

Landscape- vs Gap-level Controls on the Abundance of a Fire-sensitive, Late-successional Tree Species

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ABSTRACT

Tsuga heterophylla (western hemlock), a fire-sensitive, late-successional tree species, is an important component of old-growth forests in the Pacific Northwest, USA. In the Oregon Coast Range, however, *T. heterophylla* occurs at low densities in or is completely absent from many conifer stands. We used a cellular automata-based simulation model to explore the influences of the fire regime and gap disturbances on *T. heterophylla* dynamics at a landscape scale. The abundance of *T. heterophylla* in the simulated landscape was particularly sensitive to variation in fire return interval and fire severity. *T. heterophylla* was less sensitive to canopy gap return interval, probability of recruitment in canopy gaps, and the probability of rare long-distance dispersal events. Relatively short periods of high fire fre-

quency caused a rapid and persistent decline in the amount of *T. heterophylla* in the landscape. Based on the simulation results, we propose two new hypotheses. The first is that landscape-level constraints imposed by the frequency, severity, and pattern of wildfires will limit the potential for gap-level processes to affect *T. heterophylla* regeneration patterns at the landscape scale. The second, related hypothesis is that legacies of cumulative fire effects will have a strong influence on the subsequent development of late-successional forest structure.

Key words: *Tsuga heterophylla*; western hemlock; fire; gap dynamics; seed dispersal; old growth; simulation; historical legacy.

INTRODUCTION

Studies of forest community composition have traditionally focused on environmental gradients as the dominant factors controlling species distributions (see for example, Whittaker 1956, 1960). Current ecological theory also recognizes the dynamic nature of landscapes and the influences of spatial processes such as disturbance and dispersal on species pattern and abundance (Wu and Loucks 1995). Numerous studies have documented the effects of disturbances such as fire (Heinselman 1973) and windstorms (Frehlich and Lorimer 1991) on the spatial patterns of forest communities. Changes in

disturbance frequency (Noble and Slatyer 1980) and size (Runkle 1982; Taylor 1990) can favor species with different regeneration niches and life-history traits, causing shifts in community structure. Because seeds of many trees do not persist in the soil seed bank, the mix of species that establishes after a disturbance may be constrained by the abundance and spatial pattern of remnant seed sources (Reader and others 1995; Clark and others 1998; He and Mladenoff 1999).

Spies and Franklin (1989) proposed a simplified hierarchy that divides disturbance processes into coarse- and fine-scale dynamics. Coarse-scale dynamics are driven by large wildfires, catastrophic windstorms, and insect outbreaks that operate at spatial scales of 100 to more than 100,000 ha and at temporal scales ranging from centuries to millennia. The large canopy openings created by these distur-

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bances generate a shifting landscape mosaic of large, relatively homogeneous patches dominated by shade-intolerant species. Fine-scale gap dynamics operate within these patches, driven by windthrow, pathogens, insects, and low-severity fires that cause the death of individuals or small groups of canopy trees. These fine-scale processes are important drivers of forest succession because canopy gap formation facilitates the regeneration and growth of shade-tolerant species. Previous efforts at describing and modeling forest dynamics have typically focused on either landscape-scale patch dynamics in response to large disturbances (Baker 1992; Wimberly and others 2000) or tree population dynamics resulting from gap disturbances (Urban and Shugart 1992). Only a few studies to date have begun to address the cumulative effects of multiple disturbances operating over a range of spatial scales (see for example, Sinton and others 2000).

Wildfires and gap dynamics both play important roles in the development of old-growth forests in coastal regions of the Pacific Northwest, USA. The large openings created by fires facilitate the regeneration of *Pseudotsuga menziesii* (Douglas-fir), *Alnus rubra* (red alder), and *Tsuga heterophylla* (western hemlock), whereas the smaller opening created by gap disturbances are primarily colonized by *T. heterophylla* (Spies and Franklin 1989). The presence of multiple gaps in a range of sizes and developmental stages leads to the development of a complex, multilayered forest structure that is a distinctive characteristic of old growth (Franklin and Spies 1991). Although *T. heterophylla* is generally assumed to be the dominant late-successional tree species across most of the region (Franklin and Dyrness 1988), field research has shown that this species often has a patchy distribution, particularly in the Central Oregon Coast Range. A study of unmanaged conifer stands in the Coast Range found that half of these stands lacked *T. heterophylla* regeneration, and 31% did not have any *T. heterophylla* in the overstory (Schrader 1998). Data from permanent forest inventory plots tell a similar story, with *T. heterophylla* absent at 55% of sites in the Coast Range (J. Ohmann unpublished). Low levels of *T. heterophylla* in many areas have generated concern that young forests may not develop the same structures observed in existing old-growth forests and have raised questions about the ecological factors responsible for these landscape patterns.

The main goal of this study was to explore the influences of disturbance and seed source limitations on *T. heterophylla* abundance by developing a spatially explicit, multiscale simulation model. Our

overarching hypothesis was that variability in the fire regime and the gap disturbance regime could account for the low levels of *T. heterophylla* found in many areas. Specific objectives were to (a) develop a conceptual model of *T. heterophylla* landscape dynamics that incorporated disturbance and dispersal across multiple scales, (b) design a computer program to simulate the basic elements of this conceptual model, (c) assess model sensitivity to various disturbance and life-history parameters, and (d) use the model to examine temporal trends in *T. heterophylla* abundance following periods of increased fire frequency.

