ELSEVIER

Ecological Modelling 127 (2000) 183–205

ECOLOGICAL MODELLING

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# Disturbance and succession in a coniferous forest of northwestern North America: simulations with DRYADES, a spatial gap model

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Accepted 21 September 1999

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## Abstract

In this paper we describe a model of forest development that has been adapted for use in a coniferous forest of northwestern North America. The simulator, DRYADES, is a spatial gap model used to examine the effects of disturbances of different types, sizes, and frequencies in mature Douglas fir dominated forests on zonal sites of the Coastal Western Hemlock drier maritime (CWHdm) subzone of British Columbia. Simulation exercises were carried out to test the following (not mutually exclusive) hypotheses in relation to forest compositional variations observed within the study area today: (1) disturbance-mediated succession can accelerate the conversion of early successional forest communities dominated by pioneer tree species (e.g. Douglas fir) to later successional associations; (2) when present in the canopy, long-lived, tall, pioneer species such as Douglas fir strongly influence stand dynamics, regardless of the type of canopy disturbance; (3) silvicultural practices that emulate the autogenic natural disturbance regime of small canopy gaps will maintain a late-successional character at the stand level. Model simulations of forest successional dynamics suggested that: (1) repeated, small-scale disturbances such as light windstorms or small patch harvesting can accelerate the rate of tree species replacement by accelerating forest succession; (2) large-scale disturbances such as infrequent severe fires set back succession to an earlier seral stage dominated by Douglas fir; (3) clear-cutting without Douglas fir planting accelerates forest succession towards a western hemlock/western redcedar forest; (4) on mesic sites in the CWHdm subzone, Douglas fir will not dominate stand dynamics, unless there are infrequent, severe fire disturbances; (5) the creation of small openings through partial harvesting did not allow shade intolerant species to re-establish naturally and dominate the forest stand dynamics. It was concluded that modelled successional dynamics and composition of these forests are largely a function of the initial competitive interactions and the relative shade tolerance of species involved. © 2000 Elsevier Science B.V. All rights reserved.

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PII: S0304-3800(99)00208-2

*Keywords:* Forest gap model; Coniferous forest; Forest dynamics; Forest management; Forest succession; Partial cutting; Spatial simulation model

## 1. Introduction

The landscape of the Pacific coast of North America is dominated by coniferous species that are globally unrivaled in the size of individual trees and in the biomass accumulated in forest stands (Waring and Franklin, 1979). These stands include species such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don.), which are a common feature in coastal forests. In British Columbia, they occur at low to middle elevations, mostly west of the coastal mountains, and belong to the Coastal Western Hemlock (CWH) zone, the rainiest biogeoclimatic zone in the province (Meidinger and Pojar, 1991).

Although the CWH zone is an important biogeoclimatic zone in British Columbia, both geographically and economically, studies of long-term vegetation dynamics in forests of this zone have been quite limited and have generally focussed on moist, mature ecosystems (Daniels, 1994; Arsenault and Bradfield, 1995; Lertzman et al., 1996). The lack of successional studies on zonal sites of the drier maritime subzone (CWHdm) may have resulted partly from the belief that the major stand development work had already been performed in the past. General descriptions of succession following large-scale disturbance in Douglas fir/western hemlock forests have been available for many decades in the Pacific Northwest (Munger, 1930, 1940; Isaac, 1943). In these, Douglas fir is described as rapidly occupying burned sites, followed by reinvasion of the more shade-tolerant and fire-sensitive western hemlock and western redcedar (Franklin and Hemstrom, 1981). Establishment of western hemlock and western redcedar is believed to continue indefinitely under the canopy of the Douglas firs, and ultimately these species replace the Douglas firs which are lost to windthrow, pathogens, or other agents of mortality (Franklin and Hemstrom, 1981).

These descriptions of Douglas fir succession were followed by more detailed studies that focused mainly on secondary succession following clear-cutting and slashburning (McMinn, 1951; Morris, 1958; Yerkes, 1960). Other studies were specifically designed to document the early stages of succession (Müeller-Dombois, 1960, 1965; Kellman, 1969; Dyrness, 1973; Long, 1977). More recently, studies have dealt with the patterns and mechanisms of species abundance and replacement following disturbance (Gagnon, 1985; Klinka et al., 1985; Halpern, 1988, 1989; Halpern and Franklin, 1990). Others have focused on the relationships between species diversity and succession (Zobel et al., 1976; Schoonmaker and McKee, 1988), vegetation development following harvesting (Houseknecht, 1976; Karakatsoulis and Kimmins, 1993), and stand structural diversity versus successional stages (Kuiper, 1988). Studies of gap-phase dynamics have been implemented in the Cascade range (USA) (Stewart, 1986a,b, 1988; Spies and Franklin, 1989; Canham et al., 1990; Spies et al., 1990; Bradshaw and Spies, 1992), and in southern British Columbia (Daniels, 1994; Arsenault and Bradfield, 1995; Lertzman, 1992; Pearson, 1995). In summary, there has been a shift of interest in the study of forest dynamics toward small-scale disturbances, but there have been few studies of forest dynamics following disturbances of different types, spatial scales and frequencies on zonal sites of the CWHdm subzone.

Three reasons may explain the difficulty of investigating forest succession in coniferous forests of coastal British Columbia: (1) the time scales involved in ecosystem development; (2) the history of stands with long-lived species is difficult to reconstruct, and; (3) the possibility of changes in site conditions among stands that have experienced different disturbances (Dale et al., 1986; Keenan, 1993). One way to overcome these difficulties is to use computer models in order to help organize current knowledge and ideas about the way ecosystems develop and function. Implications of this empirical and theoretical understanding can be investigated, and hypotheses can be tested that are difficult or impossible to explore through empirical means (Yarie, 1990). Computer models have been used to study forest succession in the Pacific Northwest (Dale et al., 1986; Burton and Cumming, 1991; Keenan, 1993). They also have been used to assess the consequences of alternative silvicultural strategies over multiple rotations (Hansen et al., 1995).

In this paper we describe a spatial simulator of forest development for south coastal British Columbia. The simulator, DRYADES is a gap model (Botkin, 1993) with spatial enhancements allowing simulation of a range of patch sizes and edge effects. DRYADES is used to examine the effects of disturbances of different types, sizes, and frequencies in mature Douglas fir dominated forests on zonal sites of the CWHdm subzone. Simulation exercises were carried out to to test the following (not mutually exclusive) hypotheses in relation to forest compositional variations observed within the study area today:

1. Disturbance-mediated succession can accelerate the conversion of early successional forest communities dominated by pioneer tree species (such as Douglas fir) to later successional associations (Abrams and Scott, 1989);
2. when present in the canopy, long-lived, tall, pioneer species such as Douglas fir will strongly influence stand dynamics, regardless of the type of canopy disturbance (Dale et al., 1986);
3. silvicultural practices that emulate the autogenic natural disturbance regime of small canopy gaps will maintain a late-successional character at the stand level (Lertzman et al., 1996).

## 2. Description of DRYADES

DRYADES (Fig. 1) is derived from the SPACE model (Busing, 1991, 1995), a spatial, neighborhood model of forest dynamics that employs a fine-scale (0.5 m) grid on a plane ($\geq 0.4$ ha). The SPACE model was modified for use in south coastal British Columbia by adding: (1) crown depth and an empirical bole ratio (bole length divided by total tree height) estimation function; (2) a new leaf area estimation function based on pipe-model theory; (3) a revised height–diameter allometry; (4) a modified diameter growth function; (5) soil moisture effects on tree growth and recruitment; (6) a probability function of having good or bad seed crop years; (7) natural, exogenous disturbance effects such as fire and windthrow; (8) silvicultural prescriptions such as tree harvesting (using one or a combination of the following: tree species, diameter, height, and location), and tree planting (with user specification of plantation year and density); and (9) input tree list and stem map data (optional). These modifications and additions are described in more detail in the following sections.

### 2.1. Tree growth

As in most forest gap models, diameter at breast height (dbh) is a key state variable in DRYADES. The fundamental growth equation of gap models (Botkin, 1993), which represents change in tree volume as being proportional to the square of the diameter times the height, serves as a driving function of the model Eq. (1):

$$\frac{\partial D^2 H}{\partial t} = G\,L\left(1 - \frac{D\,H}{D_{\max}\,H_{\max}}\right) \tag{1}$$

where $G$ is a growth rate (maximum cm$^3$ wood volume $\cdot$ m$^{-2}$ leaf area), $L$ is the tree leaf area (m$^2$), $D$ and $H$ are dbh (cm) and height (cm), the subscripts denoting species maxima. Diameter growth through time is simulated using the equation proposed by Urban (1993). This equation incorporates leaf area, maximum tree size, and current tree size, and is derived by substituting a Chapman–Richards equation for height (Eq. (3)), and solving for d$D$ when d$t$ is 1 year (Urban, 1993):

$$D_{\mathrm{inc}} = \frac{G\,L\left(1 - \dfrac{DH}{D_{\max}\,H_{\max}}\right)}{D\,H_{\max}(-D\,b_2\,b_3\exp(b_2\,D)(1-\exp(b_2\,D))^{(b_3-1)} + 2(1-\exp(b_2\,D)))^{b_3}} \tag{2}$$

where all $D$ and $H$ parameters are in cm and $b$'s are parameters of the Chapman–Richards (Eq. (3)) tree height allometry:

$$H = b_1(1 - \exp^{(b_2 D)})^{(b_3)} \qquad (3)$$

where $b_1$ is maximum height ($H_{\max}$, m), and $b_2$ and $b_3$ determine the shape of the curve.

In DRYADES, two approaches can be used to estimate leaf area from cross-sectional sapwood area. In the first approach, diameter at the base of the live crown (dblc, cm) is predicted using quadratic taper equations (Eq. (4)) estimated for British Columbia species (Kozak et al., 1969):

$$\text{dblc} = D\left[a_0 + a_1\left(\frac{\text{hblc}}{H}\right) + a_2\left(\frac{\text{hblc}^2}{H^2}\right)\right]^{0.5} \qquad (4)$$

where $D$ is dbh, hblc is the height at base of live crown, $H$ is the total height, and the $a$'s are regressed parameters (Urban, 1993).

