ANALYSIS OF SILVA: A MODEL FOR FORECASTING THE EFFECTS OF SO₂ POLLUTION AND FIRE ON WESTERN CONIFEROUS FORESTS

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(Accepted for publication 1 December 1983)

ABSTRACT

Kercher, J.R. and Axelrod, M.C., 1984. Analysis of SILVA: a model for forecasting the effects of SO₂ pollution and fire on western coniferous forests. *Ecol. Modelling*, 23: 165–184.

A forest succession simulator, SILVA, has been developed for the mixed-conifer forest type of the Sierra Nevada, California, to simulate the effects of SO_2 and fire on forest dynamics. SILVA was developed by extensively modifying a northeastern U.S. simulator. The state variables of the model are the diameters at breast height (dbh) of each tree on a forest stand.

Ponderosa pine is found to be a relatively stable dominant for the site used in the simulations. White fir and sugar pine are relatively stable subordinate species. Incense-cedar shows a slowly fluctuating time-series.

Sensitivity analyses suggest that parameters determining growth rates are of major importance and changes in such parameters can often produce a relative effect on basal area larger than their relative change. Factors affecting fire induced mortality are of lesser importance. The effects of competition change the relative magnitude of the calculated sensitivities during the time course of the simulation. Relative rankings of parameters according to their sensitivities also change during the time course of the simulation. Those parameters that exhibit large changes in sensitivity are also important in determining the outcome of competition.

We investigated the convergence of the means of the time series of each species. The dominant ponderosa pine converged relatively rapidly with the number of runs. The subordinate species such as white fir converged much more slowly.

Work supported by the U.S. Fish and Wildlife Service under Interagency Agreement FWS 14-16-0009-969, in part by the Environmental Protection Agency, and in part by the Department of Energy under contract No. W-7405-Eng-48

INTRODUCTION

A forest succession simulator, SILVA, has been developed (Kercher and Axelrod, 1984) for the mixed-conifer forest type of the Sierra Nevada, California, to simulate the effects of SO_2 (Kercher and Axelrod, 1982) and fire on forest growth and succession. The model, SILVA, traces the development of each tree from seedling to death and constructs the population age and size structure for each species during the course of the simulated time period. Likewise, the species composition of the entire vegetative community can be followed as it changes in time. The model simulates the competitive interactions occurring between individual members of the forest stand and translates effects at the individual tree level into effects at the community level by simulating the interactions between individuals and between each individual and the environment.

We have followed the modeling approach of Botkin et al. (1972), who developed a northeastern U.S. simulator (JABOWA) for forest succession. In that approach, growth for each tree is modeled deterministically as a difference equation in diameter at breast height, dbh. The difference equation has annual time steps; each change is a function of the initial dbh for each tree, environmental variables, and competition by other trees. Botkin et al. (1972) modeled seedling recruitment and tree mortality by a Monte Carlo technique. Shugart and West (1977) adapted JABOWA to simulate southeastern U.S. succession and made modifications involving seedling recruitment and species that reproduce vegetatively. This model, FORET, was used by McLaughlin et al. (1978) and West et al. (1980), to simulate impacts on succession and species composition due to growth suppression by SO_2 . Emanuel et al. (1978) analyzed the frequency characteristics of the time-series of the FORET model.

Kercher and Axelrod (1984) developed SILVA from JABOWA by: (1) estimating a new set of parameters appropriate for mixed-conifer forests; (2) modifying the algorithm for establishment of young trees to bring it into agreement with field observations in the mixed-conifer forest; (3) introducing of fire ecology including: (a) dynamics of litter; (b) frequency of occurrence of fire; (c) calculation of fire intensity; (d) scorch height; and (e) probability of death from fire; (4) introducing of effect of water stress on growth following Reed (1980); (5) introducing of pollution effects (Kercher and Axelrod 1982).

SILVA has deterministic growth, competition, an extrinsic size-dependent stress, and population sizes determined by random variables (establishment and death). We want to investigate this complicated model in sufficient detail to be able to characterize its behavior and to understand its response to change.

MODEL DESCRIPTION

A complete description of SILVA may be found in Kercher and Axelrod (1982, 1984). Therefore we shall only give a brief synopsis of model structure.

We are considering the forest vegetation of the lower to middle elevations of the Sierra Nevada. The six major tree species are: ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiania*), incense-cedar (*Libocedrus or Calocedrus decurrens*), and California black oak (*Quercus kelloggi*).

