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RESEARCH ARTICLE

Changing temporal patterns of forest carbon stores and net ecosystem carbon balance: the stand to landscape transformation

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Abstract Short- and long-term patterns of net ecosystem carbon balance (NECB) for small, relatively uniform forest stands have been examined in detail, but the same is not true for landscapes, especially those with heterogeneous disturbance histories. In this paper, we explore the effect of two contrasting types of disturbances (i.e., fire and tree harvest) on landscape level NECB by using an ecosystem process model that explicitly accounts for changes in carbon (C) stores as a function of disturbance regimes. The latter were defined by the average disturbance interval, the regularity of the disturbance interval (i.e., random, based on a Poisson frequency distribution, or regular), the amount of C removed by the disturbance (i.e., severity), and the relative abundance of stands in the landscape with unique disturbance histories. We used the model to create over 300 hypothetical landscapes, each with a different disturbance regime, by simulating up to 200 unique stand histories and averaging their total C stores. Mean NECB and its year-to-year variability was computed by calculating the difference in mean total C stores from one year to the next. Results indicated that landscape C stores were higher for random than for regular disturbance intervals, and increased as the mean disturbance interval increased and as the disturbance severity decreased. For example, C storage was reduced by 58% when the fire interval was shortened from 250 years to 100 years. Average landscape NECB was not significantly different than zero for any of the simulated landscapes. Year-to-year variability in landscape NECB, however, was related to the landscape disturbance regime; increasing with disturbance severity and frequency, and higher for random versus regular disturbance intervals. We conclude that landscape C stores of forest systems can be predicted using the concept of disturbance regimes, a result that may be a useful for adjusting estimates of C storage to broad scales that are solely based on physiological processes.

Keywords Landscape · Carbon · Disturbance · Fire · Harvest · NECB · NPP · Model

Introduction

Calculating the net rate of organic accumulation or loss from ecosystems is important for measur-

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ing and managing net changes in carbon (C) storage and for assessing C budgets. The Net Ecosystem Carbon Balance (NECB) of an ecosystem represents the net flux of C entering or leaving an ecosystem and this metric implicitly incorporates all fates of C including fluxes due to disturbances (Chapin III et al. in press). Calculating NECB for forests over broad areas can be used to evaluate whether landscapes are a net source (negative NECB) or sink (positive NECB) of C, which may ultimately guide forest C management. Changes in NECB have been evaluated on daily and seasonal timescales using eddy flux covariance (Law et al. 2000) and through successional time using chronosequences (Janisch and Harmon 2002; Wirth et al. 2002), but most of these studies have been at local scales (5–1,000 ha). Less is known about how NECB varies as spatial extent increases. At the scale of the globe, seasonal changes in CO_2 concentration yield insights into how NECB changes over the course of a year (Tans et al. 1990), generally reflecting the physiologically driven temporal patterns observed at a more local scale. However, over successional timeframes (i.e., 10s to 100s of years) it is particularly challenging to understand how estimates of NECB can be scaled from measurements in single, homogeneous areas (e.g., forest stands) to a landscape composed of a myriad of stands with different disturbance histories.

Disturbances are known to influence forest NECB at the stand level (Janisch and Harmon 2002; Wirth et al. 2002, Bond-Lamberty et al. 2004; Law et al. 2004). Typically NECB is negative following a disturbance as the decomposing material created by the disturbance loses more C than the regrowing forest gains. Eventually growth exceeds decomposition losses and the ecosystem gains C, often for a considerable length of time (Wirth et al. 2002). If another disturbance does not occur for a very long period, then the ecosystem may come into approximate C balance and NECB theoretically approaches zero as long as the fundamental controls of production and decomposition remain relatively constant. While the long-term average may be close to zero, in practical terms it is unlikely that NECB is exactly zero in any particular year given fluctuations in local weather and finer-scale disturbances (Goulden et al. 1996).