Sapwood area at the base of the live crown is then predicted using sapwood thickness–diameter relationships (e.g. Lassen and Okkonen, 1969). In

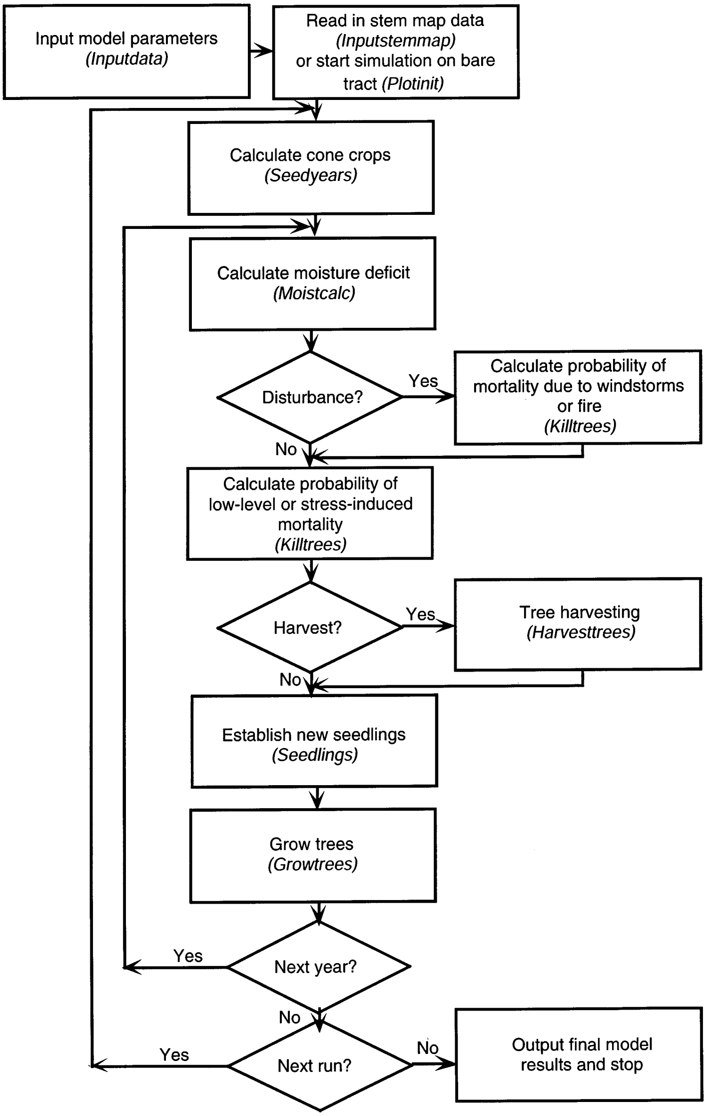

Fig. 1. Sequential order of computations in DRYADES. Program subroutines are noted in italics and parentheses.

Table 1
Parameters for the available light growth multiplyer function (Eq. (7)) for each light tolerance class as adopted from Urban (1993)

| Shade tolerance class | Parameter $t_1$ | $t_2$ | $t_3$* |
|---|---|---|---|
| Very tolerant | 1.02046 | 4.16533 | 0.03 |
| Tolerant | 1.04689 | 3.29031 | 0.06 |
| Intermediate | 1.12598 | 2.43920 | 0.09 |
| Intolerant | 1.25977 | 1.78588 | 0.12 |
| Very intolerant | 1.57851 | 1.18855 | 0.15 |

* Photosynthetic light compensation point.

the second approach, sapwood area is predicted as a function of dbh using a modified Chapman–Richards equation (Mailly, 1998):

$$SA = spa_1(1 - \exp^{(-spa_2\,D)})^2 \quad (5)$$

where $spa_1$ and $spa_2$ are regressed parameters, and $D$ is the diameter at breast height (dbh, cm). Leaf area:sapwood area ratios (LSR, Waring and Schlesinger, 1985) are then used to compute leaf area. This method of calculating leaf area yields realistic estimates, and does not overestimate leaf area for large trees such as when a power function is used (Urban, 1993).

In most forest gap models, a tree's total leaf area is situated at the top of its stem and the vertical distribution of foliage is ignored. Exceptions include the FORSKA (Leemans and Prentice, 1989; Leemans, 1991; Prentice et al., 1993) and ZELIG (Urban, 1993; Weishampel and Urban, 1996) models. In these, leaf area is distributed between the top height and the bole height (i.e. the bottom of the live canopy), which is zero at first but rises irreversibly through self-pruning when light levels fall below the photosynthetic compensation point. In DRYADES, a tree's leaf area is also distributed between the top height and bole height. Unlike other models, a species-specific, empirical equation predicting the bole ratio of each tree as a function of neighborhood competition is used (Ritchie and Hann, 1986; Mailly 1998):

$$BR = \frac{1}{[1.0 + \exp^{(br_1 + br_2 \cdot H + br_3 \cdot \ln BAL + br_4 \cdot H/D)}]} \quad (6)$$

where BR is the bole ratio, $H$ is the tree height (m), ln BAL is the natural log of stand basal area for trees whose diameter is greater than that of the subject tree (m$^2$ ha$^{-1}$), $D$ is the tree diameter (cm), and br's are species-specific parameters to be estimated. Height at base of crown is obtained by multiplying total tree height by the bole ratio.

The original light response function (Eq. (7)) found in most gap models is also used in DRYADES to estimate available light for each tree:

$$ALGM = t_1(1 - \exp^{-t_2(AL - t_3)}) \quad (7)$$

where ALGM is the available light growth modifier, AL is the available light at the top of the tree, and $t$'s are tolerance class parameters. DRYADES includes five curves that translate available light into photosynthetic capacity based on shade tolerance (Table 1; Urban, 1993) Maximum diameter increment is related to the available light at the top of each tree using one of the five response curves for each species. Available light is calculated according to the Bouguer's law (Iqbal, 1983):

$$AL = PHI \cdot \exp^{(-k \cdot SLA)} \quad (8)$$

where AL is the light available to the tree, PHI is the light at the top of the canopy (value is always 1.0, i.e. 100%), $k$ is an extinction coefficient that for many forest canopies has a value of about 0.4 (Jarvis and Leverenz, 1983), and SLA is the total shading leaf area index (m$^2$ m$^{-2}$) in the tree's neighborhood. The tree's neighborhood includes all the trees which are included in a radius of 10 m centered on the focal tree. Only the foliage (leaf area) which is above the current height of the target tree is used in the equation to compute SLA.

The inclusion of soil moisture in the diameter increment equation is necessary because of the major influence of available moisture on tree growth in the Pacific Northwest (Franklin and Waring, 1980; Dale et al., 1986). The soil moisture growth multiplier (drought response function) is the same as that proposed by Pastor and Post (1985) for the LINKAGES model; it decreases as a square-root function as maximum tolerable drought is approached:

$$\mathrm{SMGM} = \left[\frac{\mathrm{DroughtTol} \cdot \mathrm{TGS} - \mathrm{FJ}}{\mathrm{DroughtTol} \cdot \mathrm{TGS}}\right]^{0.5} \tag{9}$$

where SMGM is the soil moisture growth multiplier, DroughtTol is the species-specific drought tolerance parameter (ten times the maximum proportion of the growing season that a species can tolerate soil moisture below the wilting point, Table 3), TGS is the total duration of the growing season (days), and FJ is the fraction (%) of the growing season when soil is below wilting point. The variables SMGM, TGS, and FJ are computed in the model for each simulation time step.

The overall growth reduction in DRYADES is obtained using a multiplicative approach (Botkin et al., 1972). Maximum diameter increment is first reduced by taking into account a crowding effects growth multiplyer (CEGM) associated with maximum neighborhood biomass:

$$\mathrm{CEGM} = 1 - \frac{\mathrm{SBIO}}{\mathrm{SOILQ}} \tag{10}$$

where SBIO is the total neighborhood biomass, and SOILQ is the maximum above-ground biomass of the forest type (Busing, 1991). Above-ground woody biomass (bole, bark, live branch, dead branch) is estimated using a power function that relates the sum of these components to dbh (Gholz et al., 1979; Feller, 1992; Urban, 1993). Growth is further reduced by multiplying the diameter increment by available light and soil moisture growth modifiers.

### 2.2. Tree establishment

Seedling regeneration involves probabilistic simulation of seed production, ubiquitous seed dispersal as well as recruitment based on species-specific parameters of seedling abundance and tolerance to shading. Each year a species can have a good or poor seed crop, but seedlings establish only in good seed years (Keane et al., 1989). A Monte Carlo method (Kercher and Axelrod, 1984a,b) is used to determine good seed crop years, where ProbSeedCrop is the probability of a good seed crop. Each year a random number is generated and, if it is less than ProbSeedCrop, a good seed crop is simulated. This process is blocked for a number of years after a good seed crop. The number of blocked years (BlockYears) is based on the assumption that trees must store sufficient energy reserves before generating another seed crop.

Regeneration is not allowed on tracts lacking adult-sized trees except when dispersal is likely, i.e. when the species dispersal probability (Disp, ranging from 0 to 1, low to high) is greater than a random number with a probability of occurrence between 0 and 1. When adults of a species are present on a simulation tract or when seed dispersal occurs, Nsedl attempts at regeneration are made (Busing, 1995), where Nsedl is the maximum number of recruits per year following disturbance by fire. In cases when tree harvesting occurs, the default value of the maximum number of recruits per year is switched to NsedlHarv, to reflect changes in species' substrate preferences. During each attempt at seedling regeneration, a potential recruit is assigned a $x, y$ coordinate using a random number generator. To ensure that the regeneration environment of each potential recruit is adequate, the leaf area index (LAI, $m^2$ leaf area per $m^2$ ground area) is calculated for each circular neighborhood defined by Kradius, a species-specific neighborhood radius related to the gap size requirement of a species (Busing, 1991). Seedling input only occurs when (Mailly 1998):

$$\mathrm{LAI}_{\mathrm{neighborhood}} < \mathrm{LAItol} \tag{11}$$

where $\mathrm{LAI}_{\mathrm{neighborhood}}$ is the leaf area index of the regeneration neighborhood ($m^2$ leaf area per $m^2$ ground area), and LAItol is the LAI tolerance of a species ($m^2$ leaf area per $m^2$ neighborhood area). The maximum number of seedlings regenerated (Nsedl) is reduced if drought occurs:

$$\mathrm{Nsedl}^* = \mathrm{Nsedl} \cdot \mathrm{SMGM} \tag{12}$$

where Nsedl is the default value of the maximum number of recruits per year, SMGM is the soil moisture growth modifier, and Nsedl* is the product of SMGM and Nsedl, rounded to the nearest whole number. Finally, a time lag (Ltime, years) between seedling input and recruitment at sapling size is employed (Busing, 1995).

### 2.3. Tree mortality

As in most gap models, tree death in DRYADES occurs in two ways: (1) low-level mortality, i.e. tree mortality is a probabilistic function of maximum age for the species; (2) stress-induced death, i.e. if the growth of a tree falls below a critical limit ($<5\%$ of the maximum potential rate), its probability of mortality increases such that there is only 1% survival over 10 years. Mortality by disturbance events such as fire and windstorm is simulated as in Dale and Hemstrom (1984). Fire is modelled as an event with high probability of death for small trees (Dale et al., 1986), depending on the tolerance of the species to fire (Table 2). The probability of a tree surviving a fire is related to the intensity of the fire, and fires of different intensities can be simulated. In DRYADES, all species have an increasing probability of death from wind as tree size increases (Table 2). Species are divided into two groups of windstorm resistance (Dale et al., 1986), depending on rooting depth and crown structure (Minore, 1979). Finally, vegetative regeneration is modelled to occur following tree death (Busing, 1991). If a dead tree is within a certain diameter range, a sprout may replace the tree. The probability of replacement by sprouting is species-specific.