CONCEPTUAL FRAMEWORK

Wildfire was historically the predominant coarse-scale disturbance in Pacific Northwest forests (Agee 1993). Fire regimes exhibited considerable regional variability. Fires in the Central Washington Cascades were mostly high-severity stand-replacing burns with a return interval of more than 400 years (Hemstrom and Franklin 1982). In comparison, the drier Central Oregon Cascades had fire return intervals ranging from 95 to 149 years, with a larger proportion of low-severity fires (Morrison and Swanson 1990; Weisberg 1998). The fire regime of the central Oregon Coast Range was a mixture of high- and low-severity burns, with an average fire return interval of 271 years (Impara 1997). *T. heterophylla* has thin bark, shallow roots, and flammable foliage, and is considered a fire-sensitive "avoider" species (Agee 1993). A model incorporating crown and bole damage predicted 99% postfire mortality of *T. heterophylla* for a typical stand in the Northern Rocky Mountains (Peterson and Ryan 1986).

Survival of *T. heterophylla* and other fire-sensitive species is often spatially restricted to remnant forest patches that either escape fire entirely or burn at low severity (Camp and others 1995). *T. heterophylla* produces lightweight seeds that can disperse for hundreds of meters from these remnant patches into openings created by fires or other coarse-scale disturbances. Some *T. heterophylla* seeds released from a box kite at 60-m elevation in a 20-kph wind traveled more than 1100 m, although 80% of the seeds fell within 670 m of the release point (Issac 1930). A study of *T. heterophylla* dispersal from a remnant forest edge reported similar distances, with 87% of the seeds traveling less than 1000 m (Pickford 1929). Because *T. heterophylla* does not form a persistent seed bank (Burns and Honkala 1990), seeding establishment patterns are correlated with patterns of seed rain, resulting in a gradient of

decreasing seedling density with distance from seed source (Harris 1967).

In the intervals between fires, disturbance regimes are dominated by small canopy gaps. In the Central Oregon Cascades, most gaps are formed when trees die standing, creating canopy openings ranging from 25 to 300 m² in size (Spies and others 1990). Bole breakage by wind is the primary gap-forming agent in coastal forests, creating gaps up to 850 m² in size (Taylor 1990). Although small in size, canopy gaps occur with greater frequency than large fires and can therefore disturb an equally large area over time (Spies and Franklin 1989). *T. heterophylla* seedlings can establish underneath a closed forest canopy and survive for a century or more in suppressed form (Schrader 1998), but typically they require one or more gap disturbances to reach the forest canopy (Spies and others 1990). When gap formation does not disturb the forest floor, *T. heterophylla* advance regeneration is released from overstory competition for light and moisture and growth increases rapidly (Alaback and Tappeiner 1991). Higher light and moisture levels following gap formation also increase rates of tree seedling establishment. The abundance and spatial pattern of *T. heterophylla* seedlings vary with canopy gap size and with the abundance and pattern of various microsites such as litter, mineral soil, and dead wood (Gray and Spies 1996, 1997).

Recruitment in canopy gaps will only occur if advance regeneration is present or if reproductively mature individuals are near enough to disperse seeds into the gap. When *T. heterophylla* establishes in open conditions following a large disturbance, dominant trees typically reach reproductive maturity within 30 years (Burns and Honkala 1990). Small, suppressed individuals produce only a small number of cones compared to larger individuals in dominant canopy positions (Schrader 1998) and can functionally be regarded as nonreproductive juveniles. Dispersal distances tend to be much shorter in closed canopy forests than into large openings because of slower wind speeds and physical interference from neighboring trees. In one study, most *T. heterophylla* seedlings were found within 10 m of a parent tree, with a maximum distance of 18 m (Schrader 1998). Rare long-distance dispersal events will also occur (Greene and Johnson 1995), but traditional empirical studies cannot detect these events because the maximum distance sampled is usually 1000 m or less. A few long-distance dispersal events might lead to greatly increased rates of population spread by creating new dispersal foci from which *T. heterophylla* can expand into areas of the landscape that are other-

wise inaccessible to distance-limited seed dispersal (Shigesada and others 1995).

SIMULATION MODEL

Because of the large spatial scales and long time intervals required to study landscape dynamics, experimental and observational studies are difficult to implement. Simulation modeling provides an alternative for studying these complex large-scale systems (Baker 1989). We developed a simple cellular automata-based model driven by a small set of parameters, suitable for exploring general hypotheses about the population dynamics of *T. heterophylla* at a landscape scale. Similar modeling approaches have proven useful for studying the influences of fire regimes on the population viability of fire-sensitive shrubs (Bradstock and others 1996), demonstrating how spatial interactions contribute to cyclic dynamics in European beech forests (Wissel 1992), exploring the effects of spatial factors on the coexistence of trees and grass in semiarid savannas (Jeltsch and others 1996), and examining the influences of disturbance and dispersal on species coexistence (Green 1989).