SILVA was written in ANSI FORTAN using the structured programming technique as a guideline. A rationale of this approach and a complete description of the implementation and use of SILVA, are given by Axelrod and Kercher (1981). JABOWA (Botkin et al. 1972) was the basic foundation from which SILVA was developed. Therefore SILVA, like JABOWA, is a computer code that uses the Monte Carlo approach. This means that certain events, such as fire occurrence and birth and death of trees, are probabilistic events. Each time such an event is possible, e.g., it is possible for a tree to die every year, the computer decides whether or not it occurs by comparing a random number with the probability of occurrence. The probability of the event occurring is usually a function of state of the system at the time the event is possible. Each run of a Monte Carlo code is one realization of all possible time courses of the system. Therefore the simulation must be repeated many times to determine the central tendency or variations of the time behavior of the system.

The structure of the code is shown in Fig. 1. Control in MAIN follows the arcing arrow counterclockwise. First MAIN calls TREDTA which reads in the species-specific parameters describing reproduction, growth, and mortality; SITDTA reads in environmental variables; and CNTRL reads in control parameters such as the number of years of simulation and initial conditions. CALCNT calculates growth parameters from data read in by TREDTA. DIST generates an initial distribution of trees. SITE calculates environmental characteristics such as potential and actual evapotranspiration, degreedays, etc. SITE also calls WRSTRS which calculates the growth response to water stress. START sets the initial number and sizes of the trees for each species at the beginning of year 1. CYCLES generates a table of the good and bad seed-crop years for each species. RINGS generates a table of years with fires. The seed-crop table and the fire table are generated using the Monte Carlo method. The parameters used in generating these tables are based on data from the literature on the incidence of seed crops and fires in the Sierra. There are two versions of SILVA: one calculates the pollutant effect on the basis of the seasonal average concentration of pollution; and



Fig. 1. Structure of computer model of forest growth. Each box is a subroutine performing functions described in the text. Subroutines that communicate are connected, with the calling subroutines displayed above those called. the other translates the pollutant effect on the basis of the productivity injury due to successive episodes of pollutant visitation during a growing season. SEASO2 is in the version of the code based on the seasonal average concentration of SO₂. SEASO2 enables the user to specify up to two successive trends in SO₂ concentration over the time span of the simulation. SEASO2 calculates the seasonal average concentration for each year during the simulation. POLLUT calculates the effect on tree growth of the seasonal average SO₂ concentration for each year.

EPISOD calculates growth reduction in the successive episode version of SILVA. In this version, it is assumed that the same injury to primary production occurs for all years.

MAIN then begins the time-development calculation of the stand by calling BIRTH, GROW, FIRE, and KILL successively for the number of years under consideration, MXYRS. BIRTH determines reproduction on the stand; GROW calculates growth in dbh and height for each tree; FIRE calculates size of fires and fire damage; KILL causes trees to die based on ecological risk, lack of growth, and fire damage. BASAL sums up the basal area for each species. AVG keeps a running average of each species' basal area for all preceding runs. OUTPUR generates an output data file containing calculation results. BIRTH and KILL both use a worker subroutine, ADD, which does the accounting in adding or subtracting trees on the stand. GROW calls subroutine SHADE, which determined the leaf area index (LAI) above each tree. SHADE calls SORTP to order all trees by height. FIRE is the control subroutine for fire effects. It calls FUEL, which calculates the moisture content of fuels both live (brush) and dead (litter). FUEL gets the biomass loadings from BRUSH and LOAD. BRUSH calculates the dynamics of brush growth. LOAD calculates standing crop of litter using the increment added to litter by fallen needles and the decay of litter and duff. FIREMD calculates fire intensity based on fuel loadings (Albini, 1976). INJURY is then called by FIRE to calculate the height of crown scorch given the fire intensity. RISK is called by INJURY to calculate probability of damage due to fire. BRNOFF is then called by FIRE to reduce the fuel loadings due to the fire.

The equations of the model are summarized in Table I. In Table II, we give an index of the input variables, relating them to the equations in Table I.