### 2.4. Climate drivers

The patterns of annual temperature and precipitation are entered into the model in the form of monthly means and standard deviations on the site to be simulated as adopted from Pastor and Post (1985, 1986). Soil moisture is given in terms of dry days (Pastor and Post, 1985), i.e. days when the supply of water is inadequate for tree growth. The supply of water is determined in terms of the maximum amount of available soil water (ASW, cm):

$$\mathrm{ASW} = \mathrm{FC} - \mathrm{DRY} \qquad (13)$$

where DRY is the wilting point (cm), and FC is the field capacity (cm) specific for a particular soil texture. Soil water is calculated as a monthly water balance, which is affected by precipitation and evaporation. Evaporation in terms of potential and actual evapotranspiration is calculated from solar radiation and air temperature using a modified form of the Priestley–Taylor equation as adopted from Bonan (1989). Monthly solar radiation is calculated once at the beginning of each simulation by attenuating incoming solar radiation for atmospheric effects, partitioning this into direct beam and diffuse components, and adjusting for slope and aspect (Bonan, 1990).

### 2.5. Silvicultural prescriptions

Enhancements to the basic version of SPACE (Busing, 1995) were required to simulate the types of silvicultural prescriptions currently used and being considered by forest managers. Modifications were also implemented to facilitate simulation experiments, as well as data collection and analysis. Harvesting scenarios from single-tree selection to clear-cut harvesting can be simulated at any year of a simulation, using one or a combination of the following tree variables: tree species,

Table 2
Probability of death of a tree following a fire[a] and after a windstorm[b] as a function of tree dbh as adopted from Dale and Hemstrom (1984)

| Fire | | Wind | |
|---|---|---|---|
| Tolerance class | Probability of death | Tolerance class | Probability of death |
| Fire tolerant | $P = [\exp(-0.00255 \cdot \mathrm{dbh})] \cdot \mathrm{FireIntens}$ | Wind tolerant | $P = [1.6 - \exp(-0.00255 \cdot \mathrm{dbh})] \cdot \mathrm{StormIntens}$ |
| Fire intolerant | $P = [\exp(-0.00053 \cdot \mathrm{dbh})] \cdot \mathrm{FireIntens}$ | Wind intolerant | $P = [1.9 - \exp(-0.00053 \cdot \mathrm{dbh})] \cdot \mathrm{StormIntens}$ |
| Does not survive | 1.0 | – | – |

[a] The intensity of the fire can be adjusted by the parameter FireIntens (fire intensity, 0–1).

[b] The intensity of the storm can be adjusted by the parameter StormIntens (storm intensity, 0–1).

diameter, height, and spatial coordinates. Planting of 1-year-old seedlings of different species is also possible, requiring input data specifications of planting time (year) and rate (number of seedlings per ha).

## 3. Parametrizing the model

Table 3 gives a complete list of species parameters used in the routines for tree establishment and growth. The values were obtained from the literature or from field measurements. Maximum age and diameter were chosen for each species to represent high, but not the highest, recorded trees of a species. Parameters of the height–dbh and of the bole ratio relationships were estimated by non-linear regression analysis of tree and plot data from study sites and stands which were located in south-western British Columbia (Mailly, 1998). In order to adequately simulate height growth of long-lived, coastal, western conifer species, the height–dbh regression data set was expanded to include larger trees not found in the study area (Garman et al., 1995). Diameter growth of the four species was initially adjusted for agreement with field measurements by altering the growth scaling constant ($G$). Final calibration involved setting $G$ so that for each species, the simulated stand quadratic diameter at breast height was within a 5–10 cm range measured in the actual stands (Mailly, 1998). Probability of seed dispersal on tracts lacking mature trees was estimated from Pickford (1929), to reflect the range of seed dispersal distances of each species. Values of climatic parameters (Table 4) were taken from the literature. The light extinction coefficient was set at 0.4, and maximum above-ground woody biomass was set at 750 mg ha$^{-1}$ (Grier and Logan, 1977). The area of the simulation plot was set at 1 ha (100 × 100 m). The neighborhood radius was set at 10 m. The soil chosen for the simulations was a sandy loam, with a depth of 1 meter, field capacity (FC) of 18 cm, and permanent wilting point (DRY) of 9.5 cm.

## 4. Model testing

DRYADES's performance was compared with measured stand data following fire and clear-cut harvesting (Mailly, 1998) using calibration data described above. In order to adequately simulate slow re-establishment of trees following a severe fire disturbance, a regeneration delay of 35 years is modelled during which the number of potential recruits (Nsedl) is reduced to only 5% of its maximum value. Model outputs of all conifer species were well within the range of measured stand data following both fire and clear-cut harvesting disturbances (basal area in m$^2$ ha$^{-1}$, Fig. 2). An exception to this was the simulated basal area for western hemlock for the clear-cut origin stands ($\sim 28$ m$^2$ ha$^{-1}$) compared with the measured stand values (32–40 m$^2$ ha$^{-1}$, Fig. 2).

In order to test the model's ability to adequately simulate tree planting and stand self-thinning, DRYADES' performance was compared with traditional growth and yield data. A Douglas fir stand was planted (1000 stems ha$^{-1}$) and grown for 100 years, and the output (density and basal area) compared with growth and yield tables, i.e. 1000 naturally regenerated trees, site index 34 m at age 50 (Mitchell et al., 1992). The Douglas fir stand established as a plantation experiences mortality and growth patterns similar to a naturally regenerated stand in the absence of any thinning or other management (Fig. 3).

## 5. Simulation experiments

### 5.1. Design

The simulation model was used to compare successional trends following various natural and man-made disturbances. The long-term effects of fire, windthrow, clear-cut logging (with and without Douglas fir planting), and group selection harvesting were compared with a simulation with no disturbance agents. The model is initiated with the stand attributes of a 125-year-old forest that established after a burn (0.25 ha

Table 3
Species parameters employed in the DRYADES model*

| Variable | *Pseudotsuga menziesii* | *Tsuga heterophylla* | *Thuja plicata* | *Betula papyrifera* |
|---|---|---|---|---|
| $A_{max}$ | 1000[e] | 500[k] | 1000[k] | 120[a] |
| $D_{max}$ | 300[k] | 225[k] | 300[k] | 76[a] |
| $H_{max}$ $(=b_1)$ | 68.04[g,d] | 60.92[g,d] | 50.05[g,d] | 36.99[g] |
| $b_2$ | −0.01613[g,d] | −0.01942[g,d] | −0.01785[g,d] | −0.07069[g] |
| $b_3$ | 0.78940[g,d] | 0.79336[g,d] | 0.75149[g,d] | 1.70082[g] |
| $G$ | 1400[g] | 1150[g] | 700[g] | 1500[g] |
| $T$ | 3[k] | 5[k] | 4[k] | 3[k] |
| SPRTND | 0 | 0 | 0 | 0.30[f] |
| SPRTMN | 0 | 0 | 0 | 10[a] |
| SPRTMX | 0 | 0 | 0 | 32[c] |
| DroughtTol | 4[k] | 3[k] | 3[k] | 3[a] |
| WindTol | 2[c] | 1[c] | 2[c] | 1[j] |
| FireTol | 2[c] | 0[c] | 1[c] | 0[j] |
| Disp | 0.7[h] | 1.0[h] | 0.9[h] | 1.0 |
| LAItol | 4.0[g] | 5.8[g] | 5.8[g] | 4.0[g] |
| Ltime | 10[g] | 15[g] | 15[g] | 10[g] |
| Nsedl | 39[g] | 18[g] | 19[g] | 12[g] |
| NsedlHarv | 12[g] | 35[g] | 26[g] | 12[g] |
| Kradius | 36[g] | 18[g] | 24[g] | 36[g] |
| ProbConeCrop | 0.45 | 0.60 | 0.60 | 0.50[b] |
| BlockYears | 1 | 1 | 1 | 1[b] |
| $wd_1$ | 0.1758[k] | 0.0813[k] | 0.0332[k] | 0.0260[k] |
| $wd_2$ | 2.3320[k] | 2.5638[k] | 2.6933[k] | 2.9950[l] |
| LSR | 0.47[m] | 0.41[m] | 0.56[m] | 0.20[i] |
| $spa_1$ | 1637.7[g] | 2781.7[g] | 2404.1[g] | 2009.2[g] |
| $spa_2$ | 0.0190[g] | 0.0183[g] | 0.0181[g] | 0.0254[g] |
| BRK | 0.89[k] | 0.96[k] | 0.95[k] | 0.95[k] |
| $br_1$ | 1.91160[g] | 1.64715[g] | 1.04652[g] | 0.51291[g] |
| $br_2$ | −0.02990[g] | −0.01855[g] | 0.00000[g] | −0.03456[g] |
| $br_3$ | −0.29239[g] | −0.39337[g] | −0.01598[g] | −0.12156[g] |
| $br_4$ | −0.42917[g] | 0.00000[g] | −1.46509[g] | 0.00000[g] |

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* Species parameters employed in the DRYADES model: $A_{max}$, species' maximum age (year); $D_{max}$, species' maximum diameter (cm); $H_{max}$, species' maximum height (m); $b_{2-3}$, height allometry parameters; $G$, scalar of potential growth; $T$, light tolerance class (1 = very intolerant, 5 = very tolerant); SPRTND, probability of a sprout replacing a tree following death; SPRTMN, SPRTMX, lower and higher limit of sprouting tree diameter (cm); DroughtTol, drought tolerance class ($\times 10 = \%$ of growing season which can be survived under a water deficit); WindTol, wind tolerance class (1 = intolerant, 2 = tolerant); FireTol, fire tolerance class (0 = does not survive, 1 = intolerant, 2 = tolerant); Disp, probability of seed dispersal to tracks lacking reproductively mature individuals (all four values are estimates); LAItol, leaf area index tolerance = leaf area index (LAI, $m^2\ m^{-2}$) above which no seedling recruitment can occur; Ltime, time lag between seedling establishment and recruitment; Nsedl, maximum number of recruits per year; NsedlHarv, maximum number of recruits per year following harvesting; Kradius, radius of the regeneration neighbourhood area (0.5 m units); ProbConeCrop, probability of having a good cone crop; BlockYears, number of blocked year(s) before another cone crop; $wd_{1-2}$, parameters for the relationship between woody biomass and dbh; LSR, leaf area:sapwood area ratio at breast height; $spa_{1-2}$, parameters for the relationship between sapwood area and dbh; BRK, bark parameter (inside bark = BRK*dbh outside bark); $br_{1-4}$, parameters for bole ratio function.

