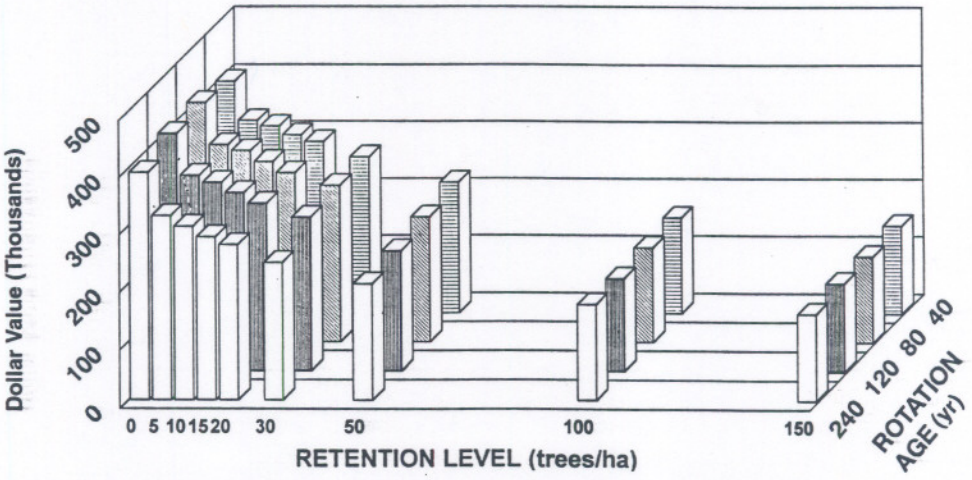

FIG. 7. Mean cumulative value of wood products per hectare (including harvested trees plus trees standing at the end of the simulation period) over the 240-yr simulation across nine levels of canopy tree retention and four rotation ages. Data are expressed in 1989 real dollars.

TABLE 6. Means (standard error in parentheses) of cumulative wood products value in dollars per hectare at year 240. Means with similar superscripts do not differ significantly. Superscripts represented by letters apply across rows. Superscripts represented by symbols apply along columns.

	Rotation age			
Retention level	240 yr	120 yr	80 yr	40 yr
0 trees/ha	393 676.6^{a} (1784.0)	411 719.2^{b} (1577.8)	416 257.2^{b} (1140.2)	402 335.3^{ab} (651.7)
5 trees/ha	317 523.9 (5868.6)	338 602.9^{a} (2253.4)	341 816.7^{*a} (3355.9)	333 786.3^{*a} (2632.3)
10 trees/ha	299 443.3 (5960.8)	326 058.0^{a} (2187.0)	331 642.3^{*a} (2006.8)	323 521.2^{*a} (1363.1)
15 trees/ha	281 149.5 (4873.1)	308 359.6^{a} (3376.9)	312 548.9^{a} (2466.0)	308 324.0^{a} (2691.8)
20 trees/ha	267 457.0 (4288.3)	289 397.0^{a} (6151.1)	293 184.9^{a} (2976.9)	296 661.5^{a} (3793.4)
30 trees/ha	236 534.4 (3156.0)	265 175.0^{a} (2898.5)	270 893.1^{a} (2552.9)	269 739.4^{a} (2700.2)
50 trees/ha	199 416.5^{a} (7704.6)	206 759.7^{ab} (8303.8)	215 562.8^{b} (4235.7)	225 304.1 (6461.3)
100 trees/ha	163 830.8^{a} (2378.2)	158 529.5^{*a} (3634.7)	162 275.3^{a} (3855.9)	163 058.1^{a} (4239.4)
150 trees/ha	148 219.3^{a} (3494.7)	151 038.9^{*a} (1678.1)	147 312.1^{a} (2000.6)	150 246.6^{a} (3104.1)

was less than for data from natural stands in the vicinity of the study area (Fig. 1). This is to be expected, however, because these field data are from a wider range of conditions than was modeled. Beyond stochasticity in weather, mortality, and regeneration (considered in the model), variance in the field data additionally resulted from heterogeneity in soils, slope, aspect, elevation, and disturbance history. Given these differences in conditions, the variance generated by ZELIG seems reasonable for our forests.