Model Structure

Cellular automata models simulate landscapes in a discrete-space, discrete-time framework, with each cell taking on one of a finite set of possible states (Wolfram 1984). The landscape was modeled as a 100 × 100 grid of cells, each encompassing 0.25 ha (50 m × 50 m). Cells were assigned to one of the following four classes (Figure 1): (1) cells with reproductively mature *T. heterophylla*, (2) cells with juvenile (nonreproductive) *T. heterophylla*, (3) forest matrix cells (containing no *T. heterophylla*) without canopy gaps, and (4) forest matrix cells with one or more canopy gaps. To give the model more ecological realism, we relaxed some of the assumptions of classical cellular automata. In addition to the discrete cell states, we tracked the age of *T. heterophylla* cells to model the transition from juvenile to reproductive states. Instead of assuming that cells interacted only with neighboring cells, we allowed spatial interactions across the entire grid to reflect the potential for long-distance dispersal following fires. Finally, instead of a deterministic rule set, cell transitions were based on probabilistic rules and equations that reflected the stochasticity inherent in disturbance and dispersal processes. Landscape dynamics were modeled as a series of 10-year time steps. At each time step, the age of every cell was incremented 10 years and gap disturbances and

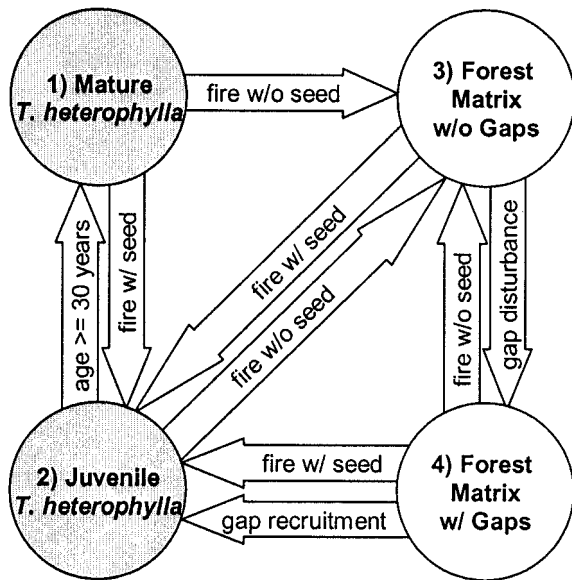


Figure 1. State and transition diagram for individual cells in the *T. heterophylla* landscape dynamics simulator. Circles denote the four states for model cells; arrows represent the possible transitions among states.

gap-phase recruitment were simulated. Juvenile *T. heterophylla* cells became mature *T. heterophylla* at age 30 (Figure 1). If a fire occurred during a time step, fire patterns and postfire recruitment were also simulated. The proportion of cells containing *T. heterophylla* was recorded at the end of each time step and written to an output file (source code for the computer model available on request from M.C.W.).

Fire Regime

The number of fires occurring in a 10-year time step, f_t , was modeled as a Poisson random variable with a mean of $10/\text{FRI}$, where FRI equaled the mean number of years between fires. If f_t was equal to 0, no fires occurred during time step t . Fires burned across the entire landscape and were modeled as mosaics of high- and low-severity patches. The proportion of the landscape burned at high severity was specified by the fire severity parameter, FSEV. The spatial heterogeneity of fires was controlled by the PATCH variable, which specified the number of low-severity patches left by each fire. The size of each low-severity patch was then computed as the total area of low-severity fire divided by the number of low-severity patches. The location of each remnant patch was centered on a randomly selected cell, and the shape of each remnant patch was approximately circular.

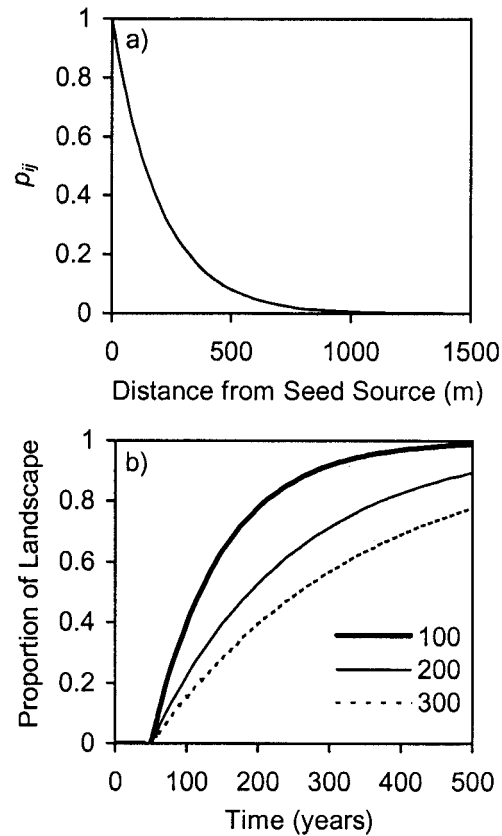


Figure 2. Probability functions used in the *T. heterophylla* patch dynamics model. a Probability of *T. heterophylla* establishment as a function of distance from seed source when $\text{FDISP} = 0.005$. b Expected cumulative proportion of the landscape with canopy gaps for three values of the gap return interval parameter (GRI).

T. heterophylla survived fires only in low-severity patches. After a fire, *T. heterophylla* could establish in the cells burned at high severity, with recruitment probabilities modeled as a function of distance from seed sources. Only cells containing reproductively mature *T. heterophylla* could disperse seeds. Probability of recruitment in a given cell, i , was assumed to decrease as a negative exponential function of distance from a seed source, j :

$$p_{ij} = \exp(-\text{FDISP} \cdot d_{ij}) \quad (1)$$

where p_{ij} equaled the probability of successful dispersal from cell j into cell i , d_{ij} equaled the distance from cell j to cell i in meters, and FDISP was the dispersal parameter. Because no data were available on establishment probabilities relative to distance from seed source, we parameterized the dispersal curve with $\text{FDISP} = 0.005$ (Figure 2a) to reflect the general finding that most *T. heterophylla* seeds fall

within 600 m of a seed source, with relatively few seeds traveling further than 1000 m (Pickford 1929; Issac 1930; Harris 1967). Each reproductively mature *T. heterophylla* cell, j , was assumed to have an independent probability of dispersing into an unoccupied cell, i , with the total probability of establishment computed as

$$p_i = 1 - \prod_{j=1}^m (1 - p_{ij}) \quad (2)$$

where m was the total number of seed sources in the landscape. A uniform (0, 1) random number was generated for each unoccupied cell, i , and recruitment occurred where this number was less than p_i . We also simulated background dispersal, which was independent of the density and pattern of seed sources and allowed for the possibility of rare, long-distance dispersal events. A second uniform (0,1) random number was generated for each burned cell, and recruitment occurred where this number was less than BDISP, the background dispersal parameter. Cells where recruitment was successful were initialized as juvenile *T. heterophylla* cells with age = 0 (Figure 1). Otherwise, cells were initialized as forest matrix cells with no canopy gaps.

