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Research article

Modeling multiscale effects of light limitations and edge-induced mortality on carbon stores in forest landscapes

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Abstract

Analyses of carbon (C) dynamics at broad scales usually do not consider spatial interactions. The assumption is that C dynamics can be modeled within homogenous (i.e., even-aged) patches and then summed to predict broad-scale dynamics (an additive approach). The goal of this paper is to elucidate the scales over which this additive approach is sufficient to explain observed C dynamics at broad scales. We define emergent "behaviors" (vs. emergent "properties") as those behaviors that cannot be predicted solely from the additive properties of units at a finer scale. We used a forest process model to check for possible emergent behaviors due to pattern-process interactions at multiple levels, from the patch to the landscape. Specifically, using artificial forest landscapes with various spatial structures, we estimated the relative effects of edge-induced, tree mortality (mainly due to wind) and light limitations on C dynamics. Emergent behaviors were observed at all levels examined, indicating that emergent behaviors did not cease as one proceeded from the patch to the landscape level, as we had expected. However, the magnitude of the emergent behaviors depended on the level of spatial interaction considered as well as the type and intensity of the processes included. In all simulations, interactions of light and wind processes resulted in significant emergent behaviors only when parameters controlling wind mortality were set to the highest levels observed in the literature. In one simulation, the magnitude of emergent behaviors differed among the landscapes, indicating that interactions among patches may not be accounted for by an additive correction for edge effects unless spatial interactions are addressed. The implication is that some C dynamics in fragmented landscapes may not be captured at broad-scales using an additive approach, whereas in other cases spatial interactions are small enough to be ignored.

Introduction

Quantifying the exchange of C between the terrestrial biosphere and the atmosphere is necessary to constrain the global C budget and potentially manage for C sequestration (e.g., Brown 1996; Schultze et al. 2000; Watson et al. 2000). As a result, estimates of C exchange over broad scales are needed to validate regional and global C models. Since it is impractical to directly measure C flux for every ecosystem over a broad area, it is necessary to make assumptions about how to scale local information derived from select sites to a larger area.

A simple way to scale information to broader extents is through an 'additive' approach (Baker 1989) and, traditionally, many C flux research projects have been attempted in this way (e.g., Cohen et al. 1996; Houghton et al. 2000). Carbon flux has a strong vertical component in that C is transferred from the biosphere to the atmosphere through decomposition and respiration, and from the atmosphere to the biosphere through photosynthesis. Thus, when accounting for the net C flux of an ecosystem, the balance of vertical inputs and outputs should indicate the directionality of C transfer, either into the ecosystem or the atmosphere. In an additive approach, by knowing the net C flux of each landscape patch, and multiplying the fluxes by the area of each patch, it should be possible to calculate the net landscape flux.

However, most broad-scale physiological models of C dynamics ignore horizontal processes affecting C flux, which may be important in spatially heterogeneous landscapes. Recent evidence suggests that horizontal exchanges of C can be significant at short and long time-scales, resulting in error if not accounted for. For example, eddy correlation techniques were designed to measure the vertical flux of CO_2 and water vapor between the vegetation, soil, and atmosphere over an ecosystem. However, due to horizontal movement of air masses, the source area of the measured fluxes does not necessarily equal the "footprint" of the eddy flux tower (Kaharabata et al. 1997; Desjardins et al. 1997; Wofsy et al. 1993; Goulden et al. 1996). Moreover, the source area may change at time scales of hours (differing wind directions) to decades (changing land types and/or age-class structure), making it difficult to control for horizontal heterogeneity. At longer time-scales, observational research on forest edge effects also indicates important horizontal effects on C stores. Particularly, increased light at forest edges causes a difference in the competitive advantage of different species and life forms (Ranney et al. 1981; Lovejoy et al. 1984; Williams-Linera 1990), each of which may have a different capacity to store C. Increased exposure to wind at forest edges may increase rates of tree-mortality, also affecting C stores. The interaction of light and wind processes can affect C storage at forest edges in ways that are not immediately intuitive. For example, although windthrow typically causes an increase in the abundance of light-tolerant species (Chen et al. 1992; Lovejoy et al. 1984), Sinton et al. (2000) showed that shade-tolerant species were favored after a windthrow event because the old-growth Douglas-fir they replaced were particularly sensitive to wind mortality. Thus, the interaction of ecological processes across a forest boundary, in this case light and wind, may result in complex behaviors that are not predictable by examining processes independently.

The horizontal interactions can be linear or non-linear across a forest boundary (edge or gap). If the change in a process is linear, the response at the edge is a result of the degree of mixing of the two neighboring patches (the "matrix effect" of Lidicker (1999)). An additive model can handle this linear change. By contrast, if the change is non-linear (enhanced, diminished, or asymptotic), the response of the system at the edge cannot be explained completely by the mixing of the two neighboring patches. For example, Parsons et al. (1994) observed non-linear responses of nitrogen cycling in forest gaps, potentially as a result of root intermingling and/or mycorrhizal linkages. When non-linear responses are observed across patch boundaries, averaging the properties of the neighboring patches (a traditional additive approach) is not sufficient to predict behavior at broad-scales (Lidicker 1999). Therefore, landscape-level estimates of C flux may diverge from patch-level estimates if these horizontal interactions are included. This discrepancy between patch-level and landscape-level results may be considered "error" at the broader landscape scale. We suggest that the cause of this perceived error might be due to previously unrecognized pattern-process interaction, that causes what we call "emergent behavior".

We define emergent behavior as behavior that cannot be predicted solely from the additive properties of units at a finer scale. The term differs from the more commonly used "emergent property" (e.g., Salt 1979) in that a property defines the *state* of the system, whereas a behavior defines the *actions of* the system. Thus, landscape-level emergent behaviors are behaviors at the landscape scale that cannot be predicted solely from the additive properties of the patches. If emergent behavior is important, landscape C flux may be dependent on patch topology, as it affects process interactions.

Despite a generally accepted notion that spatial heterogeneity is important (King et al. 1991; Risser 1999), it is difficult to determine at what scale, and under what circumstances, this is so. The goal of this research is to elucidate the scales over which assumptions of spatial homogeneity will hold. In this paper, we use a forest process model (STANDCARB) to simulate the effects of wind mortality and light limitations on C storage within different artificial landscape structures. Our general research question is: can landscape C storage be predicted using the additive approach, whereby the value of the landscape is equal to the area-weighted sum of the properties of the patches? Specifically, does the interaction of these two processes (light and wind) result in non-linear interactions among patches that are not predictable using additive approaches? Finally, if emergent behaviors (practically defined here for our simulation experiments as: the differences beyond the expected variation of an additive model) are present at one spatial scale, do they cease to be important at broader scales?

There were two specific objectives with this modeling exercise. The first objective was to analyze the effect of cell-to-cell interactions at the stand scale. Here, a cell is approximately 0.03 ha, which represents the area that would be occupied by a typical mature tree in the Pacific Northwest (or, if not occupied, a forest gap). Cell-to-cell interactions are determined by examining results within a homogenous landscape, i.e., where there is only one type of patch and thus no patch-to-patch interactions. The second objective was to analyze the effects of patch-to-patch interactions at the landscape scale. A patch represents a collection of relatively homogenous cells within a simulated landscape. Patch size ranged from 0.03 ha to approximately 5 ha, depending on the type of artificial landscape being simulated. Interactions between patches are determined by examining results within heterogeneous landscapes, where there is a mix of old and young age-classes on the landscape. We also examined the effect of patch structure in a landscape, i.e., the arrangement of patches, as it might affect possible emergent behavior at the landscape scale. By comparing results at two scales of interaction, our goal was to determine if C storage was predictable using an additive approach, or, conversely, whether emergent behaviors due to the interaction of light and wind processes were evident.

Methods

Model Description

STANDCARB version 2.0 (Harmon and Domingo 2001; Harmon and Marks 2002) was used in these simulations. This model simulates the dynamics of live and dead pools of C in mixed-species, mixed-age-class, forest stands and is also able to simulate the effects of harvests or fire on C storage. STANDCARB is similar to gap models since each stand is simulated with many replicate cells, which are then averaged to obtain stand values. In addition, STANDCARB can be parameterized for specific species based on characteristics defining their growth, mortality, and decomposition. As a result, the species composition changes through time during succession in response to the species' competitiveness. STANDCARB is also similar to many ecosystem-process models in that growth, mortality, decomposition, and other significant ecosystem processes are calculated in response to abiotic factors such as climate and site characteristics. Temporally, STANDCARB is run on an annual time step for all live and dead C pools through succession, although climate variables, affecting tree establishment, growth, and decomposition are computed monthly.

Within each cell in STANDCARB, there are 4 vegetation layers (upper tree, lower tree, shrub layer, and herb layer), each of which has up to 7 live pools, 8 detrital pools, and 3 stable C pools (Figure 1). For example, the upper and lower tree layers are comprised of 7 live pools: foliage, fine-roots, branches, sapwood, heartwood, coarse-roots, and heart-rot.

Each tree layer can be a different species, whereas the shrub and herb layers are each represented by a single "species." Live C pools transfer material to their detrital counterpart to account for the pools available for decomposition processes. Dead sapwood and dead heartwood are additionally separated into snags and logs so that the effects of position on microclimate can be modeled. All detrital pools in a cell can potentially add material to the three, relatively decay-resistant, stable C pools: stable foliage, stable wood, and stable soil.

Here, we describe a modification to STANDCARB that allows the model to calculate tree exposure to wind at each cell and to increase natural tree-mortality rates in proportion to increased tree exposure. With this change, cells in STANDCARB can interact spatially with both light and wind, which affects growth, decomposition, and mortality processes within cells.