TABLE 7. Means (standard error in parentheses) of mean bird species richness (species per hectare) over the 240-yr simulation. All means across rows are significantly different ($P < 0.05$), except those with similar superscripts. The significance of the difference among means along columns cannot be displayed graphically because of low values in the middle of columns.

	Rotation age			
Retention level	240 yr	120 yr	80 yr	40 yr
0 trees/ha	12.7 (0.04)	11.1 (0.02)	10.7 (0.03)	9.7 (0.02)
5 trees/ha	14.0^{a} (0.05)	13.9^{a} (0.07)	13.5 (0.07)	13.3 (0.04)
10 trees/ha	14.1^{a} (0.03)	14.0^{a} (0.06)	13.7 (0.06)	13.4 (0.05)
15 trees/ha	14.1^{a} (0.01)	14.0^{a} (0.03)	13.8 (0.05)	13.3 (0.03)
20 trees/ha	14.1^{a} (0.02)	14.0^{a} (0.04)	13.9 (0.02)	13.4 (0.04)
30 trees/ha	14.3^{a} (0.02)	14.1^{a} (0.02)	14.1^{a} (0.02)	13.5 (0.04)
50 trees/ha	14.3^{a} (0.16)	13.8^{b} (0.18)	14.3^{a} (0.16)	13.7^{b} (0.10)
100 trees/ha	14.5^{a} (0.03)	14.4^{b} (0.02)	14.5^{ab} (0.04)	14.7^{a} (0.02)
150 trees/ha	14.2^{a} (0.07)	14.2^{a} (0.01)	14.3^{a} (0.03)	14.6 (0.02)

We initially chose to simulate five replicates of each treatment for logistical reasons. Five replicates of 100 plots across 36 treatments for 240 yr of this computationally intensive model required considerable run time and generated a great deal of data. This number of replicates turned out to be appropriate for the statistical analyses; differences among treatments were greater than differences within treatments for many, but not all, comparisons.

Another limitation of complex computer models is error propagation. In our case, error in the economics or bird models may compound error in the forest simulator, resulting in economic and bird outputs that are inaccurate or highly variable. Perhaps the best way to assess the level of uncertainty is to verify model outputs against independent data (Oreskes et al. 1994). We did this for ZELIG output (Fig. 1), but data were not available to verify the economic and bird outputs. A second strategy is to assess the sensitivity of model output to error in model parameter estimates. This, too, was infeasible because of the large number of parameters used in ZELIG and in the economics model. However, we do not feel that error propagation is a problem in this application, for two reasons. First, variation in the economic and bird response variables was not greater than in the ZELIG outputs. Ranges of the coefficient of variation (CV) for ZELIG outputs were: DENSITY (0–51.4%); DBHMEAN (0–28.5%); and DBHSD (0–23.7%). The range in CV for the economic variable cumulative wood products value was 0.4–8.9%. Bird richness had a range of 0–12.4%. Hence, the differences among replicates did not escalate from one model

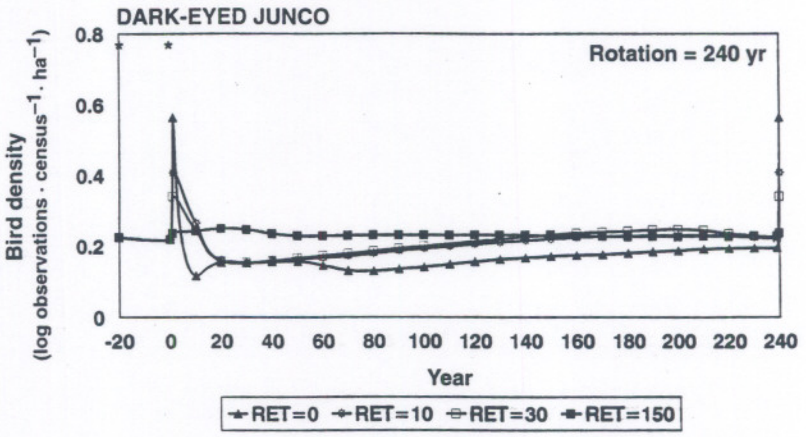

FIG. 8. Simulated density of Dark-eyed Junco for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

to the next. Secondly, differences among treatments were considerably greater than differences among replicates. Thus, the conclusions of the study are likely to hold even if some error propagation did occur.