RESULTS AND DISCUSSION

Simulation results

Full discussions of various simulations of SILVA are found in Kercher and Axelrod (1982, 1984). The model has been compared to observations

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Synopsis of equations in SILVA categorized by subroutine and process

Process	Equation number	Equation
Subroutine GROW		
Growth of each tree	(1.1a) ^a	$\frac{d(D^{2}H)}{dt} = aL[1 - D \cdot H/(HM \cdot DM] r(A) Q(DEGD) S(BAR) W(\tau) GR(SA)$
		$a =$ growth constant for each species; L = leaf area of tree; D = dbh; H = height of tree; HM = maximum height species attains; DM = maximum dbh species attains; $r =$ reduction of growth for suboptimal light; A = light at tree; Q = reduction in growth for suboptimal growing-degree-days; DEGD = growing degree-days; S = reduction in growth due to competition for edaphic resources; BAR = total basal area or stand; W = reduction in growth due to water stress; $\tau =$ actual/potential evapotranspiration; GR = reduction in growth due to pollution stress; SA = seasonal average pollutant concentration.
		Botkin et al. (1972) choose a such that:
	(1.1b) ^a	D = 0.667 DM when time = 0.5 AGEMX
		AGEMX = maximum observed age of species.
Height of tree	(1.2a) ^a	$H = 137 + b^2 D - b_3 D^2$
	(1.2b) ^a	$b_2 = 2(HM - 137)/DM$
	(1.2c) ^a	$b_3 = -(HM - 137)/DM^2$
Light attenuation	(1.3) ^a	$\mathbf{A} = \exp(-k_{\alpha} \sum \mathbf{LAI})$
		$k_{\alpha} = \text{constant}$ for light extinction in the canopy; Σ (sum) is over all trees taller; LAI = leaf area index.
Leaf area index	(1.4) ^b	Σ LAI = Σ L/PLTSIZ

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Leaf area of tree	(1.5) ^b	$\mathbf{L}_i = C_i \mathbf{D}_{ii}^{\alpha}$
		C_i , α_{1i} = constants for species <i>i</i> .
Response to climate	(1.6) ^a	$Q = 4(DEGD - DMIN)(DMAX - DEGD)/(DMAX - DMIN)^2$
		DMIN = minimum value of growing degree days for range of species; DMAX = maximum value.
Response to competition	(1.7) ^a	$S = 1 - BAR/(SOILQ \cdot PLTSIZ)$
for soil nutrition		SOILQ = maximum carrying capacity.
Response to water stress	(1.8) ^b	$W = 1 - (\frac{WSM - \tau}{WSM - WSO})^{NWS}$
		WSM = value of τ at which W is maximum; WSO = lower limit of range of tolerance in τ ; NWS = exponent relating linear function of τ to tree response.
Subroutine POLLUT		
Response of growth to pollution	^b (1.9)	$GR(SA) = 1 - PL \sum_{k=1}^{M} W_k \sum_{j=1}^{k} (SA_j - CR)$
		SA_{j} = average pollutant concentration in year <i>j</i> ; <i>k</i> = age class of needles; <i>M</i> = oldest age class of needles; <i>W</i> _k = contribution that needles of age class make to productivity; PL = sensitivity of growth to pollution.

Subroutine CYCLES

Quality of year for seed production

Parameters p and r are species-dependent. Monte Carlo technique used for determination of specific year's seed production by comparing p to a random Good seed year has probability p. Good year followed by r-1 blocked years. number chosen from a uniform distribution between 0 and 1.

Footnotes, see p. 175.

TABLE I (continued)		
Process	Equation number	Equation
Subroutine RINGS		
Determination of fire years		Probability of fire year is 0.2 from data on frequency of occurrence. Each fire year is followed by 2 blocked years.
Subroutine BIRTH		
Probability of survival by moisture condition	(1.10a) ^b (1.10b) ^b	$P_s = 1 - \exp(-\gamma_1 \text{ LAI})$ moisture stress intolerant = $\exp(-\gamma_2 \text{ LAI})$ moisture stress tolerant $P_s(I)$ = probability of survival of species I ; γ_1 , γ_2 = empirical constants.
Number of seedlings established for year	(1.11) ^b	$N(I) = \text{SDLNGS}(J) \cdot P_s(I)$ N = number of trees of breast height added; SDLNGS(J) is nominal number of trees introduced.
Subroutine KILL		
Determination of death		Monte Carlo technique used, testing each tree each year against total probability of death
Death due to random ecological factors and inherited weaknesses	(1.12a) ^a	$PD_E = 4/AGEMX$
Death due to suppressed growth	(1.12b) ^a	$PD_G = 0.369$ if $\Delta D < 0.01$ cm
Probability of all non- fire death	(1.12c) ^b	$PD_{T} = PD_{E} + PD_{G} - PD_{E} PD_{G}$