[a] Bonan (1989)).

[b] Brinkman (1974).

[c] Dale et al. (1986).

[d] Garman et al. (1995).

[e] Garman et al. (1992).

[f] Hutnik and Cunningham (1965).

[g] Mailly (1998).

[h] Pickford (1929).

[i] Pothier and Margolis (1991).

[j] Safford et al. (1990).

[k] Urban (1993).

[l] Wang et al. (1992).

[m] Waring et al. (1982).

stand, replicated four times to yield a 1.0 ha plot, Mailly, 1998). The resulting 1 ha stand includes 256 Douglas fir between, 19 and 84 cm dbh, 240 western hemlock between 5 and 56 cm dbh, and 280 western redcedar between 9 and 57 cm dbh.

### 5.2. No disturbance

Simulation proceeds from the 125-year-old stand to climax conditions during the course of a 1875-year projection, and serves as the basis for comparison with other disturbances.

### 5.3. Fire

A severe fire occurs when the simulated stand reaches 500 years, with a fire interval frequency of 500 years (Agee, 1991). Mortality after a fire is modelled as a function of species, dbh, and fire intensity (Table 2).

### 5.4. Wind

Light windstorms occur with a frequency of 30 years. Mortality after a light windstorm is modelled as a function of species, dbh, and storm intensity (Table 2). Windstorm intensity was adjusted so that approximately 8–15% of total stand basal area was removed during each storm.

### 5.5. Clear-cut logging with or without planting

Without planting — All overstory trees are removed at stand age 200. The stand is then left to natural regeneration processes, and harvested again at 100 years intervals, until it reaches 500 years.

With planting — All overstory trees are removed at stand age 126. A plantation of Douglas fir (established at 1000 trees ha$^{-1}$) is projected to the end of each subsequent 100-year intervals, until the stand reaches 500 years. This process is repeated at the beginning of each rotation.

### 5.6. Group selection — 0.125 ha and 0.50 ha patches

In order to test the influence of small-scale harvesting on long-term successional stand dynamics in these forests, the 1 ha stand was subdivided into small patches that were harvested alternately over the course of the simulation using

Table 4
Required climatic parameters, Maple Ridge, B.C., Canada

| Month | Temperature[a] (°C) | | Precipitation[a] (cm) | | Cloudiness[b] (tenths) | Solar radiation[c] (ly day$^{-1}$) |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | Mean |
| January | 1.4 | 2.1 | 27.9 | 11.8 | 8.1 | 98.8 |
| February | 3.9 | 1.4 | 22.1 | 8.1 | 7.6 | 168.5 |
| March | 5.2 | 1.2 | 19.7 | 8.1 | 7.1 | 271.4 |
| April | 8.3 | 0.9 | 13.9 | 5.4 | 6.8 | 389.5 |
| May | 11.9 | 1.2 | 9.9 | 3.9 | 6.4 | 491.6 |
| June | 14.4 | 1.5 | 9.4 | 4.5 | 6.8 | 512.7 |
| July[d] | 16.8 | 1.3 | 6.6 | 4.9 | 4.8 | 579.5 |
| August | 16.7 | 1.5 | 7.9 | 6.0 | 5.1 | 485.0 |
| September | 14.3 | 1.8 | 12.9 | 6.8 | 5.5 | 354.6 |
| October | 9.9 | 1.3 | 22.2 | 12.4 | 7.1 | 204.0 |
| November | 5.2 | 1.3 | 28.3 | 9.4 | 7.9 | 115.3 |
| December | 2.8 | 2.2 | 33.2 | 11.9 | 8.1 | 83.1 |

[a] Environment Canada (1981).

[b] Hare and Hay (1974) for south coastal British Columbia).

[c] Calculated after Bonan (1989) and required climatic parameters.

[d] July average minimum daily temperature: 11.3°C, July average maximum daily temperature: 22.6°C, Latitude: 49° 16′ N, longitude: 122° 34′ W, elevation: 143 m.

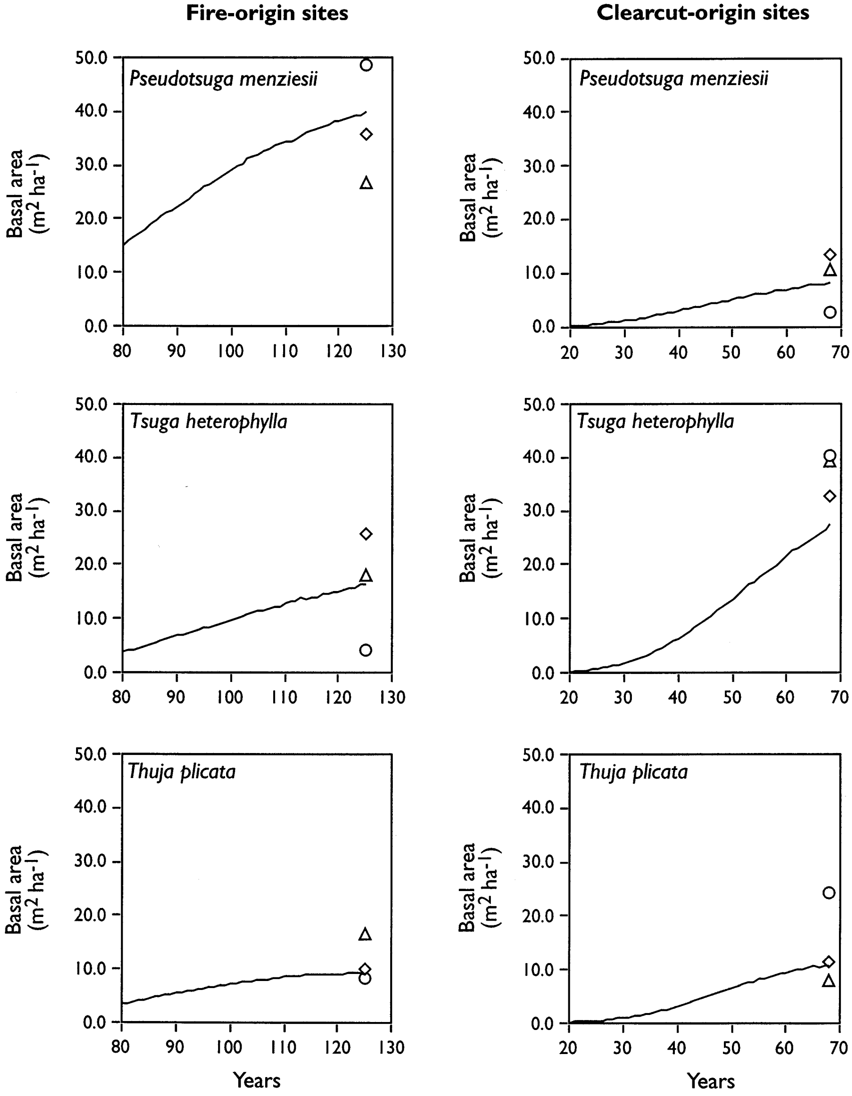

Fig. 2. Time course of simulated species basal area (last 50 years) produced by the present model (m$^2$ ha$^{-1}$, solid line) compared with measured stand basal area (Mailly, 1998) for fire-origin sites (site 1 = ◇, site 2 = ○, site 3 = △) and clear-cut origin sites (site 4 = ◇, site 5 = ○, site 6 = △).

a group selection method (i.e. a method of regenerating and maintaining uneven-aged stands in which trees are removed in small groups, Forestry Canada, 1995). A spatially-explicit light model was used to help determine the optimal size of group selection patches (Fig. 4).

0.125 ha patches — The 0.125 ha patch size (50 × 25 m) was chosen on the basis that it corresponded to the removal of approximately seven tall and contiguous mature trees (assuming each tree had a 15 m crown width). Each of the eight 0.125 ha patches (Fig. 5a) was harvested three times during the course of the 1875-year projection (i.e. every 624 years), so that at least one 0.125 ha patch harvest occurred every 78 years. This patch size results in low light levels at the ground, i.e. only about 10% of the patch area experiences light levels above 20% of full irradiance (Fig. 4).

0.50 ha patches — Each of the two 0.50 ha patches (50 × 100 m; Fig. 5b) was harvested twelve times during the course of the 1875-year projection (i.e. every 156 years); thus at least one 0.50 ha patch harvest occurred every 78 years. This patch size allows slightly more light at ground level, with more than 80% of the patch area experiencing light levels above 20% relative light intensity (Fig. 4), the optimum light level for survival of Douglas fir seedling in this biogeoclimatic subzone (Mailly and Kimmins, 1997). Using this patch size, approximately 30% of the patch area is experiencing light levels above 40%, the optimum light level for growth of Douglas fir seedling in this biogeoclimatic subzone (Mailly and Kimmins, 1997).

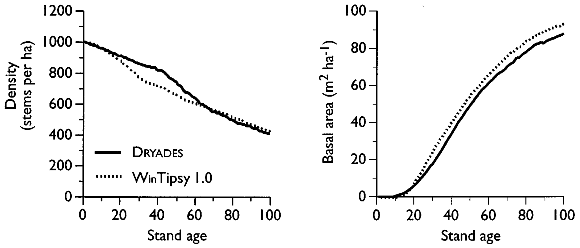

Fig. 3. Time course of stand density (stems ha$^{-1}$) and basal area (m$^2$ ha$^{-1}$) in an unthinned Douglas fir stand produced by the present model (DRYADES) and the growth and yield tables (site index 34 m at 50 years; WINTIPSY 1.0, Mitchell et al., 1992). The initial stand density was 1000 stems ha$^{-1}$.

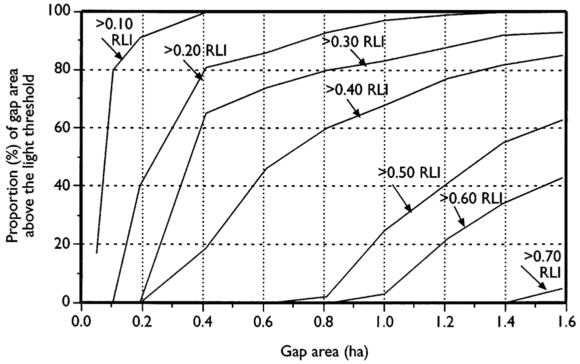

Fig. 4. Proportion (%) of simulated canopy opening experiencing light levels above specific light thresholds as a function of gap area, using tRAYci, a spatially-explicit light model (Brunner, 1998). Each line represents a specific light threshold, ranging from 0.10 to 0.70 relative light intensity (RLI) at ground level. Light simulations were performed using stem map data (0.25 ha stand; Mailly, 1998), replicated 16 times to yield a 4 ha stand. Simulated square gaps (0.05–1.6 ha) were centered in the middle of the 4 ha stand.