Stand structure and composition

The computer simulations indicated that stand-scale silvicultural manipulations strongly influence long-term forest structure and composition. These effects, in turn, have important consequences for forest productivity, economics, and bird habitat dynamics. As expected, stands produced by clearcutting remained substantially higher in tree density and lower in tree size variation than the initial old-growth forest. Intermediate levels of canopy tree retention at harvest, in contrast, resulted in stands with tree densities and diameters that were similar to the initial old-growth forest. Importantly, variation in dbh for intermediate retention levels remained below that in the initial stand for >200 yr. This suggests that when rotation length is <200 yr, it is necessary to retain multiple size classes of trees at harvest to produce stand structures typical of natural forest. Another important finding was that mean dbh under clear-cutting exceeded that of the initial forest after ≈120 yr, and increased beyond the intermediate retention treatments at ≈200 yr.

Overall, the data suggest that canopy tree retention enhances structural complexity beyond that of clear-cutting for ≈200 yr following harvest. Higher levels of retention better approximate old-growth forest structure. Beyond 200 yr post harvest, all of the retention levels converged at levels near that of old-growth forest. These findings are consistent with ecologists' predictions that advanced canopy tree retention and longer rotations are strategies for maintaining structural complexity in managed forests (e.g., Franklin 1988, Hansen et al. 1991, Swanson and Franklin 1992).

Tree species composition has not been as much at the center of the debate over forest management in the PNW. The results indicate, however, that canopy tree retention and rotation age strongly influence species composition, even when only Douglas-fir are planted

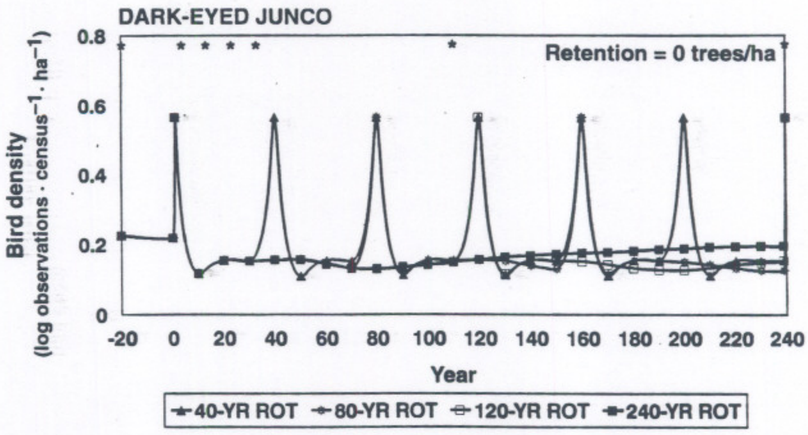

FIG. 9. Simulated density of Dark-eyed Junco for four rotation ages (ROT, in years) over the 240-yr simulation. No canopy trees were retained at harvest for these runs. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among rotation levels for all time steps except those denoted with an asterisk.

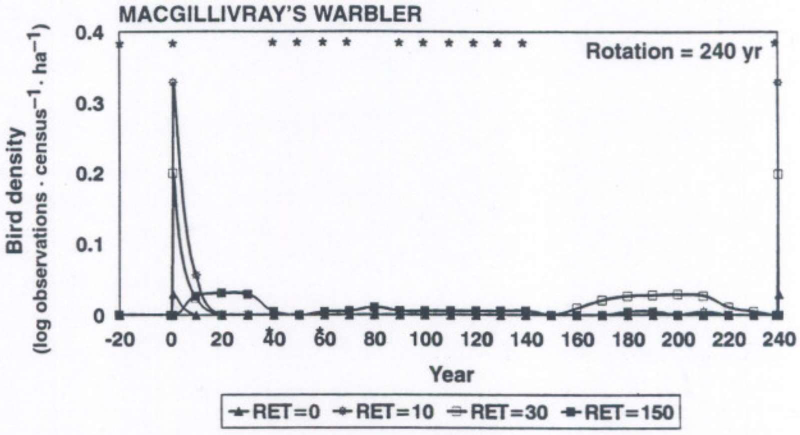

FIG. 10. Simulated density of MacGillivray's Warbler for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