Subroutine FUEL

Moisture content of deadfuel (litter) at equilibrium Subroutine LOAD	(1.13) °	$EMC = AMC \cdot RH^{BMC} + CMC exp((RH - 100)/DMC) + MMC(TMC - T_F)$ RH = relative humidity (%), T _F is temperature (°F); AMC, BMC, CMC, DMC. MMC, TMC are constants found by fitting EMC to RH and T.
Annual deposition of new litter from canopy to ground for species <i>i</i>	(1.14) ^b	$\label{eq:FN} \begin{split} \text{FN}_i = \text{FFL}_i(\Sigma \ ABM \ D_i^{\alpha_{2i}}) \ 100/\text{PLTSIZ} \\ & \text{of species} \\ \text{of species} \\ \text{FN} = \text{litterfall}; \ \text{FFL} = \text{fraction of canopy falling per year; ABM converts } D_i^{\alpha_{2i}} \ \text{to} \\ \text{biomass.} \end{split}$
Current year's litter	(1.15a) ^b	$[LN_i]_d = [LN_i]_{d-1}(1 - DKL_i - LTD_i) + [FN_i]_{d-1}(1 - DKF_i)$ DKF _i = litter decay over winter; DKL _i = loss to respiration and soil; LTD _i = conversion from litter to duff; LN _i = litter standing crop; d = current year.
Current year's duff	(1.15b) ^b	$[DN_i]_d = [DN_i]_{d-1}(1 - DKD_i) + [LN_i]_{d-1}LTD_i$ DKD _i = loss to respiration and soil; DN _i = duff standing crop.
Subroutine BRUSH		
Annual change in brush standing crop of toler- ance class I	(1.16) ^b	DELTA(I) = $\eta x(I)[1 - x(I)/X]r_1(A)$ $x(I)$ = biomass of brush class I on plot; η = growth constant for small biomass; X = carrying capacity; r_1 = factor reducing growth for suboptimal light; DELTA = increment in brush biomass.

TABLE I (continued)

Process	Equation number	Equation
Subroutine FIREMD		
Fire intensity	(1.17) ^b	FI(i) = FI(WIND, TTHETA, MOIS, FWG, RHOP, BULK, MPS, LHV, ST, SE, MEXT, PARAM)
		The full set of equations relating fire intensity can be found in Rothermal (1972) and Albini (1976). WIND = windspeed at midflame height; TTHETA = slope of stand; WIND = windspeed at midflame height; THETA = slope of stand; MOIS = fractional moisture content of fuel type <i>i</i> ; FWG = standing crop of fuel; RHOP = ovendry particle density; BULK, = bulk density of fuel type <i>i</i> ; MPS, = mean surface per unit volume of particle for fuel type <i>i</i> ; LHV, = heat content of fuel type <i>i</i> ; ST, = mineral content (fraction) of fuel type <i>i</i> ; SE, = silica-free mineral content; MEXT = moisture of extinction of fuel type <i>i</i> ; PARAM = set of internal parameters.
Subroutine INJURY		
Crown scorch height	(1.18) °	HS = $\frac{C_1(FI)^{7/6}}{\left[C_2 \cdot FI + (C_3 \cdot WIND)^3\right]^{1/2} (TKILL - T_C)}$
		$T_1 = \mu reintensity; C_1, C_2, and C_3 are empirical constants; 1KJLL = 60°C;T_c = temperature (°C)$

RISK	
outine	
Subr	

Probability of
$$(1.19a)^{t}$$
 PD = $1 - \frac{1}{e^{AO - BC \cdot DBH + D3 \cdot HS}}$ DBH > 12.7 cm death from fire of scorch
Height HS for tree of $(1.19b)^{b}$ = $1 - \frac{1}{e^{LNR}e^{AO - BC \cdot DBH + D3 \cdot HS}}$ DBH < 12.7 cm dbh, DB
Height HS for tree of $(1.19b)^{b}$ = $1 - \frac{1}{e^{LNR}e^{AO - BC \cdot DBH + D3 \cdot HS}}$ DBH < 12.7 cm dbh, DB
AO, BC, D3, and LNR are empirical constants.
Subroutine BRNDFF
Removal of litter due to $(1.20)^{t}$ U = $\frac{K_1 - K_2 MOIS}{K_3 + MOIS}$
fire U = weight loss on plot: K_1, K_2 , and K_3 are empirical constants.
 $U = \text{weight loss on plot: } K_1, K_2$, and K_3 are empirical constants.
^a Botkin et al. (1972).
^b Kercher and Axelrod (1984).
^c Anderson et al. (1972).
^b Remonal (1972).
^c Van Wagner (1973).
^f Bevins (1980).
^g Van Wagner (1972).