Gap Disturbance Regime

Canopy gaps did not occur during the first 50 years after a fire. This lag reflected the stem exclusion phase of stand development, when dense canopies prevent most light from reaching the forest floor and small canopy gaps are rapidly filled in by the expanding crowns of adjacent trees (Oliver and Larson 1990). Once a forest matrix cell reached age 50, the probability of gap occurrence during each 10-year time step was computed as $10/\text{GRI}$, where GRI equaled the mean time to gap occurrence. Cell size (0.25 ha) was larger than the size of most canopy gaps (0.0025–0.1 ha), so gap occurrence did not necessarily imply disturbance of the entire cell. Instead, it meant that one or more canopy gaps of a size suitable to allow canopy recruitment had occurred somewhere within the cell. Viewed at a landscape scale, the gap formation process reflected the transition from a young closed-canopy forest to a heterogeneous late-successional forest with increasing opportunities for overstory recruitment (Figure 2b). Once gap disturbance occurred in a forest matrix cell, the cell remained in the gap phase until *T. heterophylla* was recruited or a fire occurred.

Recruitment could occur in gap-phase cells if a seed source was present. Because the size of the

simulation cells (50 m) was larger than the 18-m maximum distance from seed source measured for *T. heterophylla* (Schrader 1998), seed was assumed to disperse only from reproductively mature *T. heterophylla* in the eight neighboring cells. Details of the recruitment processes, such as the spatial pattern of microsites and the establishment, survival, and growth of individual seedlings, were not simulated. A particular gap recruitment event could have represented either release of advance regeneration already present in the forest understory or the establishment of new seedlings. Each neighboring cell had an independent probability of dispersing into the gap-phase cell, specified by the gap recruitment parameter GREC. Total probability of gap recruitment was computed as

$$p_g = 1 - \prod_{i=1}^n (1 - \text{GREC}) \quad (3)$$

where n equaled the number of adjacent cells with mature *T. heterophylla*. A uniform (0,1) random number was generated for each canopy gap, and recruitment occurred where this number was less than p_g . Background dispersal was also modeled in gap-phase cells, with recruitment occurring if a second uniform (0,1) random number was less than BDISP. If recruitment was successful, the gap-phase cell became a juvenile *T. heterophylla* cell with age = 0 (Figure 1). Otherwise, the cell remained in the gap phase and recruitment could occur in subsequent time steps. Once *T. heterophylla* established in a cell, subsequent gap and recruitment events were not tracked; the population within the cell was assumed to be self-sustaining until fire mortality occurred.

SIMULATION EXPERIMENTS

We carried out several sensitivity analyses to examine *T. heterophylla* response to FRI (fire return interval), FSEV (fire severity), PATCH (density of remnant patches), GRI (gap return interval), GREC (gap recruitment probability), and BDISP (background dispersal probability). The goal of this experiment was to compare the relative effects of these parameters on *T. heterophylla* abundance, computed as the proportion of cells containing either juvenile or mature *T. heterophylla*. Minimum and maximum values were selected to span the ranges of likely values for each parameter based on studies of fire regimes (Hemstrom and Franklin 1982; Morrison and Swanson 1990; Impara 1997) and gap dynamics (Spies and others 1990; Taylor

Table 1. Parameter Values Used in the Sensitivity Runs and Simulation Experiment

Parameter	Description	Sensitivity Runs		Simulation Experiment
		Minimum	Maximum	
FRI	Fire return interval (y)	100	400	Varies over time
FSEV	Fire severity (% of landscape burned)	0.8	1.0	0.9
PATCH	Number of remnant patches	1	10	5
GRI	Gap return interval (y)	100	400	250
GREC	Probability of recruitment in canopy gaps	0.0	1.0	0.5
	Background dispersal (recruitment probability independent of seed source location)			
BDISP		0	0.02	0.01

The sensitivity runs used a Latin hypercube design with each parameter selected from a uniform distribution with the specified minimum and maximum values. Median values from these ranges were used in the simulation experiment, which examined temporal variation in fire frequency. Fire return intervals are not listed for the simulation experiment because a time series of fire return intervals was defined separately for the control and treatment scenarios.

Table 2. Modeling Assumptions Used in the Sensitivity Runs

Sensitivity Run	Cell Size (m)	Understory Dispersal Distance (cells)	Stem Exclusion Period (y)	Time to Reproductive Maturity (y)
BASE	50	1	50	30
G25	25	1	50	30
G100	100	1	50	30
DISP	50	4	50	30
STEMEX	50	1	0	30
REPAGE	50	1	50	0
ALL3	50	4	0	0

Cell size was varied in the G25 and G100 runs. Cell size was held constant and modeling assumptions were changed in the DISP, STEMEX, REPAGE, and ALL3 runs.