Modeling Light Processes

Light influences several processes in STANDCARB: (1) the establishment of tree species based on their light requirements, (2) growth rates through modification of foliage mass, and (3) decomposition, through influences in detritus moisture contents. To determine the direct and diffuse light reaching a particular cell, STANDCARB uses a function called NeighborLight. NeighborLight calculates the angle to the tallest tree along each of 8 cardinal transects sur-

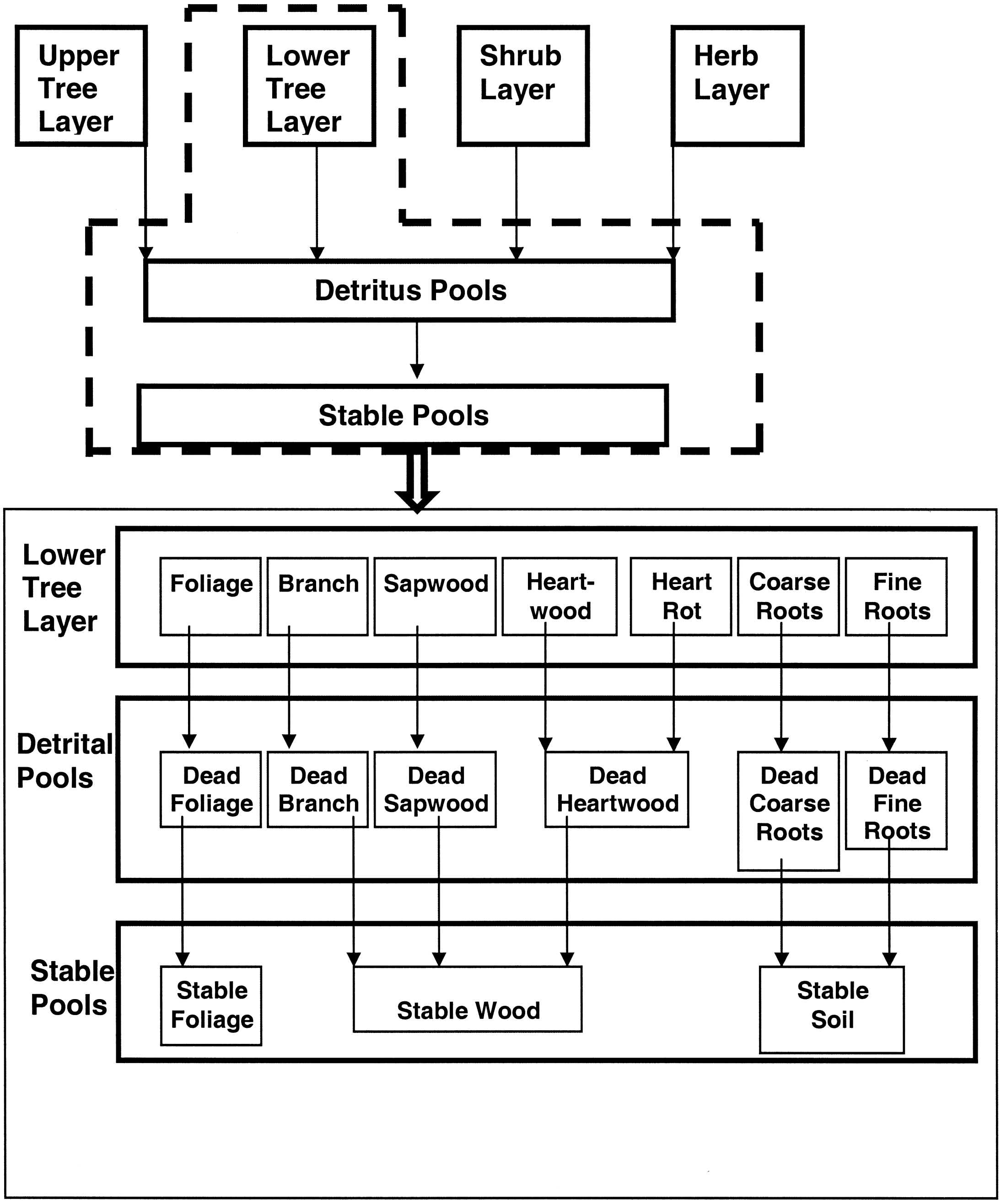

Figure 1. Conceptual structure of carbon pools and vegetation layers for STANDCARB 2.0.

rounding the cell of interest (Figure 2). By knowing the angle of the sun from the cell of interest, given information about the latitude, aspect, and slope of the site being simulated, it is possible to calculate the direct and diffuse light reaching the cell. For diffuse light, the average angle from these 8 transects is used to calculate incoming radiation. For direct light, a weighted average of the E, SE, S, SW, and W transects is used (Harmon and Domingo 2001). In addition, cell width (which can be set by the user) determines the amount of light entering a cell since, for a given height, wider cells allow more direct and diffuse light to enter. This is important because the minimum light requirements are different for differ-

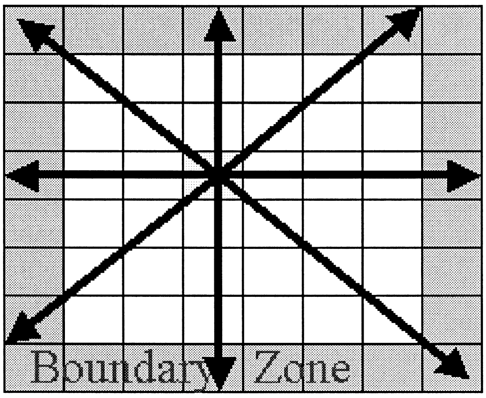

Figure 2. Arrangement of cells in STANDCARB, representing the spatial structure used to calculated light limitations and wind mortality. A boundary zone surrounds the simulation cells, representing vegetation outside of the simulation area. The arrows indicate the directions of transects used to determine shading effects and exposure to wind.

ent tree species, and the species composition will affect the amount of C that is predicted. We ran a series of simulations to test the effect of cell width of 15 m, 20 m, and 25 m on C and found a significant response of cell width on C storage, with larger cells retaining more C than smaller cells. We chose an intermediate cell width of 17 m because this width is approximately equal to the canopy width of old-growth trees in the Pacific Northwest. STANDCARB does not model light distribution through the vertical dimension of each cell; rather, light is portioned to the top layer and the amount of shading to lower layers is determined by the amount of foliage mass above the layer of interest. All simulations that are described in this paper were run with a 20×20 cell matrix, for a total of 400 cells, representing an area of 115,600 m^2 (or 11.56 ha).

Modeling Wind Mortality

We recognize that wind is an especially complex process in forest ecosystems and we do not attempt to mimic its behavior exactly. Rather, we estimated its effect by making the assumption that tree mortality is augmented by increased exposure to wind. We refer to "wind mortality" for simplification, although we imply that there is, more explicitly, an elevated tree-mortality rate where cells are more-exposed, as at patch edges. We modeled exposure as a function of slope, aspect, and tree heights, which are important factors resulting in higher mortality rates at forest edges after catastrophic wind events (Lovejoy et al. 1984; Foster 1988; Foster and Boose 1992; Chen et al. 1992).

In previous versions of STANDCARB, tree mortality is initially high due to tree competition and then decreases to a density-independent value that is a function of the maximum age of the tree species, which sets the probability that the tree will die in any given year. Here, we assumed that mortality in a cell would increase due to wind turbulence in cells that were more exposed relative to those that were more sheltered. We took advantage of the existing model structure in NeighborLight to calculate a new function, called NeighborWind, to calculate the relative exposure of trees in a cell. NeighborWind determines exposure to wind by calculating the angle from the tree height in the cell of interest to the average tree height along each of the 8 surrounding transects (Figure 2). The length of the transect (the number of cells from which average transect height is calculated) is set by the user. In these simulations, we used a transect length of 10 cells (170 m for a cell width of 17 m). NeighborWind then takes the average angle for the 8 transects. The angle is normalized so that negative numbers indicate increased exposure (the tree in the cell of interest is taller than neighboring cells, meaning it has a higher mortality rate). The transects can also be weighted by aspect so that if there is a directionality to the wind-induced mortality, it can be specified by the user. However, in this paper, all the transects received equal weighting. We then defined a new parameter, k, to equal the ratio of the maximum mortality rate at a completely exposed cell to the base mortality rate (Figure 3). We used k values equal to 2, 3, 5, or 8 times the baseline mortality rate, which are derived from estimates of increased wind mortality at edges in the literature (Laurance et al. 1998; Ferreira and Laurance 1997; Chen et al. 1992). The highest levels of increased tree mortality have been described for tropical forests, while there are fewer studies in temperate forests. Therefore, we consider the higher k-values to an upper limit of mortality values for temperate systems. Both NeighborLight and NeighborWind can be set by the user as either on or off, which allows the user to manipulate the interactions of light and wind during the simulations.