## 6. Results

### *6.1. No disturbance*

With no disturbance to the forest stand over the 1875-year projection period, Douglas fir eventually dies and is replaced by western hemlock and western redcedar (Fig. 6). Douglas fir basal area peaks at 49–50 m$^2$ ha$^{-1}$ when the stand is about 200–250 years old. It then declines to zero until the last individual dies, i.e. when it is nearly 1000 years old. The decline in Douglas fir basal area coincides with an increase in the number of regenerating western hemlock seedlings; the stand then enters the understory reinitiation phase (Oliver, 1981). At age 1000 years, the stand once dominated by Douglas fir is entirely replaced by a self-perpetuating western hemlock/western redcedar forest. Western hemlock dominates in terms of stand attributes, with values oscillating between 50 and 55 m$^2$ ha$^{-1}$, 300 and 350 stems ha$^{-1}$, and 7.1 and 7.9 m$^2$ m$^{-2}$ for stand basal area, stand density, and leaf area index, respectively (Fig. 6). Western redcedar remains a minor component of the stand, with values ranging from 7.5 to 11.0 m$^2$ ha$^{-1}$, 33 to 52 stems ha$^{-1}$, and 1.2 to 1.7 m$^2$ m$^{-2}$ for stand basal area, stand density, and leaf area index, respectively.

### *6.2. Fire disturbance*

Stand development under the severe fire disturbance scenario is somewhat similar to the forest simulation with no disturbance up until the stand is 500 years old; the fire then kills all the hemlocks, but leaves some Douglas firs and redcedars and sets successional dynamics back to a Douglas fir dominated stand (Fig. 7). Douglas fir dominance generally lasts about 470 years following a fire, after which western hemlock dominates in terms of stand basal area. The shade-tolerant western hemlock generally dominates stand density throughout the simulation, and is the major

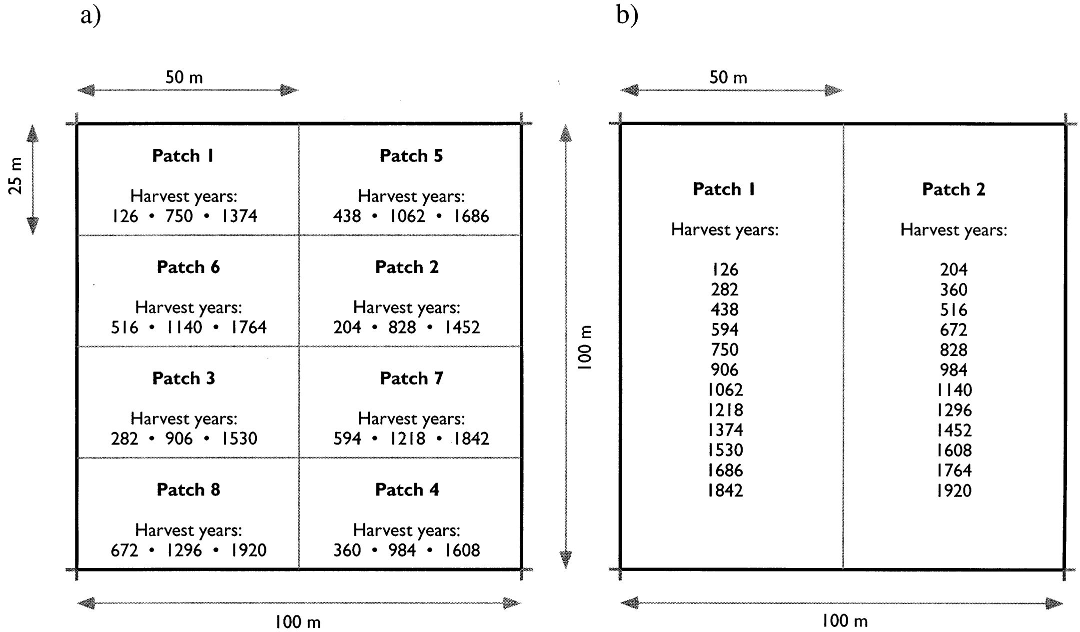

Fig. 5. (a) Location, and harvest years for each of the eight 0.125 ha patches to be harvested three times during the course of the 1875-year projection (every 624 years). (b) Location, and harvest years for each of the two 0.50 ha patches to be harvested twelve times during the course of the 1875-year projection (every 156 years).

component of the stand leaf area index approximately 400 years after fire disturbance. Redcedar is also a significant component of the stand following fire disturbance, and represents approximately 22–33% of total stand basal area (17–26 $m^2$ $ha^{-1}$), nearly 500 years after a fire episode. Interestingly, paper birch (*Betula papyrifera* Marsh.) does regenerate after a severe fire but its representation in the stand is relatively minor, with a maximum of 0.9 $m^2$ $ha^{-1}$ (40 stems $ha^{-1}$), 80 years after a fire. Although some large Douglas firs do survive after a fire episode, their small representation in the disturbed stand (ca. 6–8 individuals, 6–10 $m^2$ $ha^{-1}$) does not seem to impede the regeneration of both shade intolerant and shade-tolerant seedlings.

### 6.3. Wind disturbance

Compared with a simulation with no disturbance, frequent, light windstorms accelerate succession towards a self-maintaining, western hemlock/western redcedar forest (Fig. 8). Repeated, small-scale disturbance events such as light windstorms which removed approximately 5–10% of the stand basal area, increased the stress on the last Douglas firs which were eliminated when the stand was approximately 630 years old. Frequent, light windstorms also had the following effects: (1) they decreased the overall stand productivity at year 2000 by about 3 $m^2$ $ha^{-1}$ (i.e. from 62 to 59 $m^2$ $ha^{-1}$) compared with a scenario with no disturbance (Fig. 6), and (2) they accelerated western hemlock stand basal area dominance, which was attained at simulation year 355 (Fig. 8) compared with year 460 in the simulation with no disturbance (Fig. 6).

### 6.4. Clear-cutting

Without Douglas fir planting — When the stand is clear-cut harvested at age 200 years and left to natural regeneration, the site is quickly colonized by western hemlock seedlings, and to a much lesser extent by western redcedar and Douglas fir (Fig. 9). Western hemlock density peaks 50 years after the clear-cut at about 770–850 stems $ha^{-1}$. The high density of western hemlock in the stand, with its associated high leaf area index, allows this species to dominate stand basal area at the end of each rotation cycle, i.e. approximately 40 $m^2$ $ha^{-1}$, while redcedar and Douglas fir basal area are only about 10 $m^2$ $ha^{-1}$, respectively (Fig. 9). Paper birch also regenerates naturally following clear-cutting, but only achieves a maximum of 1.3 $m^2$ $ha^{-1}$ 50 years after clear-cutting, even though its density evolution pattern is similar to that of Douglas fir.

With Douglas fir planting — Clear-cut harvesting followed by Douglas fir planting with an initial density of 1000 stems per ha results in a complete dominance of the site by Douglas fir (Fig. 10). At the end of each 100-year rotation, Douglas fir basal area reaches a maximum of 86–93 $m^2$ $ha^{-1}$, while western hemlock is only 4–6 $m^2$ $ha^{-1}$. Redcedar and paper birch are nearly eliminated from the stand at the end of each rotation. Thirty years following clear-cut harvest with planting, Douglas fir's leaf area index reaches approximately 6 $m^2$ $m^{-2}$, a value slightly higher than western hemlock and western redcedar leaf area index tolerance of 5.8 $m^2$ $m^{-2}$ (Table 3). This coincides with a net decrease in stand density for these two shade-tolerant species, which decreased on average to only 35 and 8 stems $ha^{-1}$ at the end of each rotation, for western hemlock and redcedar, respectively (Fig. 10).

### *6.5. Group selection — 0.125 ha and 0.50 ha patches*

0.125 ha patches — Group selection logging using eight 0.125 ha patches, each one harvested every 624 years (Fig. 11), is comparable with a simulation with frequent, light windstorms, i.e. it accelerates succession towards a self-maintaining, western hemlock/western redcedar forest. Unlike the simulation with light windstorms, the 0.125 ha patch harvesting accelerates even more the successional trend towards a forest dominated by west-

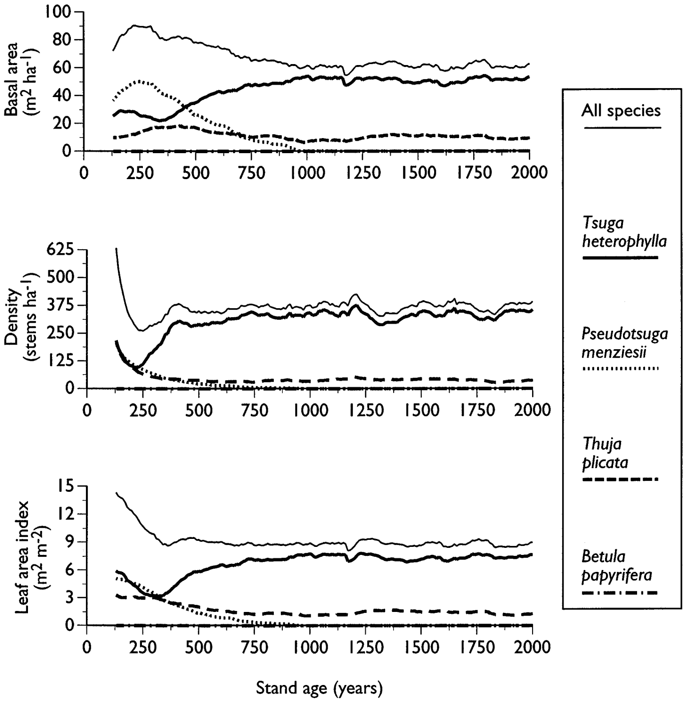

Fig. 6. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot with no disturbance.