1990) in coastal forests of the Pacific Northwest (Table 1). No data on gap recruitment or background dispersal probabilities were available. GREC was varied over the full range of possible values (0 to 1), and BDISP was varied between 0 (no background dispersal) and 0.02 (background dispersal occurs in 2% of cells during each 10-year time step).

We used a Latin hypercube sampling design (Schwartzman and Kaluzny 1987) to generate 100 parameter sets, selecting each parameter from a uniform distribution with the specified minimum and maximum values. We made an independent model run for each parameter set, starting from a randomly generated landscape pattern. The model was run for an initial 2000 years to overwrite a random starting configuration and for an additional 10,000 years in the main simulation. The mean proportion of cells with *T. heterophylla*, averaged over these 10,000 years, was computed as the response for each parameter set. To determine

whether model behavior was sensitive to spatial grain, we repeated this analysis with the cell size decreased to 25 m (0.0625-ha cells) and increased to 100 m (1-ha cells) (Table 2). All other parameters and aspects of model formulation remained unchanged. Relationships between the model parameters and the predicted responses were assessed using Spearman's rank correlation (Zar 1984) and were examined graphically using nonparametric, locally weighted regression models (Cleveland and others 1993).

We also carried out four additional sensitivity runs identical to those described above, except that several of the underlying model assumptions were relaxed. The first three runs examined the effects of increasing understory dispersal distance to four cells, eliminating the 50-year postfire period during which canopy gaps did not occur and eliminating the 30-year time lag to reproductive maturity (Table 2). The fourth run included a combination of all

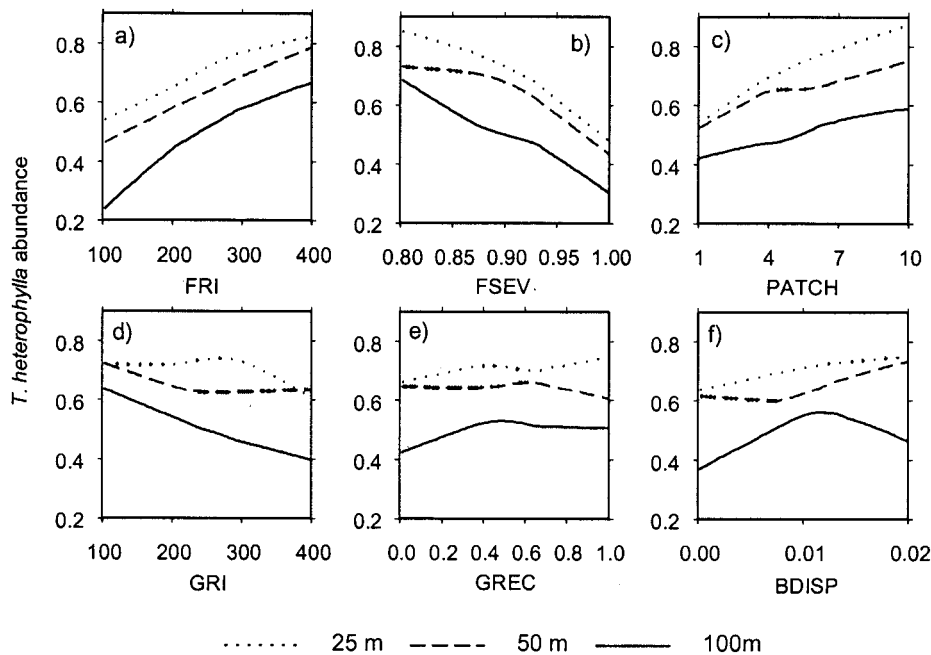


Figure 3. Locally weighted regression models predicting the proportion of cells containing *T. heterophylla* as (a) function of a fire return interval (years), (b) fire severity (proportion of landscape burned), (c) number of remnant patches, (d) gap return interval (years), (e) probability of establishment in canopy gaps, and (f) probability of distance-independent background dispersal.

these effects. All of these simulations were run at a 50-m cell size.

A simulation experiment was carried out to examine lagged responses to temporal variability in the fire regime. In the control scenarios, FRI was set at 300 years for the entire simulation. In the four treatment scenarios, FRI was set at 300 for the first 200 years; lowered to values of 50, 100, 150, or 200 for the next 100 years; and then returned to 300 for another 700 years. These treatments reflected the recent fire history in many areas of the Pacific Northwest, where the occurrence of multiple high-severity fires was associated with human settlement and dry climates in the late 19th and early 20th centuries (Weisberg 1998). In the second half of the 20th century, improved fire suppression greatly reduced fire frequency across most of the region. Parameters other than FRI were set at the median values from the sensitivity runs (Table 1). We made 100 replicate simulations of the control and each treatment scenario. Each simulation was allowed to run for an initial 2000 years to overwrite a random starting configuration. After the initialization period, mean *T. heterophylla* abundance was computed at 100-year intervals. Treatment effects were summarized by subtracting the mean abundance of the control run from the mean abundance of the treatment runs and computing the 95% confidence interval for the difference in means (Zar 1984).