In heterogeneous forested landscapes, each stand may have a different disturbance history and be in a different state of succession in relation to NECB. As a whole, the landscape may not be changing because it is responding to the landscape disturbance regime and not individual disturbances, which might be cancelled out by other areas in different states of recovery. Disturbance regimes can be characterized in part by the average disturbance interval, the regularity of disturbance events (i.e., regular or random), their severity (i.e., amount of C removed), and the resulting landscape age-class structure (i.e., the relative abundance of stands with unique disturbance histories). Several studies have shown that landscape-level ecosystem C content is affected when the disturbance regime is altered (Kurz et al. 1997–1998; Peng and Apps 1999). Theoretically, given sufficient time and landscape area, NECB should approach zero as more stands with different histories and timings are combined (Harmon 2001; Harmon and Marks 2002). For regular disturbances systematically dispersed over a landscape (i.e., a ‘‘regulated’’ system), previous modeling analysis shows this is the case (Harmon 2001). However, despite the recognized importance of disturbance at broad scales for understanding the global C cycle (e.g., Houghton 1999) there are few papers to evaluate how NECB varies within a heterogeneous landscape or one in which disturbances are random. Euskirchen et al. (2002) developed a landscape model to evaluate temporal and spatial variability in NECB (they referred to it as NEP) in a landscape mosaic and their results suggested large cyclical variations on decadal scales in a regulated system. Their model predicted continued positive NECB under certain management systems. Apps et al. (2000) modeled random and uniform disturbances across boreal forests of Saskatchewan, Canada. They concluded that random disturbances stored more C than uniform disturbances due to differences in the forest age class structure.

Here, we conducted a series of simulation experiments to reexamine variability in landscape NECB and mean C stores. Our goal was to develop a method for scaling estimates of stand-level C storage and NECB to landscapes under various disturbance regime scenarios. We were also interested in seeing if there were any simple rules that suggest which landscapes store more C. Our general assumption was that characteristics of the disturbance regime would determine average landscape C stores, NECB, and their variability. We hypothesized that disturbance interval, severity, and regularity affect stand and landscape C storage, but that NECB would approach zero for all disturbance regimes. We recognize that other characteristics of a disturbance regime may be important for understanding net C storage, e.g., the duration of the disturbance event relative to the disturbance interval, but interval, severity, and regularity are responsible for the major changes in C storage for the harvest and fire disturbance regimes that we analyzed. Specifically, we hypothesized that (1) landscape C stores would increase with increasing interval between disturbances due to the greater abundance of older stands, with higher C storage, in the landscape; (2) landscape C stores would be reduced when disturbance severity is increased given more C is removed from the system by each disturbance; and, (3) landscape C stores would be higher for random versus regular disturbance intervals because random disturbance intervals (modeled with a Poisson frequency distribution) allow stands that are older than the average disturbance interval to persist on the landscape. Moreover, we also expected that year-to-year variability in landscape NECB to be related to disturbance regime characteristics, similar to mean landscape NECB; increasing with increasing severity and frequency, and greater for random versus regulated disturbance regimes.

Methods

Model description

We developed a simple simulation model to evaluate the effect of disturbances on C stores in a landscape (Figure 1). The model calculates temporal changes in C storage in seven live pools, six dead pools, three stable pools, and one forest product pool on an annual time-step. Live pools are: foliage, sapwood, heartwood, heart-rot, branches, coarse roots, and fine roots. Live C pools transfer material to their respective detrital counterpart, although dead heartwood receives C from both heartwood and heart-rot. All detrital pools can potentially add material to one of the three relatively decay-resistant stable pools: stable foliage, stable wood, and stable soil.