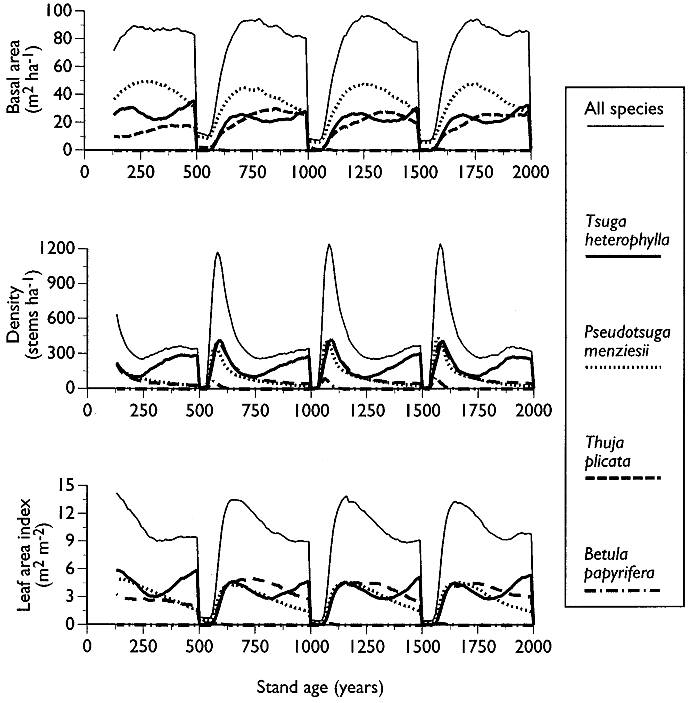

Fig. 7. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot with fire disturbance.

ern hemlock and western redcedar. Western hemlock stand basal area dominance is attained at simulation year 335 (Fig. 11), i.e. 20 years earlier than a simulation with frequent, light windstorms (Fig. 8). The decline in Douglas fir representation occurs much earlier than a simulation with no disturbance and at about the same time as a disturbance with frequent light windstorms, i.e. the last Douglas fir dies at stand age 670 (Fig. 11).

0.50 ha patches — Group selection using 0.50 ha patches (i.e. four times larger than the 0.125 patches) harvested alternatively every 156 years resulted in a much different successional dynamics compared with a simulation with smaller, 0.125 ha patches (Fig. 12). While a simulation with 0.50 ha patches still results in a self-maintaining, western hemlock/western redcedar stand, it does also allow recruitment of shade intolerant species such as Douglas fir and paper birch in the stand. The 0.50 ha patch size is not large enough, however, to allow seedlings of these species to compete with the shade-tolerant hemlocks and redcedars. Their representation in the stand is minimal, with approximately 1–55 individuals of each species contributing to less than 3 $m^2$ $ha^{-1}$ of stand basal area throughout the simulation (Fig. 12).

## 7. Discussion

In general, the model accounts well for the range of forest structures and compositions observed in the study area. Predicted stand attributes such as stand basal area and projected leaf area index are within the range of reported values for similar stands in the Pacific Northwest (Franklin and Waring, 1980). The variety of output results from the simulations (Figs. 5–11) shows the importance of the type and severity of external disturbances in driving successional stand dynamics. The model predicts that the long-term forest composition on mesic sites in the CWHdm subzone, in the absence of large-scale disturbance, is ultimately dominated by western hemlock

(Kimmins, 1997). Western redcedar is subdominant to western hemlock in the long-term simulations.

**Hypothesis 1.** Disturbance-mediated accelerated succession.

Results presented in this simulation study of Douglas fir dominated forests suggest that repeated, small-scale disturbances such as light windstorms (Fig. 8) or small patch harvesting (Fig. 12) can increase the rate of tree species replacement thereby accelerating forest succession. By contrast, large-scale disturbances such as infrequent severe fires, can set back succession to an earlier seral stage (Douglas fir stand, Fig. 7), If Douglas fir fails to regenerate following disturbance, direct development of a western hemlock/western redcedar forest can occur (Fig. 9). These results are in accordance with the findings of Hansen et al. (1995), who reported that shade-tolerant species such as western hemlock and western redcedar became dominant over Douglas fir under low to intermediate levels of tree retention and for rotations greater than 120 years.

Two mechanisms can explain a disturbance-mediated accelerated succession phenomenon in cases where small-scale disturbance destroys part of the dominant pioneer overstory: (1) disturbance releases advanced regeneration of late-successional species; and/or (2) disturbance creates environmental conditions favoring the quick establishment of shade-tolerant, late-successional species. Data from this simulation study show that both mechanisms may operate simultaneously in these forests, i.e. western hemlock advanced regeneration is released when Douglas fir stand dominance is declining (Figs. 7 and 10). At the same time, the stand leaf area index drops to a level which is favorable for the recruitment of the shade-tolerant hemlocks.

**Hypothesis 2.** When present in the canopy, long-lived, tall, pioneer species such as Douglas fir will

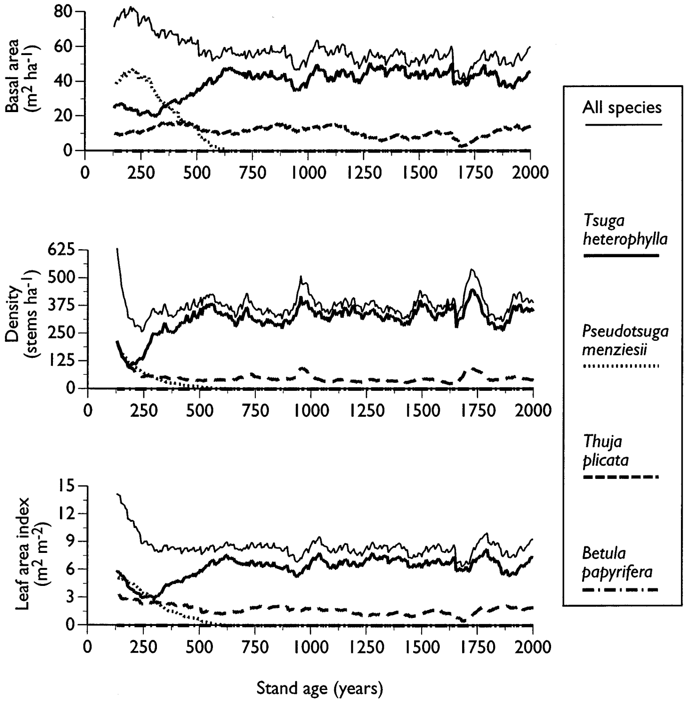

Fig. 8. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot with light windstorms initiated every 30 years.

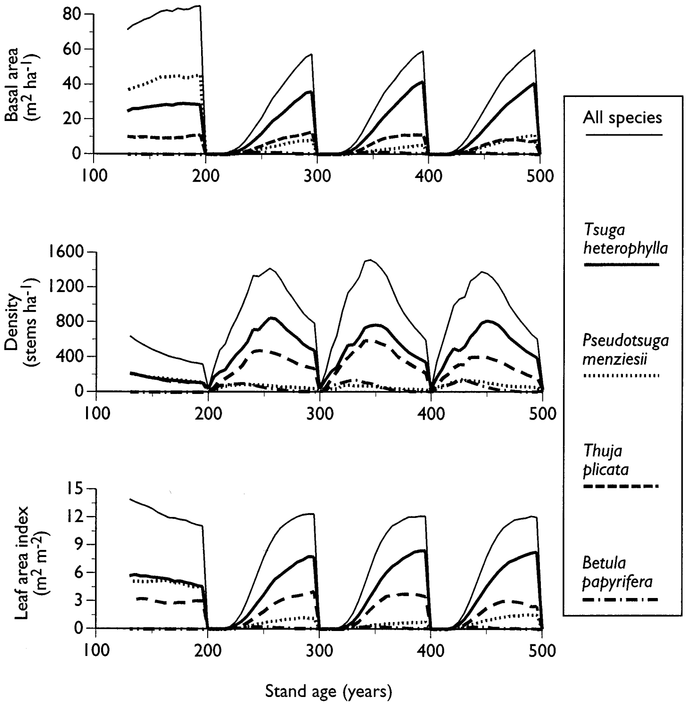

Fig. 9. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot clear-cutting with no Douglas fir planting at year 200, 300, and 400.

strongly influence stand dynamics, regardless of the type of disturbance.

The simulation results suggest that on mesic sites in the CWHdm subzone, Douglas fir will not dominate stand dynamics even though it persists in the canopy, unless there are infrequent, severe fire disturbances (Fig. 7). This result contrasts with the findings of Dale et al. (1986), which supported this hypothesis for Douglas fir dominated stands in the western Olympic Peninsula (Washington, USA) using CLIMACS, a non-spatially-explicit forest gap model. A possible explanation for the difference between the two simulation studies may have to do with how the forest canopy is represented in each model. DRYADES uses a neighborhood approach in which each tree is assigned specific $x$–$y$ coordinates on an horizontal plane. In CLIMACS, however, there is no representation of crown depth and trees are not assigned to specific locations in horizontal space. Each tree canopy in CLIMACS is represented by a disk at the top of the tree. This may lead to an exaggerated asymmetric competition for light in the model, and may make it possible for single large trees to dominate stand dynamics to an unrealistic extent (Kellomäki and Kolström, 1992). Also, overestimation of shading is a common problem in traditional JABOWA-based models because of the limited size of the simulation plot (Dale and Hemstrom, 1984; Keane et al., 1990). We suggest that a modelling approach (e.g. 0.5 m horizontal grid) capturing horizontal spatial variation and the vertical distribution of foliage within tree canopies is more appropriate when simulating the successional dynamics and crown-to-crown relationships of long-lived, tall coniferous forests.

**Hypothesis 3.** Silvicultural practices that emulate the natural disturbance regime of these forests by creating small canopy gaps will maintain late-successional character at the stand level.

Various silvicultural studies have demonstrated that the creation of different size openings in a forest canopy can promote either early- or late-successional species, thus either setting back or accelerating succession according to the size of the opening and the environmental conditions created (Minckler and Woerheide, 1965; Smith, 1986). In tall Douglas fir dominated forests of the Pacific Northwest, the creation of small openings as suggested by Lertzman et al. (1996) did not allow shade intolerant species to re-establish and dominate the forest stand dynamics as modelled in this study. Although individual shade intolerant Douglas fir and paper birch trees were able to establish and recruit in the 0.50 ha group selection patches (Fig. 12), they remained a relatively minor component of the overall stand dynamics, because of the reduced growth rate of these regenerating trees resulting from shading by the surrounding overstory (cf. also Mailly and Kimmins, 1997). The 0.5 ha patch size accelerated the transition from a mid to a late-successional stand condition. Small patches (e.g. 0.125–0.50 ha) accelerated the transition to a western hemlock/western redcedar stand even more, and maintained the late-successional character of the forest at the stand level.