following harvest. Shade-tolerant species such as western hemlock and western redcedar outcompeted and became dominant over Douglas-fir under low to intermediate levels of retention and for rotations of ≥120 yr. This effect was observed even under the lowest level of retention, 5 trees/ha (Fig. 5). Intermediate levels of retention and longer rotation should be of interest to land managers where enhancement of tree species diversity is a goal. Moreover, results suggest that where canopy tree retention is practiced (as it now is on most Federal lands in the PNW), wood production will be increased by favoring the establishment of shade-tolerant tree species rather than Douglas-fir, through natural regeneration, planting, or species-specific precommercial thinning. These species are not now as valuable as Douglas-fir, but are expected to converge in value with Douglas-fir by the year 2040 (Haynes and Fight 1992). More analysis is needed to determine the most economical planting strategy in retention units.

Wood production and economic return

Our analysis predicted that wood production drops substantially with canopy tree retention and longer rotation lengths. The greatest decrease among retention levels (75–82%) was between RET = 0 and RET = 5 (Fig. 6). Wood production did not change much between retention levels of 5 to 20 trees/ha, but decreased more rapidly at higher levels of retention. These results are consistent with simulation results of Birch and Johnson (1992), who found that stand volume growth over a 60-yr rotation for retention of 5 trees/ha was about 70% that of clear-cutting.

Rotation length had an even stronger effect on wood production than did retention level, with a rotation of 80 yr producing only 81% as much basal area as a rotation of 40 yr. These findings are explained by the fact that the fastest growing species, Douglas-fir, is intolerant of shading; its growth tends to slow after age 80 yr.

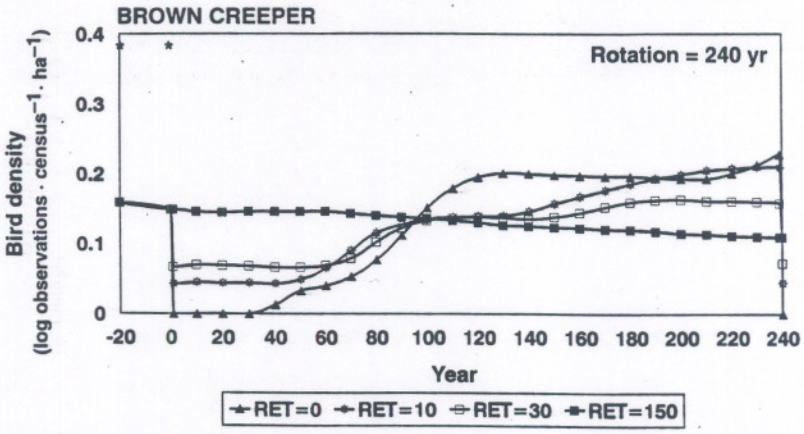

FIG. 11. Simulated density of Brown Creeper for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