Model Parameterization and Calibration

To calibrate the model, we used data from old-growth stands in the H.J. Andrews LTER permanent plot net-

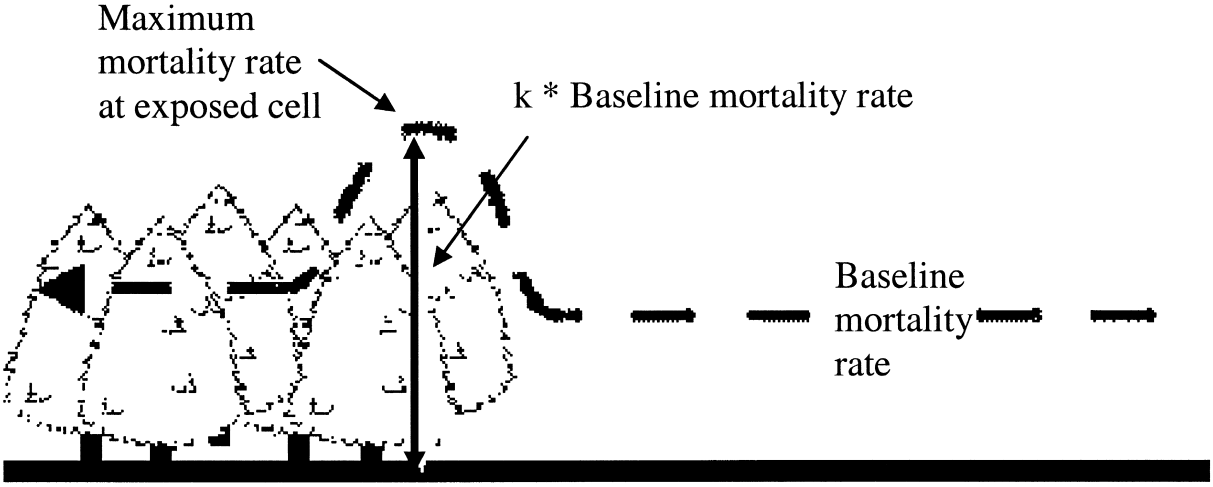

Figure 3. Graphical representation of elevated mortality rates across an edge. In *Standcarb*, k is equal to the wind mortality rate divided by the baseline ("gap-phase") mortality rate

Table 1. Parameter values used in STANDCARB simulations that varied by species

Parameter	Douglas-fir	Western hemlock
Mortality (yr^{-1})	0.009	0.011
Maximum age (yr)	1200	800
Maximum branch extension (yr)	120	100
Foliage turnover (yr^{-1})	0.20	0.25
Light establishment requirement (%)	10	5
Heartwood allocation (yr^{-1})	0.059	0.022
Coarse root to bole ratio	0.62	0.52
Branch to bole ratio	0.11	0.34
Heartwood decay (yr^{-1})	0.02	0.07

work (Acker et al. 1998) reported in Smithwick et al. (2002). The goal of this calibration was to fit the relative proportion of pools in the old-growth forest data (presumed to be at steady-state by Smithwick et al. (2002)) to the steady-state model results (average of years 500 to 1000). Then, we adjusted the model parameters in the mortality, growth, site, and decomposition driver files in STANDCARB to match the relative proportion of pools in the old-growth field data. For simplicity, we presumed an equal ratio of Douglas-fir and western hemlock tree seedlings to initiate the simulations. Some parameters that affected growth, mortality, pruning, turnover, and decomposition varied between species, affecting the differential capacity of Douglas-fir and western hemlock to store C (Table 1).

The establishment and persistence of a species in the stand is a function of the available light and mortality rates and therefore, we expected, would be determined by the particular light and wind processes included in the simulation. In particular, the species composition of a simulation would be determined by whether or not light and wind processes were allowed to interact between cells in a homogenous stand.

Model Simulation Experiments

We used STANDCARB in 1000-year simulation experiments of artificial landscapes with varying age-class structures, representing a range of possible management regimes: Landscape Y (100% Young), Landscape OG (100% Old-Growth), Landscape AIC (50% young and 50% old, Aggregated Interior Cut), Landscape AIF (50% young and 50% old, Aggregated Interior Forest), Landscape CH (50% young and 50% old, Checkerboard cut), and Landscape AD (50% young and 50% old, Aggregated Directional cut, where the upper half is cut and the lower half remains uncut) (Figure 4). For landscapes with a simulated harvest regime (all except Landscape OG), STANDCARB was run 2 times, one with a harvest regime of 50 years and one with a harvest regime of 100 years. All harvests occurred after year 500, once the species composition had stabilized. For example, the 100-year harvest patterns were prescribed at years 500, 600, 700, 800, 900, and 1000. Only years 500 to 1000 were used to calculate results. For brevity, only the 100-year simulations will be described here because results for both regimes were similar.

100%Cut
(homogenous)

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Y

100%Old
(homogenous)

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OG

50%Old/50%Young
(heterogeneous)
Aggregated
Interior Cut

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AIC

50%Old/50%Young
(heterogeneous)
Aggregated
Interior Forest

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1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
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AIF

50%Old/50%Young
(heterogeneous)
Checkerboard

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1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0
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CH

50%Old/50%Young
(heterogeneous)
Aggregated
Directional

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1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
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AD

Figure 4. Artificial landscape cutting patterns used to drive the model (0=uncut, 1=cut). Each cutting pattern was used for simulations of 100-year and 50-year harvesting regimes. Each pattern describes a landscape with either a homogenous (Y, OG) or heterogeneous (AIC, AIF, CH, AD) patch structure.

Simulations were run with one of four interactions of light limitations and wind mortality: (1) light limitations OFF and wind mortality OFF, which served as a control, (2) light limitations ON, wind mortality OFF, (3) light limitations OFF and wind mortality ON, and, finally, (4) light limitations ON and wind mortality ON, which simulated the interaction between the processes. For all simulations in which wind mortality was included, simulations were run at k set to 2, 3, 5, or 8.

We tested for statistical significance of emergent behaviors by first identifying the control (or additive) calculation for each case (detailed below and in Table 2). We then compared the control to the appropriate simulation results, in which the interactions of interest were present. We tested for statistical significance

Table 2. Description of methodology used to test for emergent behaviors at various levels of spatial interaction. C_L= carbon (C) stores for simulation with only light limitations included, C_W = carbon stores for simulation with only wind mortality included, C_{LW} = carbon stores when both were included, and $C_{\varnothing}$ = carbon stores when neither process was included in the simulation experiments. OG is the old-growth age-class structure; Y is the young age-class structure; OG*Y is any heterogeneous age-class structure, representing AIC, AIF, CH, and AD (Figure 4).

Level of Interaction	Control	Treatment	Emergent Behaviors Question
Cell-to-cell	$C_{\varnothing\text{-OG}}$ (or $C_{\varnothing\text{-Y}}$)	$C_{\text{W-OG}}$ (or $C_{\text{W-Y}}$)	Do cells interact within homogenous landscapes?
	$C_{\varnothing\text{-OG}}$ (or $C_{\varnothing\text{-Y}}$)	$C_{\text{L-OG}}$ (or $C_{\text{L-Y}}$)	
Cell-to-cell * process	$(C_{\text{W-OG}} / C_{\varnothing\text{-OG}}) * (C_{\text{L-OG}} / C_{\varnothing\text{-OG}})$	$C_{\text{LW-OG}} / C_{\varnothing\text{-OG}}$	Do the processes interact within homogenous landscapes?
	$(C_{\text{W-Y}} / C_{\varnothing\text{-Y}}) * (C_{\text{L-Y}} / C_{\varnothing\text{-Y}})$	$C_{\text{LW-Y}} / C_{\varnothing\text{-Y}}$	
Cell-to-cell * age	$C_{\text{W-OG}}$ (or $C_{\text{W-Y}}$)	$C_{\text{W-Y}}$ (or $C_{\text{W-OG}}$)	Do the process effects vary with landscape age?
	$C_{\text{L-OG}}$ (or $C_{\text{L-Y}}$)	$C_{\text{L-Y}}$ (or $C_{\text{L-OG}}$)	
	$C_{\text{LW-OG}}$ (or $C_{\text{LW-Y}}$)	$C_{\text{LW-Y}}$ (or $C_{\text{LW-OG}}$)	
Patch-to-patch	$(C_{\text{W-OG}} + C_{\text{W-Y}})/2$	$C_{\text{W-OG*Y}}$	Do patches interact within heterogeneous landscapes?
	$(C_{\text{L-OG}} + C_{\text{L-Y}})/2$	$C_{\text{L-OG*Y}}$	
	$(C_{\text{LW-OG}} + C_{\text{LW-Y}})/2$	$C_{\text{LW-OG*Y}}$	
Patch-to-patch * process	$(C_{\text{L-OG*Y}}/ C_{\varnothing\text{-OG*Y}}) * (C_{\text{W-OG*Y}}/ C_{\varnothing\text{-OG*Y}})$	$C_{\text{LW}}/ C_{\varnothing\text{-OG*Y}}$	Do the processes interact within heterogeneous landscapes?
Patch-to-patch * structure	average $(C_{\text{W-OG*Y}})$	$C_{\text{W-OG*Y}}$	Do the process effects vary with patch age structure?
	average $(C_{\text{L-OG*Y}})$	$C_{\text{L-OG*Y}}$	
	average $(C_{\text{LW-OG*Y}})$	$C_{\text{LW-OG*Y}}$	

by first calculating the standard deviation from the mean of the five replicate runs of the model for the simulation of interest. It is necessary to account for this expected variability in model results since STANDCARB has stochastic elements. We then compared the mean of the control to that of the simulation. If that difference was greater than two standard deviations, then we considered it to be significant. This is a conservative test since it implies that 95% of the observations do not overlap the mean. If, after accounting for the variability in the model, the mean of the simulation was significantly different from the control, then we considered emergent behaviors to be present.

Stand Scale

To observe the effects of light and wind processes on C stores at the stand scale, we were interested in the cell-to-cell interactions within a patch and not the spatial variability between patches. Thus, these comparisons were made independently in Landscape OG and Landscape Y, which are homogeneous patch-types.

We examined emergent behaviors among 3 types of cell-to-cell interactions at the stand scale: (1) cell-to-cell, (2) cell-to-cell * process, and (3) cell-to-cell * age (Table 2). The first interaction (cell-to-cell) reflected the interaction between cells with regard to a certain process, i.e., light or wind. The goal was to determine the relative effect of light or wind on C stores, relative to when neither is included.