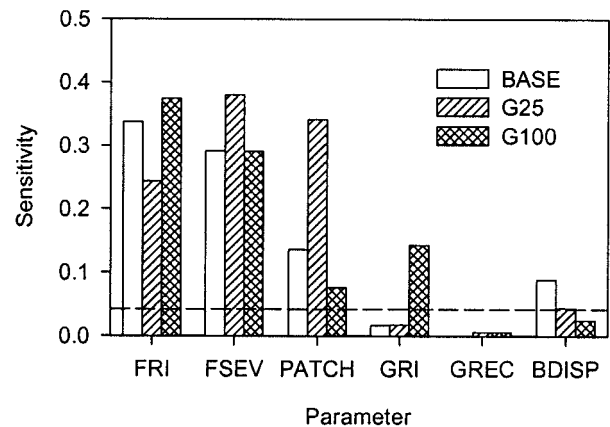


Figure 4. Sensitivity of simulated *T. heterophylla* abundance to various disturbance and life-history parameters for the base case plus two modified cell size scenarios (described in Table 2). Sensitivity was computed as the squared Spearman's rank correlation coefficient. Bars higher than the dashed line represent correlations that were statistically significant at $P < 0.05$.

RESULTS

T. heterophylla was particularly sensitive to parameters describing the fire regime (Figure 3). *T. heterophylla* abundance increased with FRI (Figure 3a), decreased with increasing FSEV (Figure 3b), and increased with PATCH (Figure 3c). *T. heterophylla* abundance also generally decreased with increasing GRI (Figure 3d), increased with GREC (Figure 3e), and increased with BDISP (Figure 3f); however, these relationships were weaker and were typically

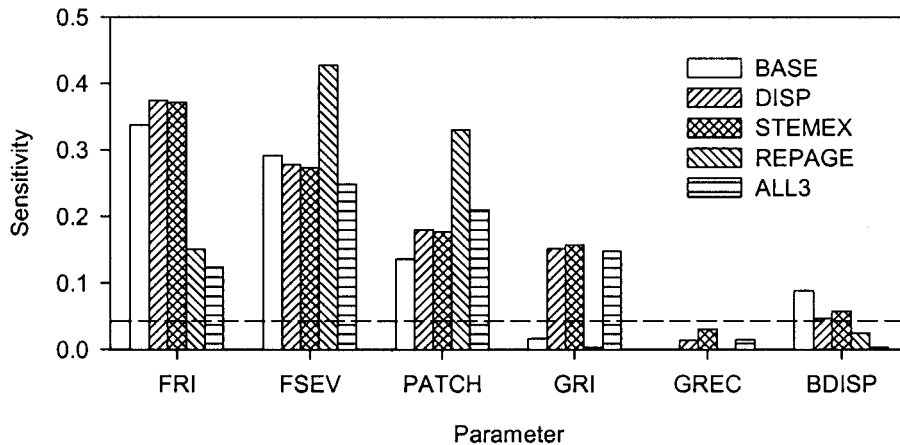


Figure 5. Sensitivity of simulated *T. heterophylla* abundance to various disturbance and life-history parameters for the base case plus four sets of altered modeling assumptions (described in Table 2). Sensitivity was computed as the squared Spearman's rank correlation coefficient. Bars higher than the dashed line represent correlations that were statistically significant at $P < 0.05$.

not significant at the $P < 0.05$ level (Figure 4). The predicted abundance of *T. heterophylla* decreased with increasing grain size (Figure 3). This phenomenon occurred because every mature *T. heterophylla* cell had an independent probability of dispersing into unoccupied cells that was not weighted by cell size. Therefore, the probability of recruitment after fire (Eq. [3]) decreased as grain size increased and mature *T. heterophylla* occupied a smaller number of larger cells. At all three spatial grains, *T. heterophylla* responses to GRI, GREC, and BDISP were much weaker than response to the fire regime parameters FRI and FSEV (Figure 4). At the 100-m grain, *T. heterophylla* had a weaker relationship with PATCH and a stronger relationship with GRI than at the smaller cell sizes.

Changing the underlying model assumptions altered the relative sensitivity of *T. heterophylla* abundance to the model parameters (Figure 5). When the understory dispersal distance was increased or the stem exclusion period was eliminated, sensitivity to GRI was much higher than in the baseline run. When the regeneration lag was eliminated, sensitivity to FRI dropped dramatically relative to the base case, whereas sensitivity to GRI was unaffected. When all three of these changes were incorporated, GRI and FRI had nearly equivalent influences on *T. heterophylla* abundance. Sensitivity to both GREC and BDISP remained relatively low under all sets of altered model assumptions.

When *T. heterophylla* response to temporal variation in the fire regime was simulated, abundance dropped 0.35 below the control level after the fire return interval was decreased to 50 for a period of 100 years (Figure 6a). *T. heterophylla* abundance eventually returned to control levels, although the 95% percent confidence interval did not consistently overlap zero until simulation year 700, 400 years after the period of high-frequency fires had

ended. *T. heterophylla* abundance showed much smaller decreases when the fire return interval was reduced to 100 years (Figure 6b). Differences between the control and treatment were negligible when the fire return interval was reduced to 150 or 200 years (Figure 6c and d).

DISCUSSION

As with any model-based research, the results of this study must be interpreted in light of the simplifying assumptions that were made. Because of our focus on disturbance and dispersal influences on *T. heterophylla* at multiple spatial scales, we did not explicitly consider effects of environmental heterogeneity. In the Oregon Coast Range, *T. heterophylla* is more abundant in the cool, moist climates of the coastal and northern areas than in warmer and drier areas in the south and along the Willamette Valley margin (Ohmann and Spies 1998). As with other species, the distribution of *T. heterophylla* may be patchier near the borders of its geographic range, where climatic conditions are less favorable and suitable habitats are restricted. The abundance of *T. heterophylla* and other shade-tolerant trees varies along topographic gradients as well, tending to be highest on moist sites located on north aspects or lower hillslope positions (Weisberg 1998).