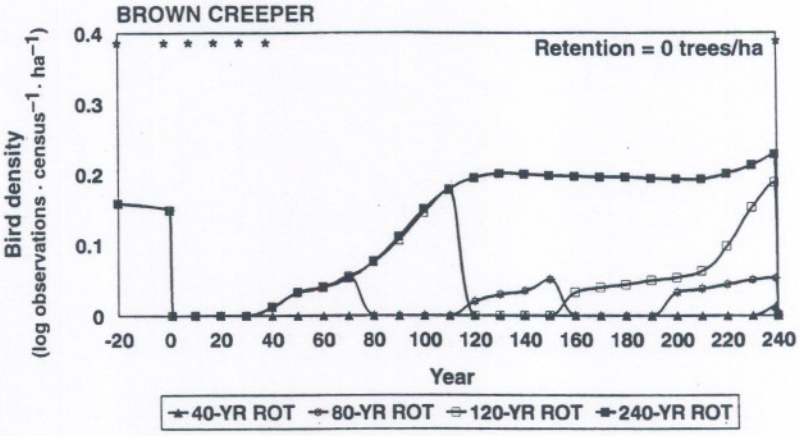

FIG. 12. Simulated density of Brown Creeper for four rotation ages over the 240-yr simulation. No canopy trees were retained at harvest for these runs. Year −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among rotation levels for all time steps except those denoted with an asterisk.

An important caveat to these findings is that our forest model did not consider the effects of traditional silviculture on nutrient availability. Ecologists have suggested that road building, logging, and rapid tree growth deplete soil nutrients and decrease long-term ecological productivity (Perry et al. 1989). Canopy tree retention and longer rotations may slow such losses in productivity (Franklin et al. 1989). Simulation studies from the PNW (Feller et al. 1983) and the northeast United States (Aber et al. 1982) indicate that short-rotation clear-cutting reduces both nitrogen availability and wood production. Empirical data in the PNW are inconclusive, however, on the effects of clear-cutting or other silvicultural practices on ecological productivity on sites of moderate to high quality (Perry et al. 1989).

Our results indicated that wood fiber volume production was not a good index of net wood products value. Wood value decreased more slowly with increased levels of canopy tree retention than did wood production. This was true in spite of the fact that the regenerating tree species favored under retention are less valuable than Douglas-fir. The higher value of large-dimension, high-quality trees in the retained overstory partially offset the lower economic productivity in the understory under retention. This effect was more pronounced relative to rotation age. In contrast to wood production, wood products value did not differ significantly across rotation age for many of the retention levels. This suggests that, in the absence of discounting, longer rotations do not reduce long-term economic returns compared with short rotations over the 240-yr period. Less frequent final harvests create less frequent, but higher individual, final harvest values. Most forest economists do discount, however, and at current rates (USDA Forest Service conventionally uses 4%/yr), longer rotations may not be as profitable as short rotations. See Lee (1993:190–195) for a thoughtful evaluation of discounting and sustainable use of natural resources.

The limitations of our economic analyses need to be kept in mind. We considered only wood products value,

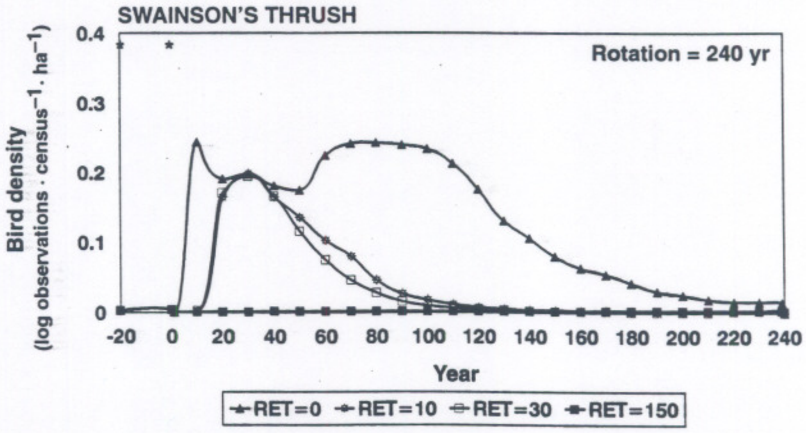

FIG. 13. Simulated density of Swainson's Thrush for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

