

Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington¹

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A model of forest development has been adapted for the Pacific Northwest. The regeneration, growth, and death of individual trees are tracked for simulated 0.2 ha plots and tree attributes are aggregated to provide stand measures. The model includes the influence of temperature, soil moisture, light tolerance, and competition on tree growth. Long-term simulations for Douglas-fir dominated forests on the western Olympic Peninsula show that the stand is eventually dominated by western hemlock with silver fir being codominant. Even after 1200 years of subsequent stand development, silver fir fails to replace western hemlock indicating that this is a self-replicating and stable community. Fire, windthrows, insect disturbance, and clear-cut logging followed by replanting are incorporated into the model as single-event disturbances to a 500-year-old forest. For those cases where large Douglas-fir survive the disturbance, stand biomass and leaf area patterns are not significantly impacted until the death of the last large Douglas-fir. The projections were all carried out to the time when the forest is dominated by western hemlock and silver fir. At that time, the differential effect of the earlier disturbance is not apparent from the forest composition, biomass, or leaf area patterns except for the insect disturbance. Following the removal of all Douglas-fir by an insect, leaf area fluctuates regularly with a period of 600 years.

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On a adapté un modèle de développement forestier pour la région nord-ouest du Pacifique. On enregistre la régénération, la croissance et la mortalité des arbres individuels sur des places d'étude simulées de 0,2 ha, et on intègre les diverses caractéristiques des arbres afin d'obtenir des valeurs pour le peuplement. Le modèle tient compte des effets de la température, de l'humidité du sol, de la tolérance à la lumière et de la compétition sur la croissance des arbres. Des simulations à long terme effectuées avec des forêts dominées par le sapin Douglas dans le secteur occidental de la Péninsule Olympique montrent ou éventuellement la forêt devient dominée par la pruche de l'Ouest avec le sapin argenté comme essence compagne. Même après une période 1200 ans, le sapin argenté ne réussit pas à supplanter la pruche, ce qui démontre qu'il forme une communauté végétale stable. Le feu, le chablis, les épidémies d'insectes et la coupe à blanc suivis de plantations sont incorporées au modèle en tant que perturbations isolées affectant une forêt âgée de 500 ans. Dans le cas où des sapins Douglas prédominants survivent aux perturbations, la biomasse du peuplement et la surface foliaire sont peu affectées, du moins jusqu'à l'élimination des derniers gros sapins Douglas. Les projections ont été poursuivies jusqu'au moment où la forêt devient dominée par la pruche et le sapin argenté. A ce moment, l'effet de la perturbation préalable n'est pas apparent sur la composition en essences, la biomasse ou la surface foliaire, sauf dans le cas d'une épidémie d'insectes. Lorsqu'un insecte détruit tous les sapins Douglas, la surface foliaire varie de façon régulière avec un cycle de 600 ans.

[Traduit par le journal]

Introduction

Although natural disturbances influence the long-term structure and stability of forests (Stephens 1956; Wright 1974; Sprugel 1976; White 1979; Oliver 1981), studying disturbance impacts usually occurs on a site by site basis. The frequency and severity of the perturbations, characteristics of surviving and invading species, and the local environment determine the repercussions of each disturbance. This study shows how a simulation model can be used to evaluate the long-term effects of abiotic and biotic disturbances on forest structure and tree

species composition. The effects of fire, windstorms, clear-cuttings, and severe insect disturbances (removal of a single species by pathogens or insects) are examined for simulated plots for the western Olympic Peninsula in Washington State. Simulating different disturbances allows comparison of stand development as a function of the type of disturbance.

Direct measurement of differences in forest structure resulting from different perturbations is difficult because of (i) the longevity of seral species and (ii) changes in site conditions among stands that have experienced different disturbances. Computer models of forest succession offer a unique way to explore succession for long time periods following different disturbances and known initial conditions. The time period for which the projected forest is considered is limited more by computer costs than by the actual stand age. Forest succession models that grow trees on an annual time step have been applied

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to decades or centuries of stand development (Dale *et al.* 1985). A second advantage of computer models is the ability to induce different disturbances in identical forests. Although there are always differences between site conditions and climatic factors in actual forests, computer models allow the user to specify identical stand structure at the start of a simulation experiment and to run the model under identical climatic conditions. This ability reduces sources of variability in the projected forest.

The computer code of a model of forest development is actually a logical statement of current hypotheses about the factors that affect tree birth, growth, and death. Experiments using such a model allow users to expand these hypotheses to their logical extension. For long-term succession where direct measurements are impossible, computer models are useful for indicating where knowledge is deficient, where the system is most sensitive, and to provide a first testing ground for hypotheses. In this paper we describe a model of forest development that has been adapted for use in the Pacific Northwest. The model is used to examine the long-term effects of disturbances of different severity to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated forests on the western Olympic Peninsula. The results are used to expand current understanding of factors affecting forest development.