We assumed that the probability of gap disturbance in a cell was the same during all time periods and was independent of gap disturbances in other cells. In addition, we assumed that dispersal in closed canopy forests only occurred between neighboring cells, with the exception of rare background dispersal events. One type of scenario where these assumptions might be invalidated is a large windstorm that blows down many small patches of trees scattered across the landscape. The same windstorm might also precipitate numerous long-distance dispersal events,

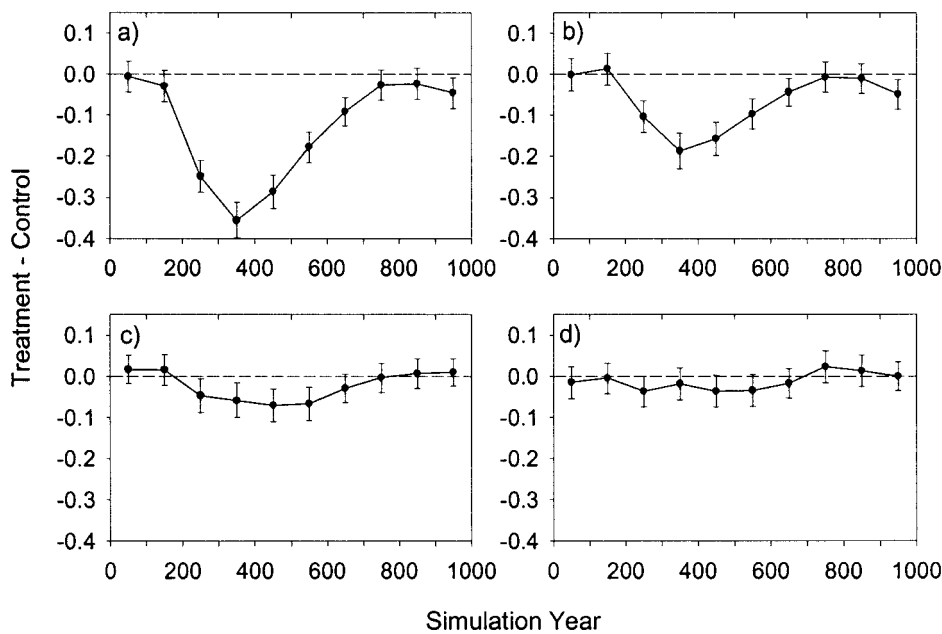


Figure 6. Differences in the proportion of cells containing *T. heterophylla* between the mean of 100 treatment runs and the mean of 100 control runs, computed at 100-year intervals for four different time series of fire return intervals (described in Table 1). The control run was made at a fire return interval of 300 years for the entire simulation. The treatment scenarios began at a mean fire return interval of 300 for years 0–200, decreased to (a) 50, (b) 100, (c) 150, and (d) 200 for years 200–250, and returned to 300 for years 250–800. Error bars represent 95% confidence intervals for the differences between mean values.

creating a pulse of overstory recruitment across large areas and rapidly expanding the distribution of *T. heterophylla*. Other ecological processes, such as competition, could also influence the rate of *T. heterophylla* dispersal. In the Oregon Coast Range, competitive clonal shrubs such as *Rubus spectabilis* can invade gaps and form dense, low canopies (Tappeiner and others 1991). If *T. heterophylla* advance regeneration is not present before gap formation, or if mature trees are not present nearby to facilitate rapid establishment of seedlings, the probability of successful establishment in the gap can be greatly reduced once the shrub layer is established.

The long temporal and large spatial scales used in the simulation experiments limit our ability to empirically validate the model. Thus, this type of model is most valuable for generating testable hypotheses about system behavior rather than making explicit predictions about specific landscapes. Based on the model simulations, we propose two hypotheses about the interrelationships of *T. heterophylla*, disturbance regimes, and dispersal limitations across multiple spatial scales. The first is that constraints imposed by frequency, severity, and pattern of wildfires will limit the potential for gap-phase processes to affect *T. heterophylla* regeneration patterns at the landscape scale. The second, related hypothesis is that forest succession will be affected by the legacy of fires that occurred prior to the most recent disturbance event.

Landscape Constraints on Gap Dynamics

Hierarchy theory emphasizes that landscape patterns and ecological processes at a given spatial and temporal scale are influenced both by the aggregate effects of finer-scale processes and the constraints imposed by larger-scale processes (Urban and others 1987). In our simulations, fire return interval, fire severity, and remnant patch density—all landscape-level disturbance parameters—typically explained more of the variation in *T. heterophylla* abundance than gap return interval, gap recruitment probability, and distance-independent dispersal probability. The high sensitivity of *T. heterophylla* to fire frequency was related to the time lag before reproductive maturity. If the landscape burned more than once within 30 years, trees established after the first fire were not reproductively mature and recruitment following subsequent fires was greatly reduced. This “double-burning” effect has been shown to have a strong influence on populations of other fire-sensitive, dispersal-limited species (Bradstock and others 1996). Increased fire severity produced smaller remnant patches that contained fewer *T. heterophylla* seed sources, leading to lower amounts of postfire recruitment. Larger numbers of low-severity patches usually increased the dispersion of remnant seed sources, expanding the spatial distribution of the postfire cohort.