The second interaction (cell-to-cell * process) reflected the interactions of light and wind processes acting together and not their individual effects. Our assumption was that an additive combination of the effects of light limitations on C stores, simulated independently (C_L), and the effects of wind mortality on C stores, simulated independently (C_W), should equal the C stores when both light and wind processes were included together in the same simulation (C_{LW}). It follows that any difference in C stores would be due to an emergent behavior, that is, behavior not predictable by a combination of the processes simulated independently.

The third type of interaction (cell-to-cell * age) determines whether cell-to-cell interactions are different between Landscape OG and Landscape Y. Our hypothesis was that older landscapes, which exhibit more tree height variability, might have in larger emergent behaviors than young landscapes, which have a more uniform canopy height distribution. Emergent behav-

	Zone name		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C9**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C8**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C7**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C6**	Cut	
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C5**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C4**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C3**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C2**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C1**		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	**C0**		EDGE
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U0**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U1**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U2**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U3**	Uncut	
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U4**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U5**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U6**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U7**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U8**		
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	**U9**		

Figure 5. Example of the zones used to calculate carbon stores within Landscape AD.

iors are indicated as significant differences between results of Landscape OG and those of Landscape Y.

Landscape Scale

To determine whether patch-to-patch interactions caused emergent behavior at the landscape scale, we used artificial landscapes with a heterogeneous patch structure. A patch ranged in size from just one cell (0.03 ha) for Landscape CH to 50% of the cells in the landscape, or approximately 5 ha for Landscapes AD, AIC, AIF. We examined 3 types of patch-to-patch interactions: (1) patch-to-patch, (2) patch-to-patch * process, and (3) patch-to-patch * structure (Table 2). The first interaction (patch-to-patch) reflects the interaction of patches within heterogeneous landscapes with regard to a certain process. Our goal was to determine whether C storage in heterogeneous landscapes is equal to the average of independent simulations of Landscape OG and Landscape Y, since heterogeneous landscapes are simply an equal mixture of old and young age-classes.

The second type of interaction (patch-to-patch * process) reflects the interaction of processes in heterogeneous landscapes. This type of interaction is similar to the cell-to-cell * process interaction, except that we are now concerned with heterogeneous rather than homogenous landscapes.

The third type of interaction (patch-to-patch * structure) reflects possible emergent behaviors due to the arrangement of patches on the landscape. To test for emergent behaviors, we compare each heterogeneous landscape to the mean of all the heterogeneous landscapes. If there are no emergent behaviors, each landscape should be approximately equal to the mean. Differences from the mean, therefore, reflect emergent behaviors caused by the spatial arrangement of the patches on the landscape.

To further explore patch-to-patch interactions, we modified STANDCARB to predict average C across "zones" of the simulated stand. The user can designate a cell or group of cells as a unique zone. Carbon stores in each zone are then the average of the C stores from each cell in that zone. Here we present results from Landscape AD, in which a zone represents one row of cells (Figure 5). In this way, average C stores could be output horizontally across the landscape, allowing modeled responses to be evaluated spatially between patches, i.e., from a cut region to an uncut region (across an "edge"). To determine whether C was changed at the edge, we calculated the average live and dead C for years 500 to 1000 (in foliage, fine-roots, branches, sapwood, heartwood, coarse-roots, and heart-rot pools), as well as their totals in each of the 20 zones. In Landscape AD, half the stand was cut every 100 years and half remained uncut. Therefore, 10 zones represented re-growing vegetation from the disturbance event (zones C0 through C9), while 10 zones represented old-growth forest (zones U0 through U9). The border of the patches was thus between zone C0 and zone U0, although the effect to which the C stores were affected by the processes was examined in zones "deeper" within each patch type.

Results

Cell-to-Cell

Within homogenous patches, light and wind processes affected total forest C stores differently (Table 3). Specifically, light limitations reduced C more than wind mortality, unless wind mortality was set very high (k=8). In the old-growth landscape (Landscape OG), light limitations caused a reduction of total C of 369 Mg C ha^{-1} from the control (1204 Mg C ha^{-1} minus 835 Mg C ha^{-1}); when wind mortality was included, total C was reduced by 114 Mg C ha^{-1} (k=2), 213 Mg C ha^{-1} (k=3), 332 Mg C ha^{-1} (k=5), and 434 Mg C ha^{-1} (k=8).

Wind mortality caused an increase in dead C stores relative to the control, while live C stores were reduced when either light limitations or wind mortality was included in the simulation. As a result, the net change in total C stores was less when wind mortality was included than when it was not due the compensatory dynamics of live and dead pools. For instance, in Landscape OG, when only wind mortality was included, live C decreased 552 Mg C ha^{-1} (825 Mg C ha^{-1} for the control to 273 Mg C ha^{-1} when k was set to 8) (Table 3) and dead C increased 100 Mg C ha^{-1} (288 Mg C ha^{-1} to 388 Mg C ha^{-1}), so the change in total carbon stores was 433 Mg C ha^{-1}(after accounting for the small change in stable pools). For brevity, only tests for total C will be presented in the results, although it should be recognized that these integrate the offsetting patterns in live, dead, and stable stores.

Emergent behaviors at the cell-to-cell level were evidenced by significant differences from the control for all simulations in Landscape OG (e.g., after accounting for 95% of the model variation) (Figure 6). When only light limitations were included, total C stores were reduced 30.3% (standard deviation (SD) = 1.3%) from the control. When only wind mortality was included (at k set to 8), C stores were reduced by 36.0% (SD = 0.8%). When both light limitations and wind mortality were included, C stores were reduced by approximately 49.3% (SD = 1.3%) (k = 8).

In contrast, emergent behaviors in Landscape Y were not consistently observed (Figure 6). For example, when only light limitations were included, emergent behaviors were not significant. When wind mortality was included, results were significant only when k was set to 5 or greater. The largest reduction (approximately 16.6% ± 0.5%) was when light and wind were both included and k was set to 5.

*Cell-to-Cell * Process*

The interaction of light and wind processes at the cell-to-cell level caused changes in species composition and therefore C stores. When wind mortality was modeled in the absence of light limitations, there was an oscillating pattern through time in species dominance between Douglas-fir and western hemlock in the upper canopy, the amplitude of which increased as the k value increased (Figure 7a). Western hemlock first appeared in the canopy after canopy closure, due to gap formation of the Douglas-fir. Typically, Douglas-fir requires higher light conditions for establishment. Thus, when light limitations were included (Figure 7b), Douglas-fir never received enough light to re-enter the upper canopy after the initial canopy closure and the canopy continued to be dominated by western hemlock. The timing of the initial transition from Douglas-fir to western hemlock was also determined by which processes were allowed to interact. When k was increased from 3 to 8 the transition to western hemlock from Douglas-fir was about 50 years earlier, indicating that western hemlock was able to dominate earlier by replacing Douglas-fir more quickly, essentially hastening the succession process.

Emergent behaviors due to the interactions of light and wind processes at the cell-to-cell level were significant when k was set to 5 or 8 but were not significant at lower levels of wind mortality (Figure 8). The direction of these differences (less than or greater than the control) differed between the old and young landscapes. In the old-growth landscape, C stores were 5.8% (± 3.1%) greater when the processes interacted when k was set to 5, and 13.7% (± 1.3%) greater when k was set to 8, compared to that calculated us-

Table 3. The effect of Neighbor functions (wind and/or light) on average carbon stores (calculated for years 500 through 1000) for different landscape cutting patterns (OG = old-growth, Y = young, AIC = aggregated interior cut, AIF = aggregated interior forest, CH =checkerboard, AD=aggregated directional; Figure 4). Standard deviations are in parentheses, rounded to nearest tenth. Only results from the 100-year cutting patterns are shown.