Previous modeling efforts for the Pacific Northwest have concentrated on changes in forest types across large areas (Loucks *et al.* 1981) or on stand management as obtained from summaries of large existing data sets (e.g., Arney 1985). The approach described in this paper allows for testing hypotheses regarding the impact of individual tree dynamics on long-term forest development. The particular impact we explore deals with disturbances.

Description of the model

The computer model CLIMACS simulates the regeneration, growth, and mortality of individual trees in western Oregon or Washington. We describe the key features of the model here; the computer code has been documented elsewhere (Dale and Hemstrom 1984). CLIMACS is based on the JABOWA and FORET models developed for deciduous forests of the eastern United States (Botkin *et al.* 1972; Shugart and West 1977, 1980). The FORET model was modified for use in the Pacific Northwest by (i) changing the species parameters, (ii) including a moisture factor in the growth equations, (iii) performing regressions for the height – diameter relationships used in the diameter increment equations, (iv) making the mortality equations dependent on successional class of the species, and (v) incorporating natural disturbances and clear-cut logging. Each of these changes is explained as it relates to the way tree regeneration, growth, and mortality are modeled.

For the model simulations, temperature growth index (TGI) and plant moisture stress (PMS) are used to characterize the site. TGI is derived from a temperature sum that relates the growth of young Douglas-fir to the daily temperature recorded during a season (Cleary and Waring 1969). The model derives TGI for each year simulated from a normal distribution around a mean value supplied by the program user. PMS, another user-supplied driving variable, is the predawn negative water potential measured near the end of the growing season and serves as an integrator of annual water status (Waring and Cleary 1967). PMS remains constant throughout a simulation run. The model proceeds on a yearly time step and can include 21 tree species that occur in the Pacific Northwest. For any one site, the few species able to exist under those environmental

conditions are present. The model was developed so as to be applicable to all of western Washington and Oregon, but, to date, has only been tested for the H. J. Andrews Experimental Forest (Hemstrom and Adams 1982) and the western Olympic Peninsula (reported here).

Tree species in the Pacific Northwest have a variety of life history traits (Franklin and Dyrness 1973; Minore 1979); to accommodate this diversity, model parameters are species specific (Table 1). For instance, alder (*Alnus rubra* Bong.) germinates under full sun, is deciduous, and lives for a maximum of 160 years. Douglas-fir also germinates under full sun, but is coniferous and lives up to 1000 years. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is shade tolerant and can live about 600 years.

Regeneration

Species available for regeneration in CLIMACS are determined depending on the existing water stress, temperature range, and geographic region of the simulated stands. For each site the user reads in TGI, PMS, and the geographic region (for the model, western Washington and Oregon are divided into four regions based on geographic distribution of the species). The species that can tolerate these conditions are defined by the species parameters (Table 1) for the degree-days and the minimum value for water stress (WMIN) and by the geographic range of each species. Actual regeneration occurs from sprouting or from seed sources in the vicinity as conditioned by species tolerance and the projected leaf area. Any available species can regenerate in openings. When the species-specific projected leaf area limit (PLA) is obtained, individuals of that species can not enter the plot (Table 1). Trees enter the stand at an average size of 10 cm in diameter at breast height (DBH), which avoids dealing with the tremendous number of small trees that may be present during early stages of succession and the influence on species turnover of the herbs, shrubs, and animal activity in the first 30 years after a disturbance. Only trees are included in CLIMACS because they are the dominant structural form after 30 years. The exclusion of small trees and shrubs from the model increases computational efficiency, but limits the applicability of the model. For questions concerning long-term stand development on sites where shrub competition does not have a major influence on tree growth, this simplification is appropriate.

Diameter increment equations

Tree growth occurs in the model by a yearly increase in DBH. The annual increment function is based on that used by Botkin *et al.* (1972), with an added expression for the effect of soil moisture on growth. Diameter growth is a multiplicative function with the following conditions: (i) growth decreases as tree size increases; (ii) growth per year is dependent on foliage area; (iii) temperature affects growth; (iv) available moisture affects growth; (v) competition influences growth; (vi) shading and shade tolerance affect diameter increment. A multiplicative function is the most common relationship used (Botkin *et al.* 1972; Shugart and West 1977; Reed and Clark 1979), but it can tend to underestimate growth if many factors are incorporated (Swartzman 1979). The functional form assumes that optimum growth is modified by the effects of temperature, moisture availability, competition, and shade tolerance, which act independently.