## 8. Management implications

Forest managers in British Columbia and in many other places in the world are under increasing pressure to manage lands for multiple ecological and sociological values in addition to timber production. The primary management practice over the last half century in coastal forests has been clear-cut logging, in which all standing trees, dead and alive, were removed during a harvest (Garman et al., 1992). Ecologists have recommended the retention of canopy trees and the lengthening of rotations in managed forests to produce larger trees, greater variability in tree size, multistoried canopies, and recruitment of large woody debris (Hansen et al., 1995). Another

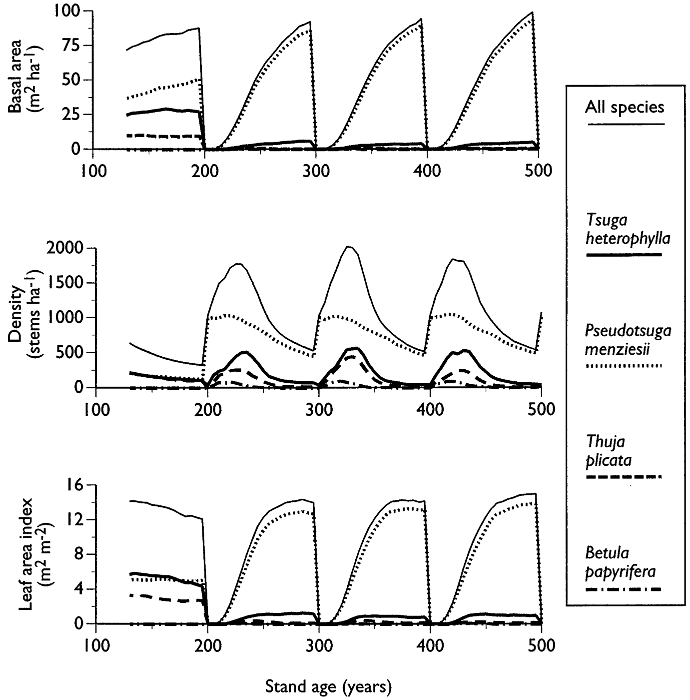

Fig. 10. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot clear-cutting with Douglas fir planting (1000 stems per ha) at year 200, 300, and 400.

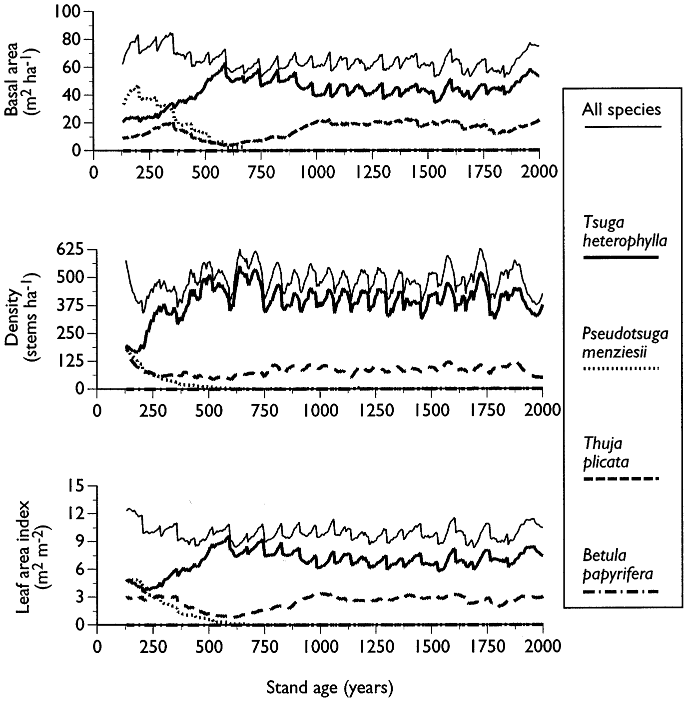

Fig. 11. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot with patch (0.125 ha) logging occurring every 78 years.

recommendation is the reduction in size of the harvest areas. Smaller patch sizes that 'mimic' autogenic disturbance processes have been proposed in place of large clear-cut areas. Findings presented in this simulation study suggest that repeated, low disturbance silvicultural manipulations would not perpetuate a Douglas fir dominated stand; in contrast, they would accelerate succession towards a western hemlock/western redcedar forest. In addition to the loss of tree species diversity in the long run, silvicultural systems that involve overstory retention may have higher layout and logging costs in comparison to clear-cutting (Kellog et al., 1991; Weigand and Burdett, 1992; Arnott and Beese, 1997). This suggests that to perpetuate the Douglas fir dominated stand condition that characterizes unmanaged forests in this area, larger cutblock sizes will be required to ensure the maintenance or re-establishment of shade intolerant species such as Douglas fir and paper birch without planting. Larger disturbance patch sizes alone may not maintain levels of Douglas fir in these stands. Because of lack of soil disturbance and the low frequency of good seed years in Douglas fir, cut areas may have to be planted. At the landscape level, a mosaic of openings of various sizes, with Douglas fir planting, in combination with some small-scale harvest to produce late-seral, structurally diverse forests, should meet society's multiple objectives.

Even though we have shown earlier (Mailly and Kimmins, 1997) that Douglas fir seedlings grow best when percent above canopy light is greater than 40%, the conclusions and the simulation results presented herein hinge on some basic assumptions on the ecology of tree regeneration. How disturbances of various sizes and types affect natural regeneration of the species involved in this zone is not fully understood. Research on the effects of disturbance patch size and substrate on the success of natural and planted regeneration of Douglas fir will add greatly to our understanding and modelling of forest dynamics in Pacific Northwest forests.

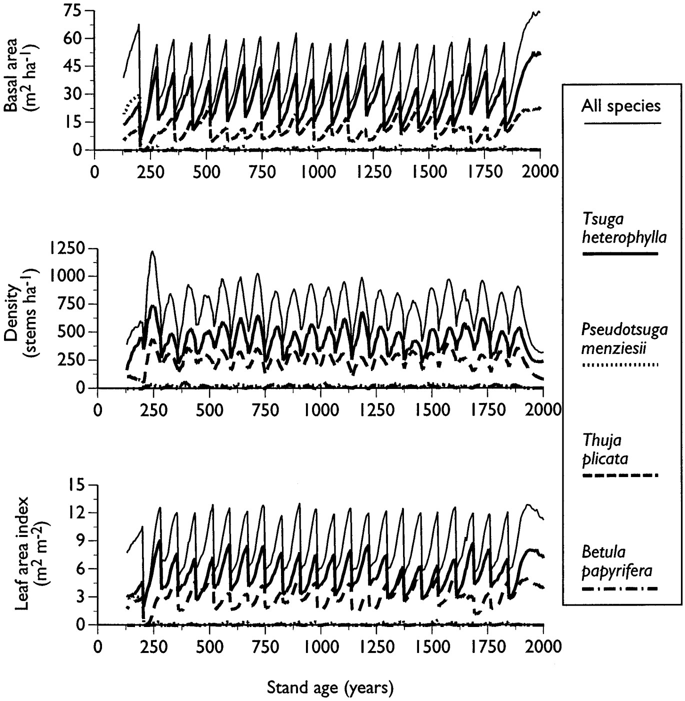

Fig. 12. Basal area, stand density, and leaf area index by species of all trees as related to stand age for a simulated plot with patch (0.50 ha) logging occurring every 78 years.

## Acknowledgements

The authors acknowledge grant support for this project from the National Sciences, Engineering and Research Council of Canada, the British Columbia Ministry of Forests. Part of this work was completed while D. Mailly was supported by a FCAR (Fonds des Chercheurs pour l'Avancement de la Recherche, Québec, Canada) doctoral scholarship. The insightful comments of R.D. Guy and P. Marshall strengthened the paper. J.-P. Ricard and J.-C. Pitre provided critical help with data collection.

## References

Abrams, M.D., Scott, M.L., 1989. Disturbance-mediated accelerated succession in two Michigan forest types. For. Sci. 35, 42–49.

Agee, J.K., 1991. Fire history of Douglas fir forests in the Pacific Northwest. United States Forest Service, General Technical Report PNW-GTR-285.

Arnott, J.T., Beese, W.J., 1997. Alternatives to clear-cutting in BC Coastal Montane Forest. For. Chron. 73, 670–678.

Arsenault, A., Bradfield, G.E., 1995. Structural–compositional variation in three age-classes of temperate rainforests in southern coastal British Columbia. Can. J. Bot. 73, 54–64.

Bonan, G.B., 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model. 45, 275–306.

Bonan, G.B., 1990. Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. Can. J. For. Res. 20, 1077–1088.

Botkin, D.B., 1993. Forest Dynamics, an Ecological Model. Oxford University Press, Oxford, UK.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Bradshaw, G.A., Spies, T.A., 1992. Characterizing canopy gap structure in forests using wavelet analysis. J. Ecol. 80, 205–215.

Brinkman, K.A., 1974. *Betula* L. Birch. In: Schopmeyer, C.S. (Ed.), Seeds of Woody Plants in the US Agriculture Handbook 450, United States Department of Agriculture, Washington, USA, pp. 252–257.

Brunner, A., 1998. A light model for spatially-explicit forest stand models. For. Ecol. Manage. 107, 19–46.

Burton, P.J., Cumming, S.G., 1991. Zelig.BC, user's guide to the prototype of a forest succession simulator for the evaluation of partial cutting options in British Columbia, B.C. Contract Report to the Ministry of Forests, Victoria, B.C., Canada.

Busing, R.T., 1995. Disturbance and the population dynamics of *Liriodendron tulipifera*, simulations with a spatial model of forest succession. J. Ecol. 83, 45–53.

Busing, R.T., 1991. A spatial model of forest dynamics. Vegetation 92, 167–179.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631.

Dale, V.H., Hemstrom, M., 1984. CLIMACS, A computer model of forest stand development for western Oregon and Washington. United States Forest Service Research Paper PNW-327.

Dale, V.H., Hemstrom, M., Franklin, J.F., 1986. Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington. Can. J. For. Res. 16, 56–67.

Daniels, L., 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia, M.Sc. Thesis. University of British Columbia, Vancouver, B.C., Canada.

Dyrness, C.T., 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54, 57–69.

Environment Canada, 1981. Canadian climate normals, 1951–1980. Temperature and precipitations. Environment Canada, Ottawa, Canada.

Feller, M.C., 1992. Generalized versus site-specific biomass regression equations for *Pseudotsuga menziesii* var. *menziesii* and *Thuja plicata* in coastal British Columbia. Biores. Technol. 39, 9–16.

Forestry Canada, 1995. Silvicultural terms in Canada, second ed. Policy, Economics and International Affairs Directorate, Canadian Forest Service, Natural Resources Canada, Cat no. Fo42–170/1995, 109 pp.

Franklin, J.F., Hemstrom, M.A., 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession. Springer–Verlag, New York, USA, pp. 212–229.

Franklin, J.F., Waring, R.H., 1980. Distinctive features of the northwestern coniferous forests, development, strucutre, and function. In: R.H. Waring (Ed.), Forests, Fresh Perspectives From Ecosystem Analysis. Oregon State University, Corvallis, Oregon, USA, pp. 59–86.

Gagnon, D., 1985. Forest vegetation of west-central Vancouver Island, British Columbia. Dissertation. University of British Columbia, Vancouver, B.C., Canada.

Garman, S.L., Acker, S.A., Ohmann, J.L., Spies, T.A., 1995. Asymptotic height–diameter equations for twenty-four tree species in western Oregon. Research Contribution 10. Forest Research Laboratory, Oregon State University, Corvallis, OR, USA.