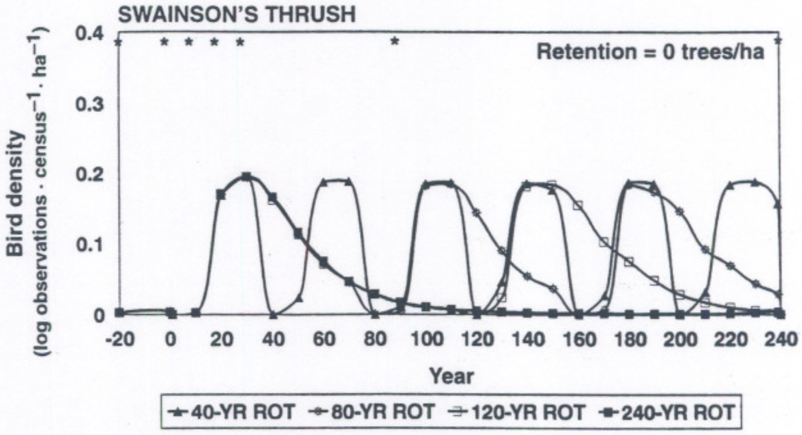

FIG. 14. Simulated density of Swainson's Thrush for four rotation ages over the 240-yr simulation. No canopy trees were retained at harvest for these runs. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among rotation levels for all time steps except those denoted with an asterisk.

not revenues generated by fishing, mushroom harvest, recreation, and other forest uses. More specific to our analyses, calculation of logging costs did not consider level of retention. Kellogg et al. (1991) found that planning and logging costs for retention of about 5 trees/ha were 12–23% higher than for clear-cutting, depending on the topography and yarding method. How these costs vary across retention levels is not known, however. Another fact to bear in mind is that prices for wood products have changed substantially since 1989, and will continue to change in the future. Large-dimension, high-quality logs have escalated faster than wood products as a whole, which may enhance the economic return of higher retention levels and longer rotations. Historically, wood prices have changed substantially from year to year, so there is no particular year that is an especially good benchmark for making long-term economic projections. Also, our pricing was for the U.S. domestic market. The international market pays relatively more for large logs. A final consideration is that we reported cumulative timber production and value over the 240-yr simulation, rather than presenting the flow of timber volume and value extracted per year. This approach allowed analysis of the relative effects of retention and rotation on wood products, but may not provide the detail on wood products flow desired by some forest economists.

Within these limitations, we offer these results as reasonable projections of the economic consequences for wood production of alternative retention and rotation scenarios. Importantly, this study demonstrates that tree species composition and log size and quality vary under alternative silvicultural regimes, strongly influence wood products value, and should be considered in analyses of forest economics.

Bird habitat dynamics

Previous studies found that bird species in the PNW respond individualistically to stand structure, being distributed across gradients in canopy closure and structural complexity (Ruggiero et al. 1991, Vega 1993, Hansen and Hounihan 1995, Hansen et al. 1995). As

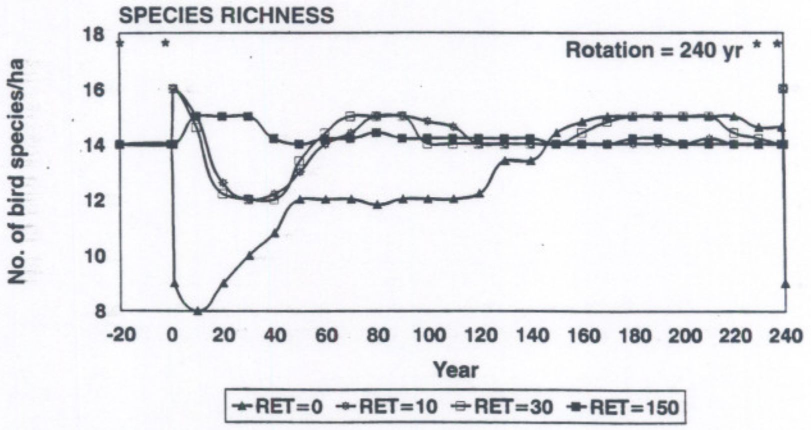

FIG. 15. Simulated bird species richness per hectare for four levels of canopy tree retention over a 240-yr rotation. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pre-treatment forest. Data values differed significantly among retention levels for all time steps except those denoted with an asterisk.