The projected diameter increment decreases as tree size increases. As a tree grows larger, a greater portion of its photosynthetic output is used in respiration and not in producing additional tissue. The volume of wood incremented is also

TABLE 2. Growth parameters used in CLIMACS

Species	Growth parameters						Regression statistics ^a		
	B_1	B_4	A_1	BB	B_2	B_3	r^2	N	DBH range (cm)
<i>Abies amabilis</i>	15 612	0.9	-3.5057	2.5744	85.60	0.22	0.98	19	16.7-62.0
<i>Abies grandis</i>	12 493	1.0	-3.7389	2.6825	76.05	0.21	—	—	—
<i>Abies lasiocarpa</i>	7 404	1.0	-3.7389	2.6825	95.18	0.78	—	—	—
<i>Abies procera</i>	54 435	0.9	-3.7158	2.7592	68.29	0.19	0.98	24	48.1-127.3
<i>Acer macrophyllum</i>	19 044	1.2	-3.4930	2.7230	55.48	0.55	—	—	—
<i>Alnus rubra</i>	103	2.0	—	—	81.68	0.54	—	—	—
<i>Arbutus menziesii</i>	5 047	1.1	-3.7080	2.6580	38.35	0.16	—	—	—
<i>Castanopsis chrysophylla</i>	15 192	1.1	-3.7080	2.6580	74.73	0.14	—	—	—
<i>Chamaecyparis nootkatensis</i>	3 135	1.1	-2.0927	2.1863	69.29	0.23	—	—	—
<i>Libocedrus decurrens</i>	2 243	1.0	-2.0927	2.1863	72.72	0.30	—	—	—
<i>Picea engelmannii</i>	3 313	0.9	-3.7389	2.6825	92.94	0.46	—	—	—
<i>Picea sitchensis</i>	12 391	1.0	-3.7389	2.6825	64.03	0.14	—	—	—
<i>Pinus contorta</i>	6 650	1.0	-2.9849	2.4287	77.63	0.52	—	—	—
<i>Pinus lambertiana</i>	12 233	0.9	-3.9840	2.6667	85.81	0.34	—	—	—
<i>Pinus monticola</i>	15 645	0.9	-4.2847	2.7180	63.79	0.16	—	—	—
<i>Pinus ponderosa</i>	14 377	0.9	-4.4907	2.7587	93.81	0.38	—	—	—
<i>Pseudotsuga menziesii</i> ^b	13 193	1.1	-3.0396	2.5951	80.44	0.23	0.96	65	22.3-200.4
					72.34	0.22	0.98	55	9.8-196.4
<i>Quercus garryana</i>	4 956	1.1	-3.4950	2.7230	52.51	0.29	—	—	—
<i>Thuja plicata</i>	3 186	1.0	-2.0927	2.1863	64.71	0.23	0.98	38	6.2-157.9
<i>Tsuga heterophylla</i> ^b	17 645	0.9	-2.1720	2.2570	81.21	0.27	0.97	39	6.8-130.0
					75.97	0.27	0.98	38	4.9-143.4
<i>Tsuga mertensiana</i>	9 098	1.0	-4.8164	2.9308	75.97	0.07	0.98	23	32.2-84.2

^aHeight-DBH regressions were performed for species when data was available.

^bParameters for the height-DBH regression equations (B_2 and B_3) are reported on a second line for trees from stressed habitats (PMS > 15 bars or TGI < 60 days).

wrapped around a larger cylinder. The portion of the diameter increment equation that predicts the optimum tree size is represented by the following equation from Botkin *et al.* (1972):

$$\Delta\text{DBH} = f \left[1 - \frac{\text{DBH}(j) \text{ HT}(j)}{\text{DBHMX}(i) \text{ HMAX}(i)} \right]$$

where DBH(j) and HT(j) are the DBH and height of tree j and DBHMX(i) and HMAX(i) are the maximum DBH and height for species i . As a tree becomes very large, this equation predicts that diameter growth approaches zero. Maximum diameter and height were chosen for each species to represent large, but not the largest, recorded trees of a species.

The height - diameter relationship is a parabolic equation following Ker and Smith (1955):

$$\text{HT}(j) = 137 + B_2(i) \text{DBH}(j) - B_3(i) \text{DBH}(j)^2$$

where $B_2(i)$ and $B_3(i)$ are species-specific parameters (Table 2). For western hemlock, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), western red cedar (*Thuja plicata* Donn. ex. D. Don), Douglas-fir, Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), and noble fir (*Abies procera* Rehd.), we developed regression equations using diameter - height data from the H. J. Andrews Experimental Forest, Willamette National Forest, in western Oregon. Because height growth is related to habitat and western hemlock and Douglas-fir were sampled in a variety of habitats, the diameter - height relationship was tested for these two species under temperature- or moisture-stressed conditions (TGI > 60 or PMS < 15) and under nonstressed conditions. In stressed stands, the regression curves predict shorter trees for a given DBH (Table 2). For the other 15 species, the constants $B_2(i)$ and $B_3(i)$ were chosen so that height is at a maximum and

the rate of change of height with respect to diameter is zero when DBH(j) is at a maximum (following Botkin *et al.* 1972). As a consequence, the rate of change in height decreases as the diameter increases.