TABLE II

 k_{α}

LHV LTD

MMC

Parameter	Equation Parameter Equation				
ABM	1.14	MPS	1.17		
AGEMX	1.1b, 1.12a	PL	1.9		
AMC	1.13	RHOP	1.17		
AØ	1.19a,b	SE	1.17		
BC	1.19a,b	ST	1.17		
BMC	1.13	ТМС	1.13		
BULK	1.17	WSM	1.8		
С	1.5	WSO	1.8		
CMC	1.13	α_1	1.5		
CR	1.9	α_2	1.14		
D3	1.19a,b	-			
DKF	1.15a				
DKL	1.15a				
DM	1.1a,b, 1.2b,c				
DMAX	1.6				
DMC	1.13				
DMIN	1.6				
FFL	1.14				
HM	1.1a, 1.2b,c				

Index of parameters of Table III to equations in Table I

1.3

1.17

1.13

1.15a.b

(Kercher and Axelrod, 1984) and proven to be realistic in its predictions. Our purpose in the discussion which follows is to analyze the internal workings of the model and to relate them to its behavioral properties. So here, we only present one example by plotting relative basal area instead of absolute basal area as done in earlier references. In Fig. 2, we show the relative basal area of the six species of ponderosa pine, white fir, Douglas-fir, sugar pine, incense-cedar, and California black oak. The figure shows the averaged result of 25 simulations run for 500 years at 5000 ft (1524 m) elevation for natural fire frequency and no SO₂ pollution. The simulations are run from clearcut at year 0 on a plot size of 400 m². The spaces between the lines indicate relative contribution of each species. Ponderosa pine dominates over the entire time period; incense-cedar slightly outperforms white fir, followed by sugar pine. California black oak is an understory tree and is eventually replaced. Douglas-fir does poorly at this site. Ponderosa pine is a relatively stable dominant under fire conditions. White fir is a



Fig. 2. Fractional share of each species contribution to total basal area. Distance between the lines is the fraction of total basal area for each species.

relatively stable subordinate species. Sugar pine exhibits a slight downward trend. Except for a brief, intermediate period of decreased relative basal area, incense-cedar shows trends for increasing importance. The sharp excursions in Fig. 2 are due to the deaths of dominating trees in one of the subordinate species, incense-cedar, white fit, or sugar pine. As useful as such results are for interpreting and displaying model behavior, it is quite clear that much detail eludes us without manipulating the model more intensively. A useful means of doing this is by sensitivity analysis.

Sensitivity analysis

We made a sensitivity analysis of SILVA by varying each species parameter individually by 10% of its original value. SILVA was run for 100 simulations for each variable tested. Each simulation was of 50-year length from clearcut initial conditions at 5000 ft (1524 m) elevation. Ponderosa pine basal area was chosen as the indicator output variable. We calculated the ratio of the fractional change of this variable to the fractional change in the varied model parameter. We define this as the sensitivity of the indicator variable.

The sensitivity Γ is defined as:

$$\Gamma = \left(\frac{PP_{new} - PP_{old}}{PP_{old}}\right) / \left(\frac{\mu_{new} - \mu_{old}}{\mu_{old}}\right)$$
(1)

where PP is basal area density of ponderosa pine (m^2/ha) and μ is some input parameter of model such as AGEMX(1), $H_m(1)$, DKL(1), etc.

The subscript 'old' indicates the variable or parameter as determined in Kercher and Axelrod (1982, 1984). The parameter with 'new' as a subscript is 10% greater than the corresponding 'old' parameter. The parenthetical subscript (1) indicates that only ponderosa parameters were varied in this analysis. The results of these calculations are given in Table III. If Γ equals 1, then a 10% change on a parameter produced a 10% increase in the

TABLE III

Sensitivity analysis of SILVA: fractional change in ponderosa pine basal area per fractional change in variable (values ranked at 10 years, 25 years, and 50 years for 100 simulations)