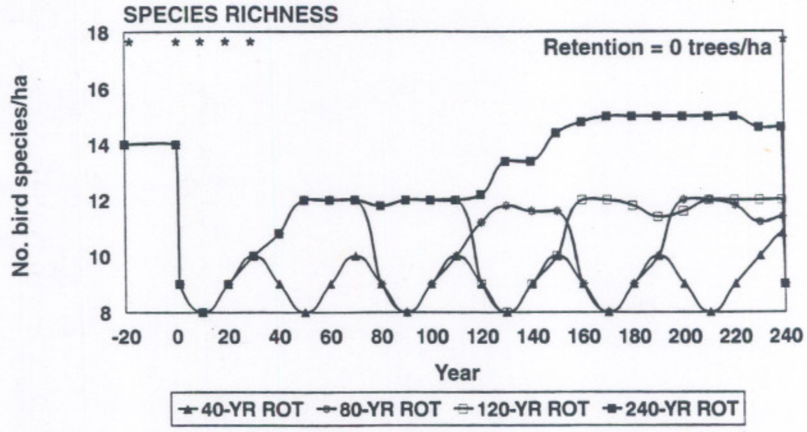

FIG. 16. Simulated bird species richness per hectare for four rotation ages over the 240-yr simulation. No canopy trees were retained at harvest for these runs. Years −20 and 0 represent years 480 and 500, respectively, of the simulated pretreatment forest. Data values differed significantly among rotation levels for all time steps except those denoted with an asterisk.

is predictable from the bird habitat functions we used, simulated bird densities differed dramatically among species across the retention and rotation levels. These results are valuable in illustrating the silvicultural strategy that is likely to favor each species. The results indicate, for example, that forest-dwelling species such as Brown Creeper will attain modest densities in the first few decades after harvest if low to moderate levels of canopy trees are retained. Interestingly though, Brown Creeper achieved higher densities under clearcutting than retention during years 100–170. This was because more of the large tree boles this species requires were available under clear-cutting during these years.

Species such as MacGillivray's Warbler are primarily associated with open-canopy stands with scattered live trees. In contrast, the predicted densities of other open-canopy species, such as Dark-eyed Junco, were inversely related to canopy tree retention level. Similarly, the simulated densities of species such as Swainson's Thrush were dramatically higher during years 50–180 in stands that were clear-cut than in stands with even low levels of retention. The predicted responses of these species to rotation length also varied with the degree of canopy closure and structural complexity they required.

Most of the bird species considered were associated with older, structurally complex stands. Hence, bird richness was highest where canopy trees were retained and under longer rotations. A threshold in bird richness was evident between clearcuts and retention units. Richness increased substantially from RET = 0 to RET = 5, and did not increase much at higher levels of retention (Fig. 17).

Some important assumptions accompany the approach we used in these bird habitat analyses. The projections were based on statistical functions that predict bird density from tree size class distribution. While this

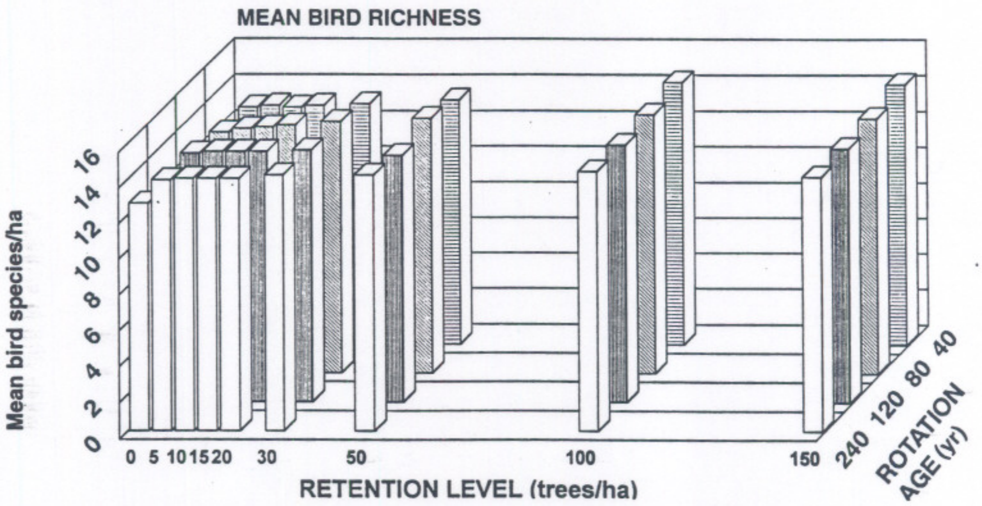

FIG. 17. Mean bird species richness per hectare over the 240-yr simulation period across nine levels of canopy tree retention and four rotation ages.