		Landscape					
Neighbor	k value	OG	Y	AIC	AIF	CH	AD
		LIVE					
None	na	825(12.5)	248(1.1)	540(4.7)	542(9.4)	541(14.7)	541(3.6)
Light	na	572(2.4)	245(0.4)	409(6.0)	395(6.2)	415(9.9)	402(10.9)
Wind	2	655(3.2)	231(0.4)	433(5.2)	439(2.7)	419(7.9)	426(6.3)
Wind	3	526(8.9)	216(0.6)	361(6.2)	366(7.2)	347(3.6)	361(4.7)
Wind	5	382(3.8)	171(0.3)	253(3.4)	260(3.2)	238(2.4)	281(2.7)
Wind	8	273(2.1)	148(0.1)	191(2.8)	195(1.7)	182(2.1)	216(1.2)
Light+Wind	2	475(6.5)	239(0.5)	354(4.6)	341(5.7)	350(3.9)	350(3.3)
Light+Wind	3	409(6.1)	233(0.5)	317(4.5)	310(5.0)	314(5.5)	312(3.6)
Light+Wind	5	341(5.9)	196(0.4)	212(1.6)	211(2.7)	208(1.8)	273(4.4)
Light+Wind	8	283(2.3)	184(12)	183(1.0)	183(1.6)	179(0.9)	237(2.0)
			DEAD				
None	na	288(3.6)	164(0.6)	226(1.6)	226(4.3)	225(4.9)	223(3.2)
Light	na	186(2.8)	158(1.3)	161(1.1)	154(1.3)	158(3.2)	162(2.7)
Wind	2	336(1.8)	182(0.2)	261(2.8)	257(2.1)	265(1.5)	262(2.4)
Wind	3	363(3.7)	198(1.1)	281(1.6)	278(3.1)	284(3.4)	281(1.8)
Wind	5	384(1.1)	205(0.6)	298(2.2)	296(1.9)	301(0.9)	303(2.4)
Wind	8	388(1.0)	223(0.2)	307(1.0)	306(1.1)	307(0.2)	316(1.4)
Light+Wind	2	194(5.1)	163(1.4)	173(1.5)	166(3.9)	172(2.4)	170(3.2)
Light+Wind	3	199(5.3)	168(1.2)	180(1.2)	173(2.5)	180(1.6)	179(2.3)
Light+Wind	5	211(2.9)	156(0.5)	159(1.1)	153(1.6)	159(1.2)	189(2.8)
Light+Wind	8	232(1.2)	167(0.8)	175(0.8)	169(1.0)	173(0.9)	205(1.2)
STABLE							
None	na	90(0.3)	72(0.4)	81(0.3)	81(0.5)	81(0.5)	81(0.3)
Light	na	81(0.4)	70(0.1)	72(0.3)	71(0.4)	72(0.5)	73(0.6)
Wind	2	97(0.5)	73(0.2)	85(0.6)	85(0.4)	86(0.2)	85(0.3)
Wind	3	101(0.5)	74(0.2)	88(0.2)	88(0.3)	89(0.2)	88(0.4)
Wind	5	106(0.2)	59(0.1)	70(0.4)	70(0.3)	71(0.2)	91(0.2)
Wind	8	109(0.1)	61(0.1)	72(0.2)	72(0.1)	72(0.1)	94(0.3)
Light+Wind	2	84(0.7)	70(0.2)	76(0.1)	75(0.8)	76(0.4)	76(0.5)
Light+Wind	3	86(1.4)	71(0.3)	79(0.5)	76(0.8)	79(0.1)	78(0.5)
Light+Wind	5	91(1.2)	52(0.1)	50(0.3)	49(0.2)	49(0.3)	81(0.8)
Light+Wind	8	96(0.5)	53(1.0)	52(0.3)	51(0.1)	51(0.2)	84(0.4)
			TOTAL				
None	na	1203(16.5)	484(2.2)	847(6.6)	848(14.1)	847(20.1)	845(7.1)
Light	na	839(5.5)	473(1.9)	643(7.4)	620(7.9)	646(13.5)	636(14.2)
Wind	2	1089(5.4)	487(0.8)	780(8.6)	781(5.2)	770(9.5)	773(8.9)
Wind	3	991(13.1)	488(1.9)	730(8.0)	734(6.5)	720(7.3)	730(6.9)
Wind	5	871(5.1)	435(1.0)	621(6.0)	626(5.4)	610(3.5)	675(5.3)
Wind	8	770(3.2)	432(0.5)	571(4.1)	573(2.9)	562(2.4)	626(2.9)
Light+Wind	2	753(12.3)	473(2.1)	602(6.2)	582(10.4)	598(6.6)	595(7.0)
Light+Wind	3	695(12.8)	471(2.0)	576(6.2)	560(8.2)	572(7.1)	569(6.5)
Light+Wind	5	643(10.0)	403(1.0)	421(3.0)	414(4.5)	415(3.3)	544(8.0)
Light+Wind	8	610(3.9)	404(1.4)	410(2.0)	403(2.7)	403(1.9)	527(3.6)

ing the additive approach. In contrast, in the young landscape, C stores were 5.2% (± 0.5%) and 4.3% (± 0.7%) lower when k was set to 5 and 8, respectively.

*Cell-to-Cell * Age*

When there was a regular harvest event across the stand (Landscape Y), the effect of light limitation and wind mortality processes was reduced compared to

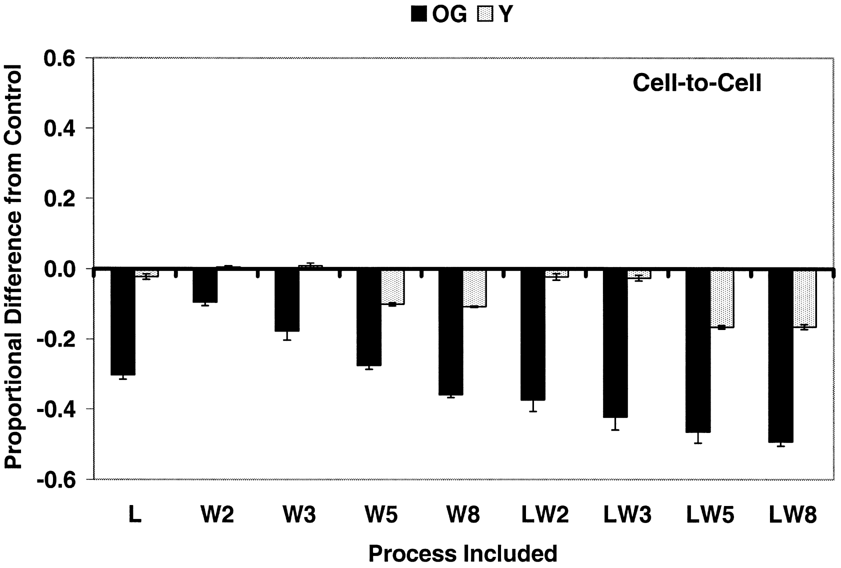

Figure 6. Emergent behaviors due (a) cell-to-cell interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation.

the older landscape (Landscape OG). For example, in Landscape OG (Figure 9a), both light limitations and wind mortality reduced C stores from the control (when neither was included), but in Landscape Y (Figure 9b), the simulations that included light limitations are indistinguishable after year 500 from the control. This indicates that light interactions were less pronounced in the younger landscape than the older landscape.

Emergent behaviors resulting from cell-to-cell interactions in Landscape OG were higher than those in Landscape Y for all simulations (Figure 10). Emergent behaviors were 28.7% (± 0.2%) higher in Landscape OG than Landscape Y when only light was included and between 30.0% (± 0.02%) and 40.0% (± 0.2%) higher when both light and wind processes interacted.

Patch-to-Patch

Results across edge zones in Landscape AD showed that C stores were affected both by light limitations and wind mortality, indicating that patch-to-patch interactions were important. The relative effect of these processes at the edge was different depending on the type of interaction included and the pools considered (Figure 11). Total live C stores (the sum of all the live pools) in the cut patch averaged 200 ± 62.7 Mg C ha^{-1} across all zones when only light limitations were included (Figure 11a). However, near the edge of the cut patch (zone C0), the total live C store was 47 Mg C ha^{-1}, a decrease of 154 Mg C ha^{-1}. The difference was negligible (1 Mg C ha^{-1}) for zones C3 to C9, indicating that most of the reduction in C stores due to light limitations was at the edge of the cut patch. When only wind mortality was included, the reductions in total live biomass at the edge compared to the average of all zones in the cut patch ranged from 2 Mg C ha^{-1} (when k was set to 2) to 78 Mg C ha^{-1} (when k was set to 8). When both light limitations and wind mortality were included, total live stores decreased at the edge of the cut patch (up to 137 Mg C ha^{-1} (k=2), similar to the simulations with only light included. In the uncut patch, for all simulations, total live C stores did not appear to change significantly across the zones. Total dead C stores (Figure 11b) showed no change across all zones in the cut patch. In the uncut patch, total dead pools were increased near the edge, from 3 Mg C ha^{-1} (with light limitations) to 19 Mg C ha^{-1} (with light limitations and wind mortality, k=2). Total C pools (total live + total dead + total stable, data not shown) showed no significant trend near the edge in the uncut patch. In the cut patch, there was a decrease in C stores near the edge, ranging from large differences such as 254 Mg C ha^{-1} when only light limitations were included and 230 Mg C ha^{-1} when both light limitations and wind mortality were included (k=5) to smaller dif-

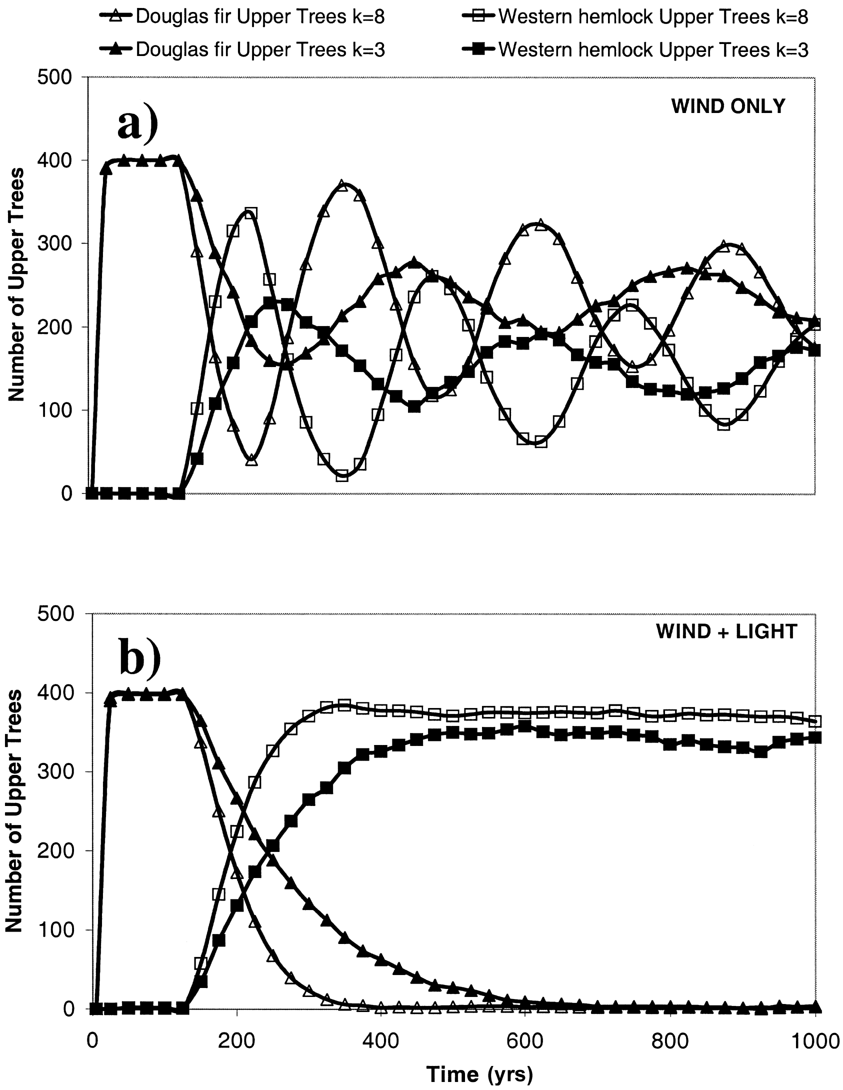

Figure 7. Effect of increasing k values on the number of upper trees for PSME (Douglas-fir, *Pseudotsuga menziesii*) and TSHE (western hemlock, *Tsuga heterophylla*) for simulations with (a) only wind mortality included and (b) both light limitations and wind mortality included

ferences such as 1 or 2 Mg C ha^{-1} when only wind mortality was included (k=2, 3, and 8).