Garman, S.L., Hansen, A.J., Urban, D.L., Lee, P.F., 1992. Alternative silvicultural practices and diversity of animal habitat in western Oregon, a computer simulation approach. In: Luker, P. (Ed.), Proceedings of the, 1992 summer computer simulation conference, The Society for Computer Simulation, Reno, Nevada, USA, pp. 777–781.

Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Research Paper 41, Oregon State University, Corvallis, OR, USA.

Grier, C.C., Logan, R.S., 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed, biomass distribution and production budgets. Ecol. Monogr. 47, 373–400.

Halpern, C.B., 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69, 1703–1715.

Halpern, C.B., 1989. Early successional patterns of forest species, interactions of life history traits and disturbance. Ecology 70, 704–720.

Halpern, C.B., Franklin, J.F., 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. J. Veg. Sci. 1, 475–482.

Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., Raphael, M.G., 1995. Alternative silvicultural regimes in the Pacific Northwest, simulations of ecological and economic effects. Ecol. Appl. 5, 535–554.

Hare, F.K., Hay, J.E., 1974. The climate of Canada and Alaska. In: Bryson, R.A., Hare, F.K. (Eds.), Climates of North America, World Survey of Climatology, 11. Elsevier, Amsterdam, The Netherlands, pp. 49–192.

Houseknecht, S.J., 1976. Vegetational composition and regeneration in three forest associations after logging in the coastal western hemlock zone. M.Sc. Thesis. University of British Columbia, Vancouver, B.C., Canada.

Hutnik, R.J., Cunningham, F.E., 1965. *Betula* (birches). In: Silvics of Forest Trees of the United States. Agriculture Handbook No. 271, United States Department of Agriculture, Washington, USA, pp. 93–99.

Iqbal, M., 1983. An introduction to solar radiation. Academic Press, Toronto, Canada.

Isaac, L.A., 1943. Reprodutive habits of Douglas fir. Charles Lathrop Pacific Forestry Foundation, United States Forest Service, USA.

Jarvis, P.G., Leverenz, J.W., 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Physiological Plant Ecology IV — Ecosystem Processes, Mineral Cycling, Productivity and Man's Influence. Springer-Verlag, Berlin, Germany, pp. 233–280.

Karakatsoulis, J., Kimmins, J.P., 1993. Vegetation development and Douglas fir growth following clear-cut harvesting in the CWHdm subzone, 10-year results from the Blaney chronosequence. Land Management Report No 81, Ministry of Forests, British Columbia, Canada.

Keane, R.E., Arno, S.F., Brown, J.K., 1989. FIRESUM — An ecological process model for fire succession in western coniferous forests. United States Forest Service General Technical Report INT-GTR-266.

Keane, R.E., Arno, S.F., Brown, J.K., 1990. Simulating cumulative fire effects in ponderosa pine/Douglas fir forests. Ecology 71, 189–203.

Keenan, R.G., 1993. Structure and function of western redcedar and western hemlock forests on northern Vancouver Island. Dissertation. University of British Columbia, Vancouver, B.C., Canada.

Kellman, M.C., 1969. Plant species interrelationships in a secondary succession in coastal British Columbia. Syesis 2, 201–212.

Kellog, L., Pilkerton, S., Edwards, R., 1991. Logging requirements to meet new forestry prescriptions. In: McNeal, J., Andersson, B. (Eds.), Forestry Operations in the, 1990's, Challenges and Solutions. Proceedings of the Fourtheen Annual Meeting of the Council on Forest Engineering, Forest Engineering Research Institute of Canada, Nanaimo, B.C., Canada, pp. 43–49.

Kellomäki, S., Kolström, T., 1992. Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. Vegetation 102, 47–68.

Kercher, J.R., Axelrod, M.C., 1984a. Analysis of SILVA: a model for forecasting the effects of $SO_2$ pollution and fire on western coniferous forests. Ecol. Model. 23, 165–184.

Kercher, J.R., Axelrod, M.C., 1984b. A process model of fire ecology and succession in a mixed-conifer forest. Ecology 65, 1725–1742.

Kimmins, J.P., 1997. Forest Ecology — a Foundation for Sustainable Management, 2nd edition. Prentice Hall, Upper Saddle River, NJ, USA.

Klinka, K., Scagel, A.M., Courtin, P.J., 1985. Vegetation relationships among some seral ecosystems in southwestern British Columbia. Can. J. For. Res. 15, 561–569.

Kozak, A., Munro, D.D., Smith, J.H.G., 1969. Taper functions and their application in forest inventory. For. Chron. 45, 278–283.

Kuiper, L.C., 1988. The structure of natural Douglas fir forests in western Washington and western Oregon. Agricultural University Wageningen Paper No 88, Wageningen, The Netherlands.

Lassen, L.E., Okkonen, E.A., 1969. Sapwood thickness of Douglas fir and five other western softwoods. U.S. For. Serv. Res. Pap. U.S. For. Prod. Lab. FPL Report Rep. No. FPL124, Madison, WI, 16 pp.

Leemans, R., Prentice, I.C., 1989. FORSKA, a general forest succession model. Meddelanden Från Växtbiologiska Institutionen 89-2, Uppsala, Sweden.

Leemans, R., 1991. Sensitivity analysis of a forest succession model. Ecol. Model. 53, 247–262.

Lertzman, K.P., 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73, 657–669.

Lertzman, K.P., Sutherland, G.D., Inselberg, A., Saunders, S.C., 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77, 1254–1270.

Long, J.N., 1977. Trends in plant species diversity associated with development in a series of Pseudotsuga menziesii/Gaultheria shallon stands. Northw. Sci. 51, 119–130.

Mailly, D., 1998. Influence of the disturbance regime on forest succession in the CWHdm subzone, B.C. Dissertation. University of British Columbia, Vancouver, B.C., Canada.

Mailly, D., Kimmins, J.P., 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. Can. J. Bot. 75, 1424–1435.

McMinn, R.G., 1951. The vegetation of a big burn near Blaney Lake, British Columbia. Ecology 32, 135–140.

Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. Ministry of Forests, Vancouver, British Columbia, Canada.

Minckler, L.S., Woerheide, J.D., 1965. Reproduction in hardwoods 10 years after cutting as affected by site and opening size. J. For. 63, 101–107.

Minore, D., 1979. Comparative autecological characteristics of Northwestern tree species — a literature review. United States Forest Service Research Paper PNW-87.

Mitchell, K.J., Grout, S.E., Macdonald, R.N., Watmough, C.A., 1992. User's guide for TIPSY, A Table Interpolation Program for Stand Yields. Ministry of Forests, Victoria, British Columbia, Canada.

Morris, W.G., 1958. Influence of slashburning on regeneration, other plant cover, and fire hazard in the Douglas fir region — a progress report. United States Forest Service Research Paper PNW-29.

Müeller-Dombois, D., 1960. The Douglas fir forest associations on Vancouver Island in their initial stages of forest succession. Dissertation. University of British Columbia, Vancouver, B.C., Canada.

Müeller-Dombois, D., 1965. Initial stages of secondary succession in the coastal Douglas fir and western hemlock zones. Ecol. West North Am. 1, 38–41.

Munger, T.T., 1930. Ecological aspects of the transition from old forests to new. Science 72, 327–332.

Munger, T.T., 1940. The cycle from Douglas fir to hemlock. Ecology 21, 451–459.

Oliver, C.D., 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3, 153–168.

Pastor, J., Post, W.M., 1985. Development of a linked forest productivity–soil process model. Environmental Sciences Division Publication No. 2455, Oak Ridge National Laboratory, Oak Ridge, TN, USA.

Pastor, J., Post, W.M., 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochem. 2, 3–27.

Pearson, A.F., 1995. Disturbance regimes in Clayquot Valley, a first approximation. Progress report to the British Columbia Forest Service, Victoria, British Columbia, Canada.

Pickford, A.E., 1929. Studies of seed dissemination in British Columbia. For. Chron. 5, 8–16.

Pothier, D., Margolis, H.A., 1991. Analysis of growth and light interception of balsam fir and white birch saplings following precommercial thinning. Ann. Sci. For. 48, 123–132.

Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol. Model. 65, 51–70.

Ritchie, M.W., Hann, D.W., 1986. Development of a tree height growth model for Douglas fir. For. Ecol. Manage. 15, 135–145.

Safford, L.O., Bjorkbom, J.C., Zasada, J.C., 1990. *Betulaceae*–Birch family. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America — vol. 2, Hardwoods. Agriculture Handbook 654, United States Department of Agriculture, Washington, USA, pp. 120–128.

Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. For. Sci. 34, 960–979.

Smith, D.M., 1986. The Practice of Silviculture, eighth ed., Wiley, New York, USA.

Spies, T.A., Franklin, J.F., 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 70, 543–545.

Spies, T.A., Franklin, J.F., Klopsch, M., 1990. Canopy gaps in Douglas fir forests of the Cascade Mountains. Can. J. For. Res. 20, 649–658.

Stewart, G.H., 1986a. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Can. J. For. Res. 16, 558–568.

Stewart, G.H., 1986b. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. Ecology 67, 534–544.

Stewart, G.H., 1988. The influence of canopy cover on understorey development in forest of the western Cascade range, Oregon, USA. Vegetation 76, 79–88.

Urban, D.L., 1993. A user's guide to ZELIG version 2 with notes on upgrades from version 1, Department of Forest Sciences, Colorado State University, Fort Collins, Colorado, USA.

Wang, J.R., Zhong, A.L., Kimmins, J.P., Tsze, M., 1992. Biomass and productivity of white birch (*Betula papyrifera* March) in the Interior Cedar Hemlock zone, B.C. Contract Report to the Ministry of Forests, Victoria, B.C., Canada.

Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204, 1380–1386.

Waring, R.H., Schroeder, P.E., Oren, R., 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. 12, 556–560.

Waring, R.H., Schlesinger, W.H., 1985. Forest Ecosystems, Concepts and Management. Academic Press, Orlando, FL, USA.

Weigand, J.F., Burdett, A.L., 1992. Economic implications for management of structural retention on harvest units at the Blue River Ranger District, Willamette National Forest. United States Forest Service Research Note PNW-RN-510.

Weishampel, J.F., Urban, D.L., 1996. Coupling a spatially-explicit forest gap model with a 3-D solar routine to simulation latitudinal effects. Ecol. Model. 86, 101–111.

Yarie, J., 1990. Role of computer models in predicting the consequences of management on forest productivity. In: Dyck, W.J., Mees, C.A. (Eds.), Impact of intensive harvesting on forest site productivity. Forest Research Institute Bulletin, Rotorua, New Zealand, pp. 3–18.

Yerkes, V.P., 1960. Occurence of shrubs and herbaceous vegetation after clear-cutting old-growth Douglas fir in the Oregon Cascades. United States Forest Service Research Paper PNW-34.

Zobel, D.B., McKee, A., Hawk, G.M., 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46, 135–156.