is the only viable approach for community scale studies (Hansen et al. 1993), habitat is known to be an imperfect predictor of bird demography (Van Horne 1983, Pulliam 1988). These statistical functions explained 9–67% (depending on species) of the variation in bird abundance in the calibration data. Obviously, other stand- and landscape-scale factors influence bird density (Hansen et al. 1993), but these factors were not considered in this study.

Another limitation is that the calibration data set for the bird habitat models did not include retention stands that had aged beyond canopy closure. This stand type is not presently found in the study area, but will be common as retention stands age. Our models predicted that birds associated with structurally complex open-canopy stands would not continue to use these stands after canopy closure. We suspect that this is not the case, and that our model underestimated bird species richness in these stands. In spite of these limitations, the habitat functions employed here reflect best current knowledge for the PNW regarding bird response to stand age and structure.

Management implications

This study is the first to offer detailed projections on the consequences of rotation age and retention level on both ecological and economic response variables in the PNW. Even so, the results tend to confirm the common belief of silviculturalists and ecologists in the region that strategies to enhance structural complexity and habitat diversity come at the expense of wood production and forest products value. Ignoring potential losses in long-term ecological productivity, our model predicted that short-rotation clear-cutting produces the highest return in wood products value. Bird species richness, on the other hand, was highest under long rotations and moderate levels of canopy tree retention. The individualistic responses of the bird species to stand structure emphasize that no particular silvicultural regime will provide habitat for all bird species. Clearly, land managers must carefully specify their management objectives and then select the silvicultural strategy or strategies most likely to achieve those objectives.

In our analyses, many of the response variables showed nonlinear behavior across levels of retention and rotation. Knowledge of these thresholds is critical to selecting management strategies that best balance conflicting objectives (see also Hof and Raphael 1993). For example, retaining 5 trees/ha would appear to best optimize mean bird richness (Fig. 17) and wood products value (Fig. 7). Similarly, longer rotations would appear to favor several bird species (e.g., Fig. 12) without reducing economic returns (if value is not discounted) (Fig. 7).

Evaluation of alternative management strategies is a key element of adaptive ecosystem management (Walters 1986, Everett et al. 1993, Hansen et al. 1993). Such analyses allow "best" strategies to be identified, implemented, monitored, and evaluated. In addition to determining how well the implemented strategies achieve objectives, monitoring and evaluation provide key information for revising management objectives and updating data bases and simulation models.

Beyond our simulation results, this study suggests that the new silvicultural strategies being implemented on Federal lands in the PNW have important consequences for key response variables such as forest structure and composition, habitat diversity, and wood products value. Yet, current databases and traditional tools are insufficient for identifying these consequences. Current forest plans probably err considerably in projections of wood production, habitat suitability, and other factors (see Birch and Johnson 1992). A vigorous program to monitor alternative silviculture on Federal lands in the PNW could help to provide a database for assessing these consequences. Some large-scale experiments on these topics are now being initiated; continued funding of these efforts is critical. New forest-planning models are also needed. Current models such as FORPLAN are not calibrated to simulate the mixed-species, mixed-age stands that are now being produced on Federal lands. FORPLAN also is not configured to consider the important effects of forest spatial patterning. New GIS-based decision support systems are now being developed to simulate multiple ecological, economic, and social response variables in a spatial context (e.g., Li 1989, Sessions and Sessions 1990, Hansen et al. 1993). Such tools can help land management agencies such as the USDA Forest Service best achieve their management goals.

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