Emergent behaviors due to patch-to-patch interactions were evidenced by differences between the C stores in heterogeneous landscapes and the C stores of independent simulations of old growth and young landscapes that were additively combined (Figure 12). However, emergent behaviors were not significant until the k value was set to 5 or 8. At these high k values, landscapes AIC, AIF, and CH had 21 or 22% (± 2.0%) less C in the heterogeneous landscapes than would be predicted from an additive approach. In contrast, landscape AD had between 4.0% (± 2.0%) and 1.0% (± 3.0%) greater total C stores.

*Patch-to-Patch * Process*

Emergent behaviors due to patch-to-patch * process interactions were significant when k was set to 3, 5, or 8 for all heterogeneous landscapes (Figure 13). Differences from the control were small when k was set to 3 (4.0% SD = 2%). When k was set to 5, landscape AIC, AIF, and CH were approximately 11.0% (SD = 2.0%) lower and landscape AD is 7.0% (SD = 3.0%) higher than the control. When k was set to

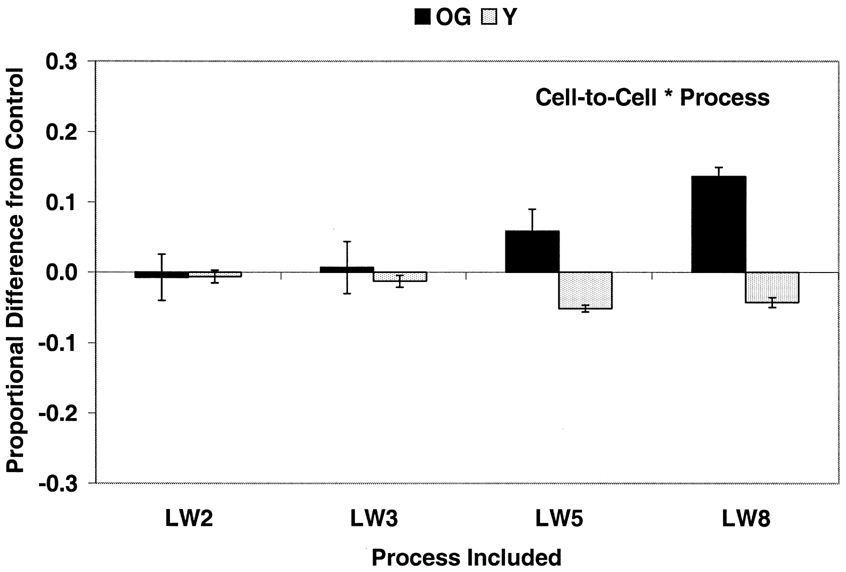

Figure 8. Emergent behaviors due (a) cell-to-cell * process interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation.

8, landscapes AIC, AIF, and CH were about 5.0% (SD = 1.0%) lower than the control, although landscape AD was 12.0% (SD = 1.0%) higher.

*Patch-to-Patch * Structure*

The arrangement of patches in heterogeneous landscapes resulted in emergent behaviors when k was set to 5 or 8 (Figure 14). The magnitude of the emergent behaviors was dissimilar among different heterogeneous landscapes; the largest differences were found when light and wind interacted. When k was set to 5 or 8, landscapes AIC, AIF, and CH had between 6.0% and 8.0% (SD = 1.7 to 3.6%) lower biomass than the average C store of the simulated landscapes. Landscape AD showed an opposite trend, being 21.0% (SD = 1.7 to 3.6%) higher than the control.

Discussion

Our modeling exercises were based on a simple analysis of only two processes, light limitations and wind mortality, which are affected by the spatial heterogeneity of tree heights of only two species, Douglas-fir and western hemlock. Simulations were also performed over artificial landscapes for simplicity and do not capture the natural complexity of real landscapes. Nevertheless, results suggest that, in some instances, interactions of these processes may lead to emergent behaviors that influence C storage at the stand-scale (based on interactions of processes among cells) and the landscape-scale (based on interactions of processes between patches).

At the stand scale, process interactions affect C storage in multiple ways. In our simulations, the variation in tree heights among cells caused limitations in regeneration and exposed some trees to more wind damage. This effect was highest for older stands because the variation in tree heights was greater than in younger stands. Most ecophysiological models only consider vertical C fluxes (such as respiration and photosynthesis) at this scale and ignore horizontal processes across cell boundaries (such as light and wind transfer). These interactions of light and wind processes among cells can lead to a change in species composition that may modify C storage depending on the differences in growth, mortality, and decomposition characteristics of the species. Thus, ignoring the effects of horizontal processes between cells on C storage could result in error in stand-scale estimates. Predicting the effects of these interactions on total C stores at the stand scale is complicated given that live, dead, and stable pools respond differently to changed wind and light conditions.

We did not include many other processes known to be potentially important across cell boundaries and which may influence C stores at the stand scale. For

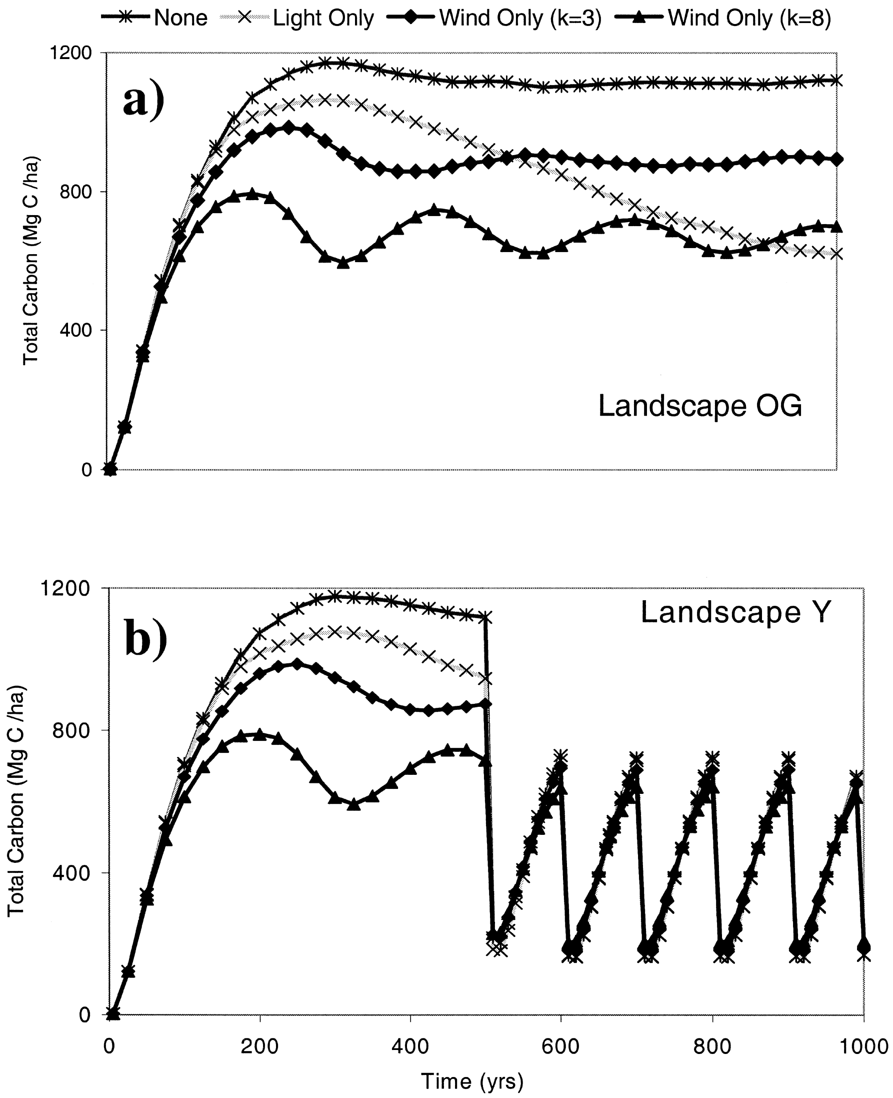

Figure 9. The trend in total carbon in (a) Landscape OG (old-growth) and (b) Landscape Y (young) through time. (Symbols: *triangle* = wind mortality included (k set to 8), *diamond*= wind mortality (k set to 3), *cross* = light included, *asterisk* = neither included).

example, we did not include the transfer of material between neighboring cells, e.g., the exchange of fallen wood, or the competition of roots belowground, due to the complex nature of these interactions. Belowground biogeochemical cycling in STANDCARB is simplistic and nitrogen cycling interactions at the edge are ignored, both of which may contribute to greater soil changes at the edge than we observed (T. Redding, T. Hayes, personal communication). In addition, wind-mortality events may be stochastic, e.g., in the form of a blowdown, whereas our modeled increases in mortality were constant through time.