Diameter growth is related to existing foliage biomass (Grier and Logan 1977). CLIMACS uses a nonlinear relationship between leaf biomass (FBIO) and growth:

$$\Delta\text{DBH} = f[B_1(i)/\text{FBIO}^{B_4(i)}]$$

where $B_1(i)$ and $B_4(i)$ are parameters adjusted from those of Reed and Clark (1979) to give reasonable diameter increments for trees 50 cm in diameter (Table 2). The relation was scaled to produce a plateau in the curve as DBH approaches 100 cm.

The effect of temperature on diameter growth is modeled with a parabolic equation that ranges from 0 to 1 (following Botkin *et al.* 1972) and reflects the effects of temperature on net photosynthetic rates:

$$\Delta\text{DBH} = f \left[\frac{4(\text{TGI} - \text{DMIN}(i)) (\text{DMAX}(i) - \text{TGI})}{(\text{DMAX}(i) - \text{DMIN}(i))^2} \right]$$

where DMIN(i) and DMAX(i) are minimum and maximum degree-days for species i , respectively (Table 1). A value of zero occurs for TGI less than the minimum degree-days or greater than the maximum degree-days. This function thus reflects the temperature range in which a species can grow.

The inclusion of the moisture index in the equation for diameter increment is necessary because of the major influence of available moisture on tree growth in the Pacific Northwest (Franklin and Waring 1980). The effect of available moisture on growth is represented by a β -function (following Reed and Clark 1979):

TABLE 3. Equations for slow growth-related mortality^a

Life history group	Conditions	Probability of surviving 1 year		Species
Long lived, early seral	DBH < 0.2DBHMX ^b	0.8866 +	$\frac{0.1029}{0.2 - 1/DBHMX} \frac{DBH - 1}{DBHMX}$	<i>Pinus ponderosa</i> <i>Pseudotsuga menziesii</i>
	DBH ≥ 0.2DBHMX	0.9895		
Short lived, early seral		0.628		<i>Acer macrophyllum</i> <i>Alnus rubra</i> <i>Arbutus menziesii</i> <i>Quercus garryana</i>
Long lived, early midseral	DBH < 0.1DBHMX	0.96496 +	$\frac{0.1029}{0.1 - 1/DBHMX} \frac{DBH - 1}{DBHMX}$	<i>Chamaecyparis nootkatensis</i> <i>Libocedrus decurrens</i> <i>Thuja plicata</i>
	DBH ≥ 0.1DBHMX	0.97556 +	$\frac{0.02339DBH}{DBHMX}$	
Long lived, early midseral with increasing mortality	DBH < 0.5DBHMX	0.8866 +	$\frac{0.1112}{0.5 - 1/DBHMX} \frac{DBH - 1}{DBHMX}$	<i>Abies grandis</i> <i>A. lasiocarpa</i> <i>A. procera</i> <i>Picea engelmannii</i> <i>P. sitchensis</i> <i>Pinus contorta</i> <i>P. lambertiana</i> <i>P. monticola</i>
	DBH ≥ 0.5DBHMX	1.0538 -	$\frac{1.1112DBH}{DBHMX}$	
Late seral	DBH < 0.1DBHMX	0.9956 +	$\frac{0.99355}{0.1 - 1/DBHMX} \frac{DBH - 1}{DBHMX}$	<i>Abies amabilis</i> <i>Tsuga heterophylla</i> <i>T. mertensiana</i>
	DBH ≥ 0.1DBHMX	1.0053 -	$\frac{0.0635DBH}{DBHMX}$	

^aCompiled from McArdle *et al.* (1949) and from unpublished data from a chronosequence of stands in the Washington and Oregon Cascades (T. Thomas, U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, Corvallis, OR).

^bDBHMX is the maximum DBH for a species as given in Table 1.

usually blow down large trees. In CLIMACS, all species have an increasing probability of death from wind as size increases (Fig. 2B). Species are divided into two groups of windstorm resistance, depending on rooting depth and crown structure (Minore 1979). After windthrow, advance regeneration may occur. To simulate advance regeneration by western hemlock and silver fir following a windstorm (Oliver 1981), existing tolerant trees grow for 15 years before new trees are introduced into the model. Windstorms of different intensities may be simulated.

A biological disturbance, such as an insect or fungal epidemic, is modeled as an event that can kill all of the individuals of one or more species independent of tree size. Species affected and mortality rates can be selected by the user.

Clear-cut logging occurs in the model by removal of all aboveground biomass. Slash burning commonly precedes planting of 1- to 3-year old Douglas-fir seedlings.

Biological support for the model

Biological support for CLIMACS is based on (i) the scientific rationale of model equations and parameter values, (ii) the applicability of the model paradigm to other forest systems, and (iii) the comparison of model output to existing data sets. Equations and parameter values are obtained from 36 publications on forest ecology and tree physiology in the Pacific Northwest (Dale and Hemstrom 1984). The CLIMACS paradigm is based on models that have been applied to the northeastern United States (Botkin *et al.* 1972), an Appalachian forest of east Tennessee (Shugart and West 1977), a mixed pine - hardwood

forest of Arkansas (Mielke *et al.* 1978), an Australian eucalyptus forest (Shugart and Noble 1981), and a montane Puerto Rico rain forest (Doyle 1981).