10 years		25 years		50 years	
Variable	Sensitivity	Variable	Sensitivity	Variable	Sensitivity
AGEMX	-2.6	AGEMX	- 1.6	α2	-2.0
WSM	-2.2	DMAX	-1.5	AGEMX	-1.8
CR	1.9	α2	-1.5	α_1	-1.6
DMAX	-1.8	ST	0.97	DMAX	-1.3
DMIN	-1.4	CR	0.95	DMIN	-1.0
α_2	-1.1	WSM	-0.92	DM	0.89
B ŪLK	-1.1	DMIN	-0.92	ABM	-0.75
LHV	-1.0	FFL	-0.85	BC	0.71
FFL	-0.95	HM	0.82	FFL	-0.67
α_1	0.88	BC	0.79	BULK	0.62
SE	-0.87	DM	0.71	WSM	-0.61
HM	0.82	AMC	0.64	С	-0.48
BC	0.64	MPS	0.63	WSO	-0.46
k _α	-0.60	SE	0.58	HM	0.44
ΑØ	-0.60	ABM	-0.54	LHV	-0.41
RHOP	-0.59	TMC	0.48	CR	-0.39
BMC	-0.52	LHV	-0.46	BMC	0.38
AMC	0.46	RHOP	0.45	KDL	0.28
ST	0.44	LTD	0.42	MMC	-0.21
DKL	-0.40	BMC	0.40	MPS	0.16
D3	-0.39	DKF	0.38	CMC	-0.16
WSO	-0.34	DKL	0.37	kα	-0.14
DM	0.33	CMC	0.35	LTD	0.13
С	- 0.29	АØ	-0.28	AØ	-0.12
DMC	-0.28	MMC	0.20	AMC	0.11
PL	-0.26	PL	0.14	PL	0.067
MMC	-0.20	DMC	0.13	DKF	-0.059
CMC	0.17	k _α	-0.13	DMC	-0.053
DKF	0.14	D3	-0.12	RHOP	-0.049
ТМС	0.14	BULK	-0.11	TMC	-0.034
LTD	-0.07	С	0.070	D3	-0.030
ABM	-0.07	WSO	-0.018	SE	-0.021
MPS	-0.01	α_1	0.008	ST	0.009

indicator variable; if Γ equals 0.1, then a 10% change in a parameter produced a 1% increase in the indicator variable. We use a subjective division of the Γ scale such that for $|\Gamma| < 0.1$, we use the term 'very insensitive'; for $0.1 < |\Gamma| < 0.5$, use the term 'insensitive'; for $0.5 < |\Gamma| < 1.1$, the term 'sensitive'; and for $|\Gamma| > 1.1$, the term 'very sensitive'. If a particular parameter is found to be sensitive, it means that it must be accurately known to produce accurate model results. The sensitivity of a parameter is indicative of whether the most important processes of the model are governed by that parameter. We have ordered the results for 10, 25, and 50 years.

We see that α_2 , AGEMX, DMAX, and DMIN are consistently ranked high as important parameters. DMAX and DMIN are important because they determine the growth response to temperature factors of climate. Changes in these parameters should have their maximum impact if DEGD in eq. 1.6 (Table I) has a value which corresponds to a rapidly changing Q. For DEGD near the value (DMAX + DMIN)/2, Q should be slowly changing and the basal area response should be relatively insensitive. Apparently for the value of DEGD in this simulation, basal area of ponderosa pine is quite sensitive to changes in Q. The negative sign for both DMIN and DMAX indicates that DEGD < (DMAX + DMIN)/2. AGEMX is the overall most important variable in sensitivity of basal area change. AGEMX is used by the model in two ways. AGEMX is used to calculate the probability of ecological death (eq. 1.12a, Table I) and is used to calculate the growth rate coefficient a in eq. 1.1a, Table I. For greater maximum observed age, AGEMX, a lower growth rate is set. The effect on sensitivity of a lower growth rate is probably larger than is the effect due to changes in the death rate. To first order, an increase in AGEMX in eq. 1.12a should produce a decrease in PD_{F} and a corresponding increase in basal area. (This argument ignores the resulting increase in competition which would accompany an increase in PD_{E} , so the positive effect would not be as large as a naive calculation would suggest.) However, the negative sign of the sensitivity for AGEMX is derived from the decrease in the growth rate and thus we suggest that, in the short term, eqs. 1.1a and b are more important than is eq. 1.12a in determining sensitivity of AGEMX. DM and HM also set the growth form and growth rate. DM enters the model in eqs. 1.1a, 1.2b and c. We see that as the time increases, basal areas become monotonically more sensitive to DM. This pattern is not observed for HM. Basal area is moderately sensitive to both DM and HM.