At the landscape scale, our results indicate that emergent behaviors due to process interactions across patches are important, even though most current C models do not include these effects. Our results indicate that interactions of processes across patches are not predictable using an additive model when the wind mortality is set to the highest levels reported in the literature. Further, our results indicate that artificial landscapes with different spatial structures resulted in different magnitudes of emergent behaviors. These emergent behaviors ranged from + 21% to − 22%, depending on the type of interaction, the

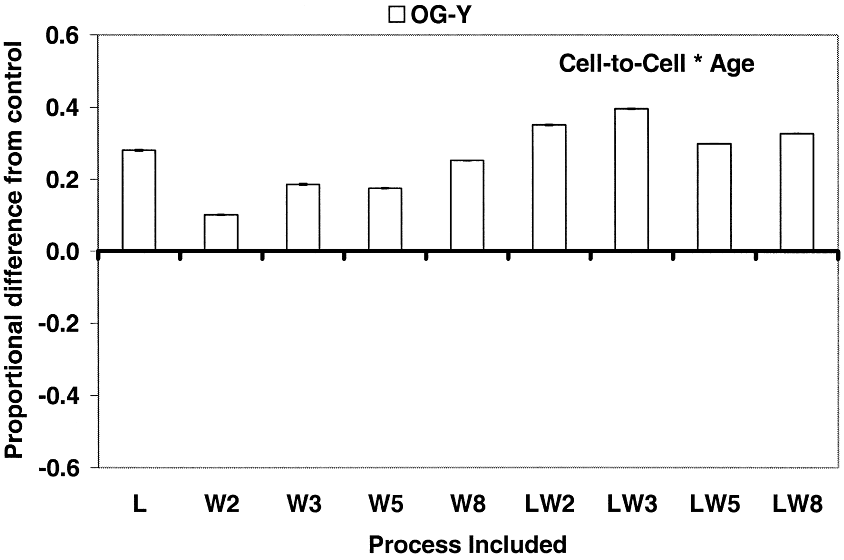

Figure 10. Emergent behaviors due (a) cell-to-cell * age interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation.

landscape structure, the type of processes considered, and the magnitude of the processes.

By simulating a zone structure within our simulated landscapes, we were able to examine the location of "edge effects" between patches due to wind and/or light. Our results indicated that the effects of light limitations were primarily located at the edge since C stores were reduced in the cut patch for at least 50 m, presumably due to shading by the uncut patch. However, we did not detect the effects of wind mortality in cut patches beyond 17 m. There may be several reasons for this. First, given the relatively coarse resolution of the cells, we may have missed finer-scale dynamics. Second, and probably more importantly, a limitation of STANDCARB is that each cell can only be affected by wind mortality once per year. Thus, there is a time step limit on wind propagation through a stand and continuous effects of wind mortality within a year cannot be simulated. In future modeling of edge effects it would be helpful to consider shorter time-steps for wind disturbances within a year.

Most models do not include spatial interactions across patches in a landscape for several reasons. First, the effect of forest edges may be minimal relative to the broad scale patterns that are of interest, in which case emergent behaviors resulting from these interactions are inconsequential. This was the case for all simulated landscapes other than Landscape AD.

Second, if processes are linear across edges, edge effects will be minimal at broad scales as edge effects are averaged out across patches. If processes are asymptotic or non-linear across edges, however, edge effects will exhibit emergent behaviors that are not predictable by the properties of the neighboring patches. We found that emergent behaviors across edges are significant at high k values (i.e., >5 times the baseline mortality rate), ranging from $+12\%$ to -11%, but are not significant at lower k values.

Third, if edge effects occur at broad scales, it may be possible to use the edge zone as another "patch"in a fragmented landscape to account for the area affected by edges. Yet, the latter solution to edges in fragmented landscapes may not be appropriate if the topological arrangement of patches on the landscape is also important. We found that, when the wind mortality was set very high (8 times the base mortality rate) the level of emergent behavior of the aggregated directional landscape (Landscape AD), was significantly different than that found in the other landscapes, by almost 28%. The different response of Landscape AD from the other landscapes may be because Landscape AD has more interior cells (unaffected by an edge) than the other landscapes. With more interior cells, both dead and live biomass increase and the relative effects of light limitations and wind mortality are reduced. Regardless of the

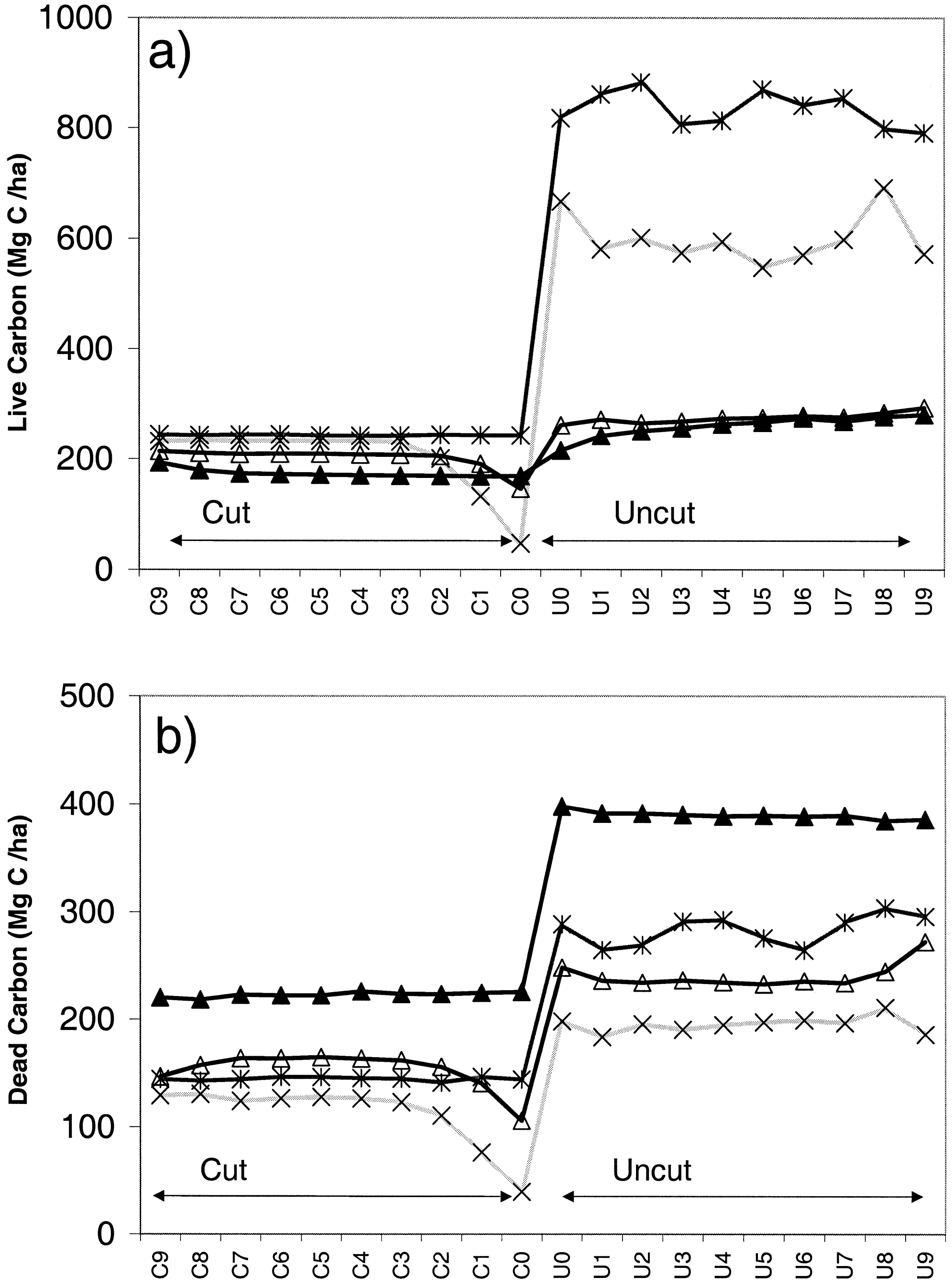

Figure 11. Effect of light limitations and wind mortality on: (a) total live and (b) total dead carbon, by zone, in Landscape AD. Zones C0 through C9 are cut every 100 years after year 500, while zones U0 through U9 remain uncut. Results are the average for years 500 to 1000 for each zone.

cause, in this landscape, an additive correction for edge area would result in error.