Comparisons of model output to data can be done in two ways (Shugart 1984). Verification refers to comparisons of projected forest attributes with measured values when some data from that site may have been used to develop the model equation or parameter values. Validation refers to comparison of model projections to an independent data set.

The model projections compare well to Douglas-fir dominated natural stands in western Oregon and on the western Olympic Peninsula. Because the species-specific parameters of CLIMACS were derived from data collected at the H. J. Andrews Experiment Forest, simulations of that forest serve as model verifications. Projections from CLIMACS for xeric and mesic Douglas-fir forests have been compared with field data (Hemstrom and Adams 1982).

Validation of CLIMACS was provided by simulations of the western Olympic Peninsula, in which the field data and model parameters are independent in both the projected and measured stands. When the model is initiated from a bare plot with the climate conditions of the western Olympic Peninsula, projected species composition is good. Both the projected and actual forests are dominated by Douglas-fir with an understory of western hemlock and silver fir. Furthermore, the size of the trees is similar for the modeled and measured stands. Predicted density - diameter distributions for the western Olympic Peninsula are not significantly different at the 0.05 level from those of the measured 500-year-old stands using cumulative

	Basal area (m ² /ha)	Tress/ha	Mean DBH (cm)
Measured stand data used to initiate the model ^a	81.5	378	50
<i>Tsuga heterophylla</i> – <i>Pseudotsuga</i> <i>menziesii</i> type ^b	87.7	400	53

^aBased on unpublished data provided by M. Huff and H. Agee.

^bFonda and Bliss 1969.

in the Hoh River Valley. On the western Olympic Peninsula soil profiles are poorly developed; soil morphology is influenced by past fire; however, soil fertility does not influence community type distribution (Fonda and Bliss 1969). The role of past disturbances on these communities has not been examined.

The simulation model is used to compare succession given various disturbances. (i) No disturbance: The 500-year-old stand proceeds to the local climax condition during the course of a 1500-year projection. This simulation serves as the basis for comparison with other disturbances. (ii) Clear-cut logging followed by planting: All overstory trees are removed and the slash burned at stand age 500. A plantation of Douglas-fir (initially established at 1250 trees/ha) is projected through 1500 years of stand development. (iii) Fire: A moderate fire and a light fire occur at year 500 in separate simulations with mortality as a function of species, DBH, and fire intensity (Fig. 2A). The moderate fire is not a stand-replacement event because in the simulation large, fire-tolerant trees such as Douglas-fir have a 40% chance of survival. The remaining stand for both fires is projected through 750 years to bring the total stand age, including the 500 years before the fire, to 1250 years. A simulation of intense fire has the same results as clear-cut logging because dead wood and nitrogen losses are not tracked in the model. (iv) Windstorm: Light and moderate windstorms, each simulated separately, occur at the start of the model projection. Trees die as a function of species, DBH, and storm intensity (Fig. 2B) and advance regeneration of shade-tolerant species occurs. About 70% of large, deep-rooted trees survive the moderate storm simulated. The wind-thrown stand is projected 750 years to bring the total stand age to 1250 years. (v) Severe insect outbreak: A pathogen or insect outbreak eliminates all Douglas-fir at the beginning of the simulation period. Patterns of leaf area index and distribution by species of stand biomass and diameter are produced by each simulation and allow comparison of succession resulting from different types of disturbances and their intensities. Modal projections chosen from a minimum of 10 replicate simulations of each disturbance are reported in this paper.

Results and discussion

The simulations offer useful insights into patterns of species composition and forest development. Although 21 tree species are included in the model, only 4 species are able to grow in the model under the prevailing temperature and moisture conditions of the western Olympic Peninsula site. Douglas-fir, western hemlock, and silver fir are all characteristic of the measured stands, but the occasional introduction of grand fir into the projections appeared to be an anomaly. We surmise that the current distribution of grand fir on the Olympic Peninsula is limited by seed-source availability and not climate and have