Foliage is important in two processes in the model. Foliage is the agent of competitive shading (eqs. 1.3, 1.4, and 1.5) and foliage is the source for the litter component of fuel for fire (eq. 1.14). We have kept the parameters for these two processes separate with designations (C, α_1) and (ABM, α_2) respectively. In the process of shading, the parameter k_{α} (eq. 1.3) expresses

the attenuation of light in the canopy. We see that at 10 years the sensitivity of k_{-} is -0.6. The minus sign implies that as light attenuation (shading) increases, basal area decreases. Now C_i multiplies k_{α} in eq. 1.3. But the sensitivity to C₁ is -0.29 which is one-half that of k_{α} . This is because we have only changed the C_1 of ponderosa pine in determining the sensitivity, whereas changing k_{α} changes the light for all trees. It is interesting that the sensitivity to α_2 is greater than to α_1 . This suggests fire effects are equal to or greater than light competition in western forests. Also the sensitivity to α_2 increase monotonically in time. This latter observation is presumably due to the fact that fire intensity from litter increases as litter is allowed to accumulate. Further evidence to support this is that ABM sensitivity increases monotonically in time rather dramatically. The difference in sensitivity between ABM and α_2 is because α_2 is an exponent. However, FFL, while relatively stable, does show a slight decrease. FFL, of all the fire parameters, does remain relatively sensitive. FFL is the fraction of a standing crop of foliage which is dropped each year (eq. 1.14). We see that the parameters having to do with fire are in a lower category of sensitivity than the parameters having to do with growth. Many of the parameters having to do with fire fluctuate rather strongly, e.g. BULK, ST, and LTD. The parameters for fire intensity often are of very low sensitivity, e.g., ST, SE, MPS. The parameters for evaluating equilibrium moisture content, a variable for fire intensity, are also often of low sensitivity and one of them CMC changes sign. This occurrence and some of the other sensitivity fluctuations may be due to competition. As CMC (eq. 1.13) increases, EMC increases. As EMC increases, fire intensity decreases. As fire intensity decreases, scorch height decreases and probability of death from fire decreases. As the latter decreases, the number of trees increases. Initially, for low tree numbers for small times, this increases basal area. However, at longer times there are more trees and competition is more limiting. In this case, an increase in tree number increases competition to the point that basal area actually decreases. This suggestion would also explain the shift we see in ST, AMC, TMC, RHOP, DMC, and SE, the latter four of which also change signs from 25 to 50 years.

The parameter with greatest decrease in sensitivity is WSM (eq. 1.8). WSM at ten years has sensitivity -2.2 which falls to -0.61 at 50 years. WSM is another growth parameter being the value of the ratio (τ) of actual to potential evapotranspiration for which growth is maximum. In our case where τ is less than WSM, as WSM increases, W decreases and hence basal area decreases. Apparently the dramatic decrease in this parameter's sensitivity between 10 and 50 years is due to competitive effects also. Possibly the strongest argument for the change in sensitivity due to competitive shading is given by the change in sensitivity of α_1 . Judging solely by this parameter's sensitivity alone, one would infer that competitive shading is relatively

unimportant at 25 years but is a dominant factor at 50 years' growth.

Finally consider the parameters regulating the response to pollution (PL, CR) (eq. 1.9). PL is the sensitivity of the growth reduction response to air pollution. We see that initially (10 years) an increase in this parameter causes a small decrease in basal area. However, at 25 and 50 years, we see an increase in basal area. CR is the threshold for the effect of pollution on growth. As CR increases, growth rates increase for individual trees. We see a monotonic decrease in the sensitivity of CR from a high of 1.9 at 10 years to a negative value of -0.39 at 50 years. This change is further evidence of competitive effects.

The sensitivity analysis is useful in determining critical processes and data that warrant further study. In this case, it suggests that the growth parameters should be given attention to assure their maximal accuracy.

Convergence of model

Inspection of the time-series of the average of 25 runs (e.g., Fig. 2) reveals the noisy character of the vegetational response of the stand. This noise is due to the stochastic nature of the birth and death processes and of the occurrence of fire. The natural question to ask is how noisy is the model? More specifically, how many runs are necessary to remove the noise from the mean output? The answer comes from examining the changes in the average response between successive runs. Let x(i, j, m) be the basal area of the *i*th species for the *j*th year for the *m*th run. Then the average response for the *i*th species in the *j*th year for N runs is:

$$\bar{x}(i,j)_{N} = \frac{1}{N} \sum_{m=1}^{N} x(i,j,m)$$
(2)