Given that our tests for emergent behaviors at the landscape scale largely examined one patch size, it would be helpful if there were a simple way to estimate the magnitude of this effect for a range of patch sizes. Assuming the relative effects of emergent behaviors are a function of the relative width of edge

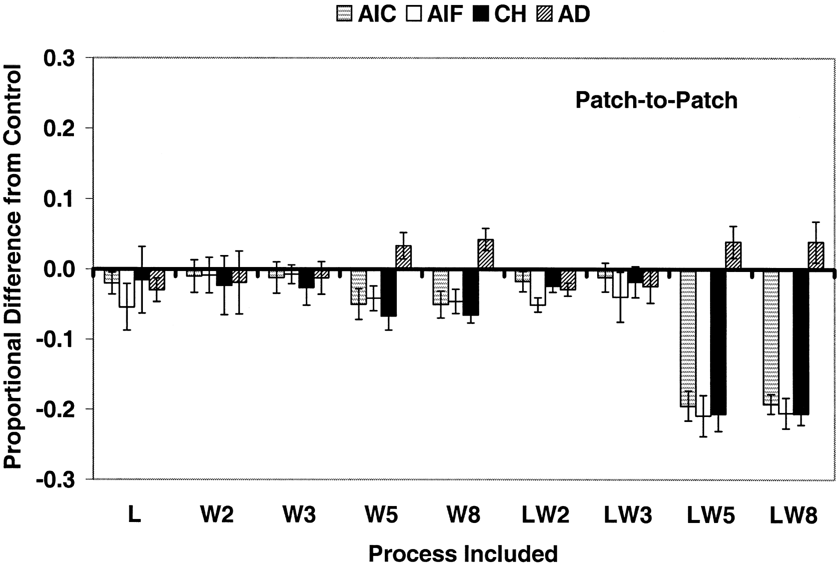

Figure 12. Emergent behaviors due to (a) patch-to-patch interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation. Landscape names described in text.

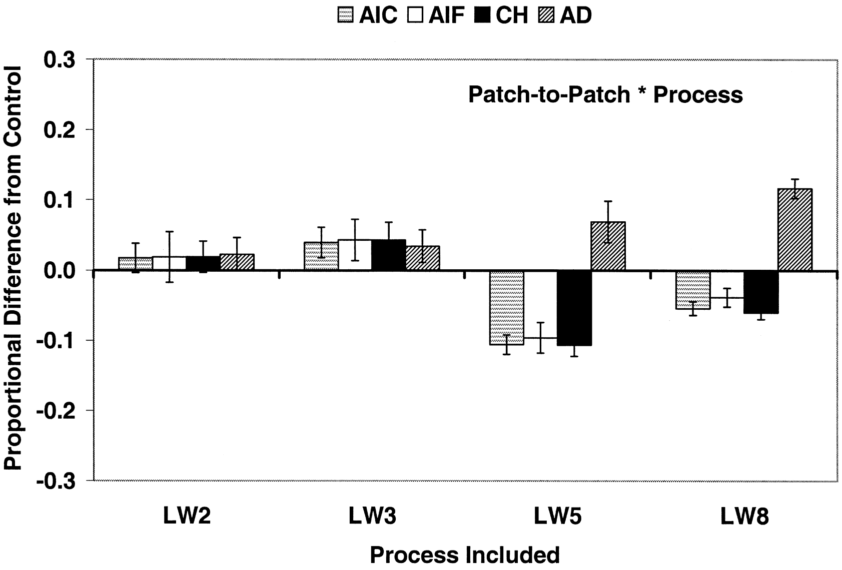

Figure 13. Emergent behaviors due to (a) patch-to-patch * process interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation. Landscape names described in text.

effects relative to patch width, we can extrapolate the effects for other square-shaped patches, assuming a constant edge width. In our simulations, the maximum edge width was approximately 51 m (3 cells into a patch 10 cells wide, where each cell is 17 m). Since the simulated patches were 170 m wide, the edge-affected area represents approximately 30% of the patch and this resulted in potential errors of ± 20% based on the emergent behaviors we observed. Typical harvest cuts may be between 20 and 40 ha, much larger than the patches simulated here, with less edge-affected area. The potential for errors is thus between 5% and 7% (Figure 15). Similarly, around larger patches, such as from natural fires, the poten-

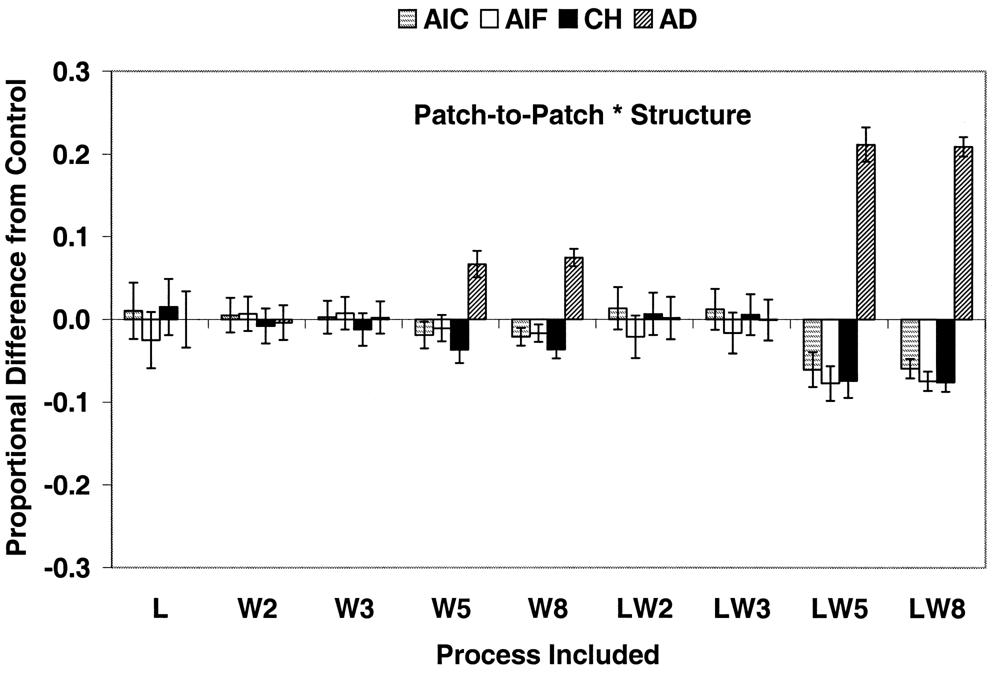

Figure 14. Emergent behaviors due to (a) patch-to-patch * structure interactions. Values represent the proportional difference of the treatments from the control. The control is defined in Table 2. Values different from 0 reflect emergent behaviors. Error bars represent two standard deviations from the mean of five repetitions for each simulation. Comparisons between bars reflect differences between landscapes, due to the different age structures. Landscape names described in text.

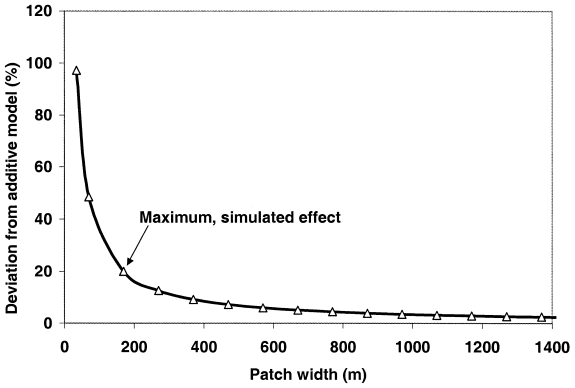

Figure 15. Results of a simple mixing model showing the potential errors caused by edge-induced, emergent behaviors for increasing patch widths. The maximum, simulated effect observed here is ± 20% at a patch width of 170 m. Calculations assume a constant edge width of 51 m.

tial for error would be from less than 1% to 4%. It should be noted, however, that the trend in forest management is to reduce the size of clear-cut patches. As the average cut size for harvests is reduced, the relative amount of edge-affected area would increase suggesting errors due to emergent behaviors might be larger than we observed.

Conclusions

Despite the increasing evidence over the short and long term that horizontal processes are important, and despite the generally recognized notion that assumptions of scale limit prediction, there have been few studies to systematically test the effect of complex, nonlinear processes at multiple scales. Here, we presented a novel, modeling analysis to assess the importance of emergent behaviors on C storage. By using artificial landscapes, and coupling them to an ecosystem process model, we provided various null models for generating predictions about C storage in fragmented landscapes (With 1997). Although the artificial landscapes used here are relatively simple, they are useful in defining situations when spatial heterogeneity may be important. Particularly, the goal of this work is to alert modelers to assumptions of spatial homogeneity, which may or may not hold when complex, nonlinear dynamics are applied in heterogeneous landscapes.

We found that spatial interactions at all levels were potentially significant and resulted in emergent behaviors in both homogenous and heterogeneous landscapes. Cell-to-cell interactions are part of many (non-point) model structures and thus these spatial interactions are straightforward to include; were this the only type of spatial interaction then additive scaling to broader scales would be possible. Similarly, if patch-to-patch interactions were the only type of interaction then we might be able to suggest a simple correction for edge zones. However, the fact that we detected emergent behaviors among landscapes with different spatial structures in one instance indicates that the spatial arrangement of patches on the landscape may be important when scaling information to broader scales. An additive correction for edge zones, therefore, may not capture the variability in patch-to-patch interactions in all cases. The potential error of not accounting for these emergent behaviors depends on the relative area of the edge relative to patch size and the magnitude of the emergent behaviors.

More understanding of how processes interact spatially at the local level may be necessary before predictions of C dynamics can be made accurately at broad scales. With this goal in mind, futher elucidation of the role of spatial pattern in influencing emergent behaviors is needed. A more precise study of landscape pattern indices (Krummel et al. 1987; Li 2000) may be useful in this effort to identify landscapes with differing potential to exhibit emergent behaviors. In addition, to predict accurately emergent behaviors in spatially heterogeneous environments, more research is needed on the processes themselves, for example to determine the effect of wind mortality at forest edges across a broader range of conditions and environments than those simulated here. This research has significant implications for C cycle modeling since C models that operate at broad scales make assumptions of spatial homogeneity, although the implications may extend to other ecological fields in which spatial scale is important.

a)

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