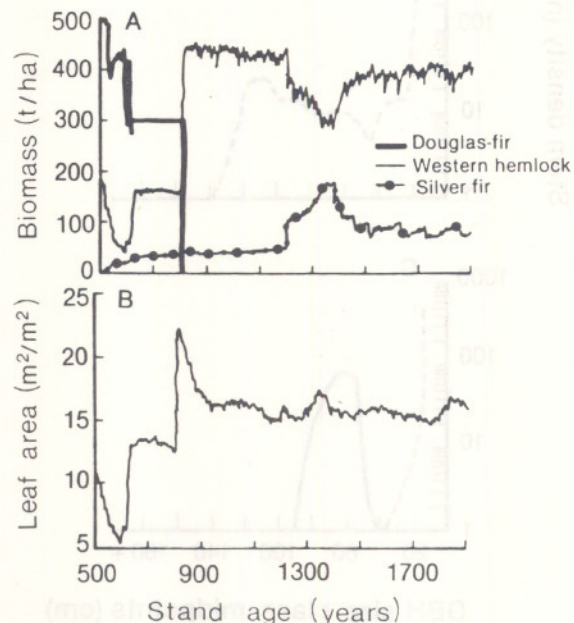


Fig. 4. Biomass by (A) species and (B) leaf area of all trees as related to stand age for a simulation with no disturbance. Initial stand structure is from a measured Douglas-fir – western hemlock forest on the western Olympic Peninsula (data provided by J. Agee). Environmental driving variables were set at TGI = 75 days and PMS = 13 bars.

removed grand fir from the potential species list for the Olympic Peninsula in the model.

The forest simulation with no disturbance

With no disturbance to the forest stand over the 2000-year period, Douglas-fir eventually dies and is replaced by western hemlock and silver fir (Fig. 4A). From years 500 to 900 there are some fluctuations in the biomass of Douglas-fir caused by mortality and changes in individual tree biomass. Because the last Douglas-fir to die on the plot is usually a large tree, there is a sharp drop in the biomass of Douglas-fir at that time. The actual stand age at the time of death of the oldest Douglas-fir varies from 750 to 1000 years for the simulations with no disturbance. At that time, advance regeneration of western hemlock causes a rapid increase in leaf area as many small, shade-tolerant trees invade the canopy (Fig. 4B). Leaf area increases from less than 15 to over 23 m²/m² within 20 years as western hemlock and Pacific silver fir quickly occupy available growing space by growing about 2.4 rings/cm diameter. The peak in leaf area drops to about 16 m²/m² as a stable size distribution of the western hemlock and silver fir is achieved as a result of natural thinning and suppression. Changes in leaf area are therefore linked to the death of the last Douglas-fir and subsequent

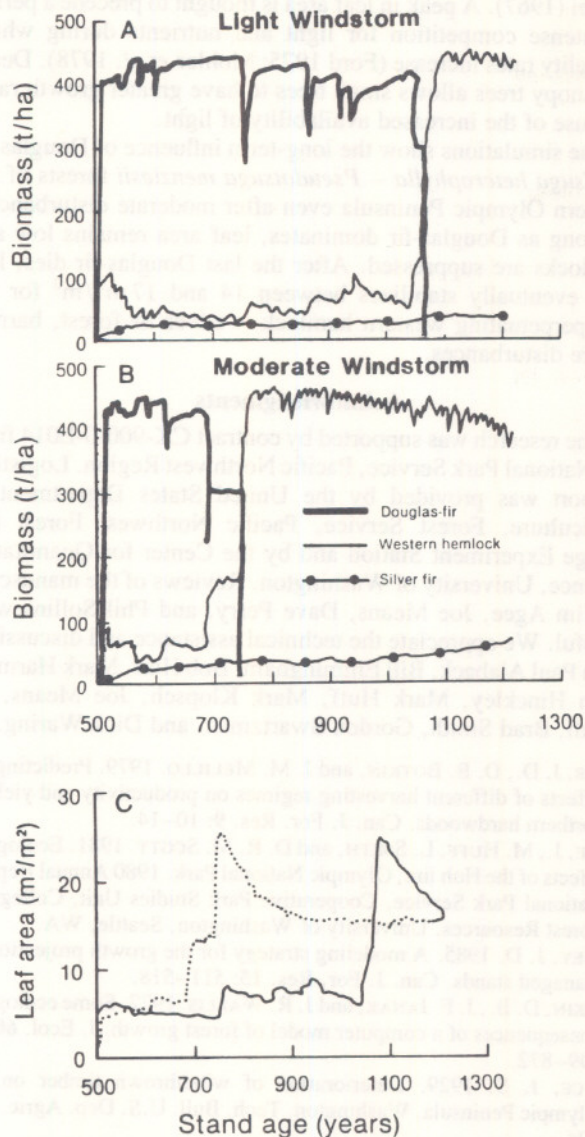


FIG. 7. Biomass by species for (A) a light windstorm and (B) a moderate windstorm for a simulated forest that was initiated at year 500 with the stand structure described in Fig. 4 and had the windstorm at year 500. (C) Leaf area of all species for the two windstorms (·····, moderate; —, light).

number of Douglas-fir in the light fire delays death of the last dominant Douglas-fir and the transition to climax forest by about 50 years as compared with the moderate fire. Removal of most western hemlock and Pacific silver fir from the stand by moderate fire affects stand dynamics for only a short period because the model assumes seed sources for both species exist outside the plot. The moderate fire simulation, however, does not reduce the dominant Douglas-fir canopy sufficiently to allow establishment of a rapidly growing seral Douglas-fir cohort. A large fire that eliminates seed sources for long distances could substantially change successional patterns by killing enough Douglas-fir to set succession back to a nearly bare plot colonized by Douglas-fir. Simulations of stand replacement fires in which all trees are killed show recovery patterns similar to those following clear-cut logging (Fig. 6).