For the $N + 1^{\text{th}}$ run, we can calculate $\overline{x}(i, j)_{N+1}$ from $\overline{x}(i, j)_N$ using:

$$\bar{x}(i,j)_{N+1} = \frac{N}{N+1}\bar{x}(i,j)_N + \frac{1}{N+1}x(i,j,N+1)$$
(3)

Equation 3 can be used to keep track of the average by cumulating two numbers, the total of x(i, j, m) summed up to N and N itself. Define the quantity ρ_{iN} as:

$$\rho_{iN} = \frac{\sum_{j=1}^{L} \left[\bar{x}(i,j)_N - \bar{x}(i,j)_{N-1}^2 \right]^{1/2}}{\left[\sum_{j=1}^{L} \bar{x}(i,j)_{N-1}^2 \right]^{1/2}}$$
(4)

where L = the number of years. Thus ρ_{iN} measures the convergence of the



Fig. 3. Convergence properties of model results for ponderosa pine. The index ρ is plotted versus the number of runs for ponderosa pine. (a) Full stochastic inputs to seed year tables, fire occurence, seedling survival, and tree mortality. (b) Seed year tables and fire occurrence table taken the same for all runs.

average response of the *i*th species in N runs. Performing new runs causes smaller changes to the average basal area on the stand for a given species, and ρ_{iN} approaches zero. It may approach zero faster for some species than for others. Figure 3a shows ρ_N for ponderosa pine for 50 runs. The convergence for 50 runs was better than for 25 runs but the difference was not great enough to warrant the increased expense associated with more runs.

Our modeling approach up to this point has been to assume that each run represents a possible history for a stand with a given set of environmental conditions in a possible forest governed by certain probabilistic events. Consider the degree of variability induced by this assumption. Suppose all the good crop years and all the fire years are known for a particular forest. Then instead of calling the subroutines that generate the tables for seed crop years and fire years for each run, suppose the user calls these subroutines only once at the beginning of the multiple runs. Thus, the variability between runs is now due only to survivorship of seedlings and trees. Figure 3b is a plot of ρ_{iN} for ponderosa pine for this case. The convergence indicator ρ_N shows a much faster drop initially for ponderosa pine, but by 25 runs, ρ_N is very similar to that found by generating new seed tables and fire tables for each run. For white fir on the other hand, peaks in ρ_N which still occurred in the neighborhood of 45 runs were reduced by approximately 35% by generating only one set of tables for seed and fire years. These results allow a tentative generalization: for the dominant species, the randomness introduced by randomizing seed tables and fire tables each year is not an important contributor after 26 runs. However, the dominated or suppressed species are very noisy and their convergence is sensitive to any change in the number of stochastic factors. This is not too surprising in view of the fact that the suppressed species are of necessity opportunistic and must take advantage of chance occurrences which allow them to survive.

CONCLUSION

We have discussed the results of analyzing a model of growth and succession in a western coniferous forest dominated by fire ecology and which includes the effects of pollutants. Our goal in this paper has been to examine the model in sufficient detail to understand its inner workings and to draw some general conclusions regarding such models which combine deterministic growth; extrinsic, size-dependent stress; and an indeterminate (random variable) number of state variables with complex interaction (competition). Consideration of long-term simulation runs suggested that a detailed sensitivity analysis should be done to assess model details and that the noise associated with the random variables in the model should be considered by determining rates of convergence for model means.

Sensitivity analysis showed that parameters directly affecting growth dominated sensitivity response. Parameters of secondary processes such as fire-induced mortality were of secondary importance in determining model results. Model interactions of competition strongly affected parameter sensitivity. This effect was age-of-stand dependent. The results for young stands (10 years) could be explained by direct extrapolation of the functional form of model equations. However, many sensitivities for later years (50 years) were not predictable by direct extrapolation and seemed counterintuitive unless competition was invoked. This seemed particularly true for parameters affecting mortality but also was true for some growth parameters, notably parameters relating the effect of pollution on growth.

The analysis of model convergence suggested that means of the time-series for basal area of ponderosa pine, the dominant species, converged rather rapidly. This convergence was enhanced by not allowing fire years and seed years to be random variables but instead to be fixed for all runs. This result was not surprising. Subordinate species had much slower convergence than the dominant ponderosa pine. To achieve the equivalent accuracy in determining their time series required considerably more runs. We conjecture that this result is indicated for many models of this type. SILVA should be classified as a gap model (Shugart and West, 1980). It would be interesting to see if the results we have obtained can be generalized to the entire family of gap models or to only a subset. We conjecture that many of the results on competition and convergence can be generalized.

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