The comparatively weak response to gap recruitment was surprising because we considered the full range of values from zero (recruitment in gaps never

occurs) to one (recruitment in gaps occurs immediately if a neighboring seed source is present). Spatial and temporal constraints on seed availability were apparently much more important than recruitment rates in canopy gaps. Increased canopy gap frequency produced more recruitment opportunities, but short understory dispersal distances and the lack of gap formation during the stem exclusion period limited *T. heterophylla* response to the gap disturbance regime. Although *T. heterophylla* abundance was sensitive to the probability of distance-independent background dispersal, rates would need to be much higher than the maximum tested in our simulations (2% of the landscape per decade) to overcome the constraints imposed by the fire frequency and severity.

Experimental research has emphasized the importance of canopy gap size, substrate availability, and competition in controlling the recruitment and growth of tree seedlings within canopy gaps (Gray and Spies 1996, 1997). Our results suggest that when tree regeneration is limited by short understory dispersal distances, its abundance at the landscape scale may ultimately be controlled by fire history rather than fine-scale habitat variables. This hypothesis could be investigated through large-scale field surveys and analyses of the relative influences of various predictors (for example, see Weisberg and Baker 1995; Kneeshaw and Bergeron 1996) on regeneration patterns. We hypothesize that for disturbance-sensitive species such as *T. heterophylla*, variables describing the effects of recent fires (stand age, abundance and spatial pattern of remnant trees) would explain more of the variability in regeneration density than variables characterizing substrate availability or the understory environment.

Disturbance History and Successional Pathways

Much of the current theory about forest succession in the Pacific Northwest has been influenced by comparisons of forest structure and species composition over a range of stand ages (Franklin and Hemstrom 1981; Spies and Franklin 1991; Huff 1995). These studies typically show that *T. heterophylla* is rare or absent in young stands and that it increases in abundance with stand age. Establishment of a *T. heterophylla* understory in maturing Douglas-fir stands has been attributed to gradual colonization as seeds disperse in from neighboring mature stands or isolated seed sources (Franklin and Hemstrom 1981). Our simulations suggest another explanation for these observed patterns. Because many young and mature stands on the landscape today established during a period of relatively high fire frequency (approximately 1840–1940) (Weisberg 1998), current low levels of *T. heterophylla*

in some of these forests may be attributable to multiple fires and seed source limitations in addition to stand age. If this is the case, then these young stands will not necessarily follow the same successional pathways or develop the same structure as the older forests.

This hypothesis could be tested by comparing stands with different disturbance histories. Forests with a history of multiple burns within a short time period should have less *T. heterophylla* than similar-aged forests that burned only once after a long fire-free interval. Although disturbance history information is difficult to obtain, ages of remnant trees, fire scars, and historical records can provide clues about events that occurred prior to the most recent disturbance. Several studies have found lower density and/or basal area of *T. heterophylla* following multiple fires than in stands that burned only once (Klopsch 1985; Poage 1995; Gray and Franklin 1997; Wimberly and Spies 2001). In all of these cases, however, disturbance history was confounded by stand age because a large, initial fire was followed by localized reburns within a few decades. Tracking changes in species composition over time would help to alleviate this bias. Thus, disturbance history studies may be particularly fruitful in areas where long-term plots have been established and data on forest change is already available.

Synthesis and Conclusions

Our results support the emerging view that landscape history, as well as current conditions, should be considered when assessing patterns of structure and composition in forest ecosystems (McCune and Allen 1985; Foster 1992; Motzkin and others 1999). Understanding the persistent effects of historical disturbances in forest communities is important because present-day human activities are creating the historical legacies of the future. For example, under current forest management practices in the Pacific Northwest, *P. menziesii* is selectively planted following clear-cutting. Although naturally regenerating *T. heterophylla* are seldom completely excluded from these plantations, low overstory densities could reduce seed availability and limit the development of multilayered forest structure as these stands age. Low levels of *T. heterophylla* and other shade-tolerant species could be particularly problematic in planted stands located in old-growth reserves on federal land, where the current management focus is on encouraging rapid development of late-successional structure.

Although the model was specifically designed to examine *T. heterophylla* dynamics under natural disturbance regimes in the Pacific Northwest, the general hypotheses derived from this work may be applicable

to other disturbance-sensitive, late-successional species in a wide range of forested ecosystems. For example, epiphytic lichens such as *Lobaria oregana* are usually restricted to patches of remnant old-growth forest following fire or timber harvest, with population expansion into the disturbed areas limited by propagule availability rather than habitat suitability (Sillett and others 2000). In the Great Lakes region, large-scale logging followed by selective cultivation of high-value tree species has been invoked as a major factor limiting seed sources and understory regeneration of *Tsuga canadensis* (Mladenoff and Stearns 1993). In the temperate rainforests of Tasmania, succession to *Atherosperma moscharum*, the predominant shade-tolerant tree species, is limited by slow dispersal rates and a sparse distribution of remnant seed sources following fire (Read and Hill 1988).

The importance of disturbance frequency and seed source limitations in structuring forest communities is well established, but researchers have only begun to consider the multiple spatial linkages among gap dynamics, fire regimes, and dispersal-limited recruitment. Many forest succession models have assumed that dispersal is ubiquitous and instead focused on environmental controls over tree establishment, growth, and mortality at the gap scale (Urban and Shugart 1992). However, recruitment and growth in canopy gaps may have a limited effect on the landscape-scale distribution of some late-successional tree species. Variability in the frequency, severity, and pattern of large disturbances may have a comparatively strong influence, with short-term increases in disturbance frequency causing persistent declines in species abundance. To effectively model the development of late-successional forest structure across large landscapes, it will be necessary to better link environmentally driven, gap-scale simulators of tree population dynamics with landscape-scale models that incorporate disturbance and dispersal in a spatially explicit framework.

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