Insect outbreak

The insect-induced removal of all dominant Douglas-fir at the

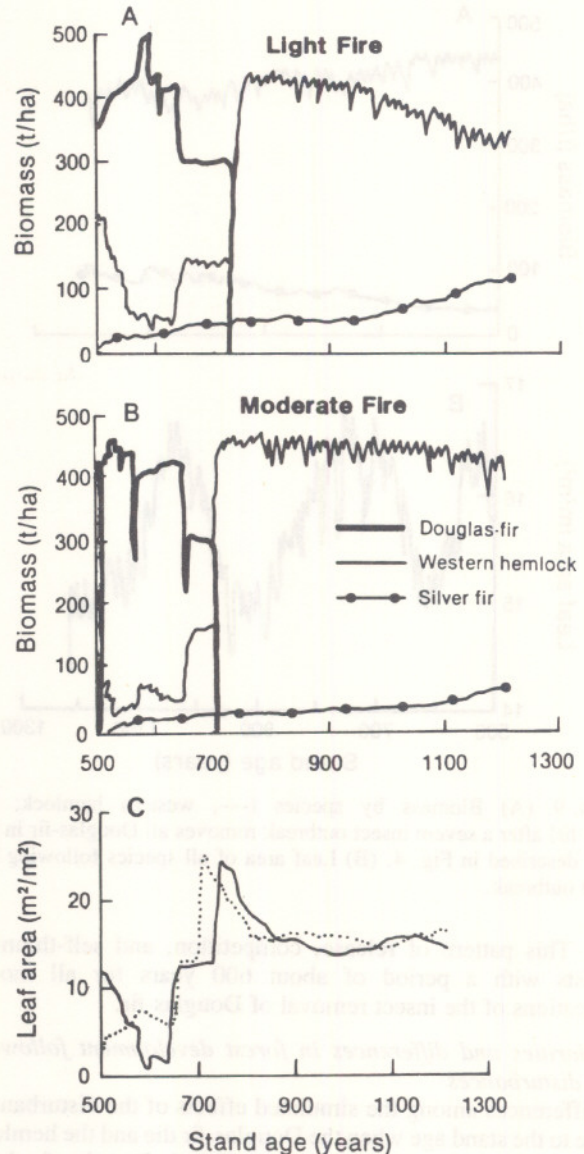


FIG. 8. Biomass by species for (A) a light and (B) a moderate fire occurring at year 500 in the stand described in Fig. 4. (C) Leaf area of all species following the two kinds of fires (·····, moderate; —, light).

beginning of the simulation period produces an immediate response by established western hemlock and Pacific silver fir (Fig. 9). Several large hemlock in the stand provide enough residual leaf area, however, to dampen the normal overshoot of leaf area during transition to climax. This is an example where population structure influences community dynamics. As the cohorts of western hemlock approach their maximum age of 600 years, mortality increases. With increasing dominance by large western hemlocks, the leaf area decreases to 15 m²/m² at about stand age 600 years, but rises after the death of the large hemlocks and subsequent release of small suppressed hemlocks. After stand age 600 years, the oscillations in leaf area appear to be part of a feedback loop involving self-thinning of overstory and release of the understory trees. As the numbers of hemlock and silver fir increase on the plot, leaf area increases. The resulting competition induces self-thinning and a subsequent decrease in leaf area. More light can then penetrate the canopy and understory trees are released, which instigates a rise in leaf

- Olympic National Park. *In* Ecological research in National Parks of the Pacific Northwest. Proceedings of the 2nd Conference on Scientific Research, November 1979, San Francisco, CA. Oregon State University, Forest Research Laboratory, Corvallis, OR.
- FRANKLIN, J. F., K. CROMACK, W. DENISON, A. MCKEE, C. MASER, J. SEDELL, F. SWANSON, and G. JUDAY. 1981. Ecological characteristics of old-growth Douglas-fir forests. U.S. Dep. Agric. Serv. Gen. Tech. Rep. PNW-118.
- FRANKLIN, J. F., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agric. Serv. Gen. Tech. Rep. PNW-8.
- FRANKLIN, J. F., and M. A. HEMSTROM. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In* Forest succession: concepts and application. Edited by D. C. West, H. H. Shugart, and D. B. Botkin. Springer-Verlag, New York. pp. 212-229.
- FRANKLIN, J. F., and R. WARING. 1980. Distinctive features of the northwestern coniferous forest: development, structure and function. *In* Forests: fresh perspectives in ecosystem analysis. Pro. Ann. Biol. Colloq. (Oreg. State Univ.), 40th. pp. 59-86.
- GHOLZ, H. L., C. C. GRIER, A. G. CAMPBELL, and A. J. BROWN. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Res. Pap. No. 41, Oreg. State Univ., For. Res. Lab.
- GRAHAM, R. L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis, OR.
- GRAHAM, R. L., and K. CROMACK. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 511-521.
- GRIER, C. C., and R. S. LOGAN. 1977. Old growth *Pseudotsuga menziesii* communities of a western Oregon watershed; biomass distribution and production budgets. Ecol. Monogr. 47: 373-400.
- HAMILTON, D. A., JR., and B. M. EDWARDS. 1976. Modeling the probability of individual tree mortality. U.S. Dep. Agric. For. Serv. Res. Pap. INT-185.
- HEINSELMAN, M. L. 1970. The natural role of fire in northern conifer forests. Naturalist, 21: 14-23.
- HEMSTROM, M., and V. ADAMS. 1982. Modeling long term forest succession in the Pacific Northwest. *In* Forest succession and stand development in the Northwest. Edited by J. E. Means. Forest Research Laboratory, Oregon State University, Corvallis, OR. pp. 14-23.
- HEMSTROM, M., and J. F. FRANKLIN. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quat. Res. (N.Y.), 18: 32-51.
- HUFF, M. H., and J. K. AGEE. 1980. Characteristics of large lightning fires in the Olympic Mountains, Washington. *In* Fire and Forest Meteorology Conference Proceedings. Vol. 6. Society of American Foresters, Washington, DC. pp. 175-181.
- KER, J. W., and J. H. G. SMITH. 1955. Advantages of the parabolic expression of height-diameter relationships. For. Chron. 3: 235-246.
- KIRA, T., and T. SHIDEI. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jpn. J. Ecol. 17: 70-87.
- LOUCKS, O. L., A. R. EK, W. C. JOHNSON, and R. A. MONSERUD. 1981. Growth, aging and succession. Dyn. Prop. For. Ecosyst. 1981. pp. 37-86.
- MACLEAN, C. D., and J. M. BERGER. 1976. Softwood tree volume equations for major California species. USDA For. Serv. Res. Note PNW-266.
- MCARDLE, R. E., W. H. MEYER, and D. BRUCE. 1949. The yield of Douglas-fir in the Pacific Northwest. Tech. Bull. U.S. Dep. Agric. No. 201. (Revised 1961.)
- MIELKE, D. L., H. H. SHUGART, and D. C. WEST. 1978. A stand model for upland forests of southern Arkansas. Oak Ridge Natl. Lab., Environ. Sci. Div. Publ. No. 1134.
- MINORE, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-87.
- MOHLER, C. L., P. L. MARKS, and D. S. SPRUGEL. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66: 599-614.
- OLIVER, C. D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3: 153-168.
- REED, K., and S. CLARK. 1979. SUCSIM: a coniferous forest simulator. Model documentation. IBP Ecosyst. Anal. Stud., Conif. For. Biome Bull. No. 11.
- SHUGART, H. H. 1984. A theory of forest dynamics: an investigation of the ecological implications of several computer models of forest succession. Springer-Verlag, New York.
- SHUGART, H. H., and I. R. NOBLE. 1981. A computer model of succession and fire response of the high altitude eucalyptus forests of the Brindabella Range, Australia Capital Territory. Aust. J. Ecol. 6: 149-164.
- SHUGART, H. H., and D. C. WEST. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the Chestnut Blight. J. Environ. Manage. 5: 161-179.
- . 1980. Forest succession models. Bio. Science, 30(5): 308-313.
- SPRUGEL, D. G. 1976. Dynamic structure of wave generated *Abies balsamea* forest in the northeastern United States. J. Ecol. 64: 889-912.
- STAEBLER, G. R. 1953. Mortality estimation in fully stocked stands of young-growth Douglas-fir. U.S. For. Serv. Res. Pap. PNW-4.
- STEPHENS, E. P. 1956. The uprooting of trees: a forest process. Soil Sci. Soc. Am. Proc. 20: 113-116.
- SWARTZMAN, G. L. 1979. Evaluation of ecological simulation models. *In* Contemporary quantitative ecology and related econometrics. Edited by G. P. Patil and M. Rosenzweig. International Cooperative Publishing House, Fairland, MD. pp. 295-318.
- WARING, R. H., and B. D. CLEARY. 1967. Plant moisture stress: evaluation by pressure bomb. Science (Washington, D.C.), 155: 1248-1254.
- WARING, R. H., and J. F. FRANKLIN. 1979. Evergreen coniferous forests of the Pacific Northwest. Science (Washington, D.C.), 204: 1380-1386.
- WHITE, P. S. 1979. Pattern, process and natural disturbance in vegetation. Bot. Rev. 45: 229-299.
- WRIGHT, H. E. 1974. Landscape development, forest fires and wilderness management. Science (Washington, D.C.), 186: 487-495.