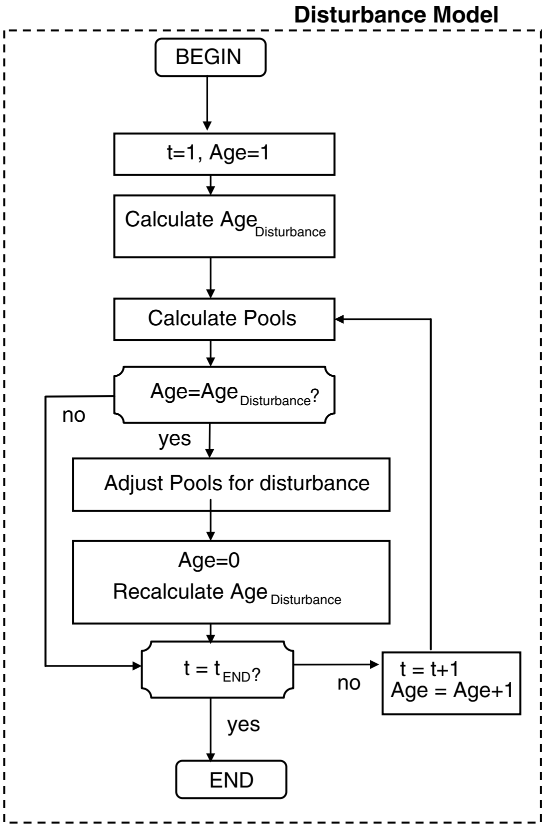
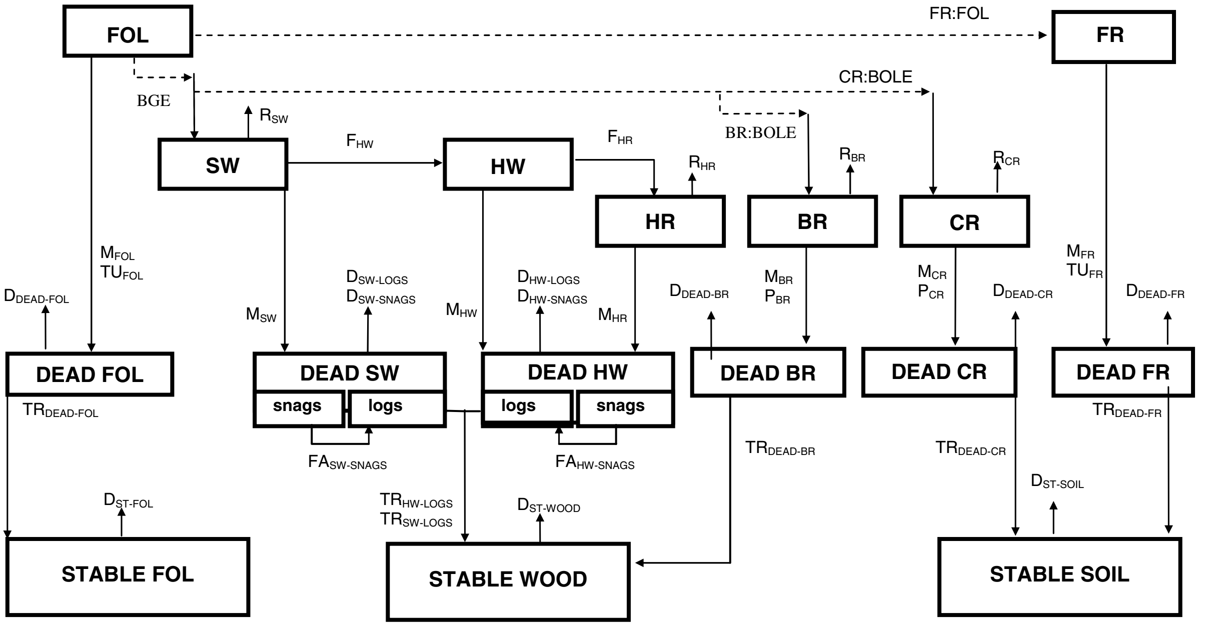


Fig. 1 Sequence of calculations used in the disturbance simulation model

The C stores for each pool are a function of the stores in the previous year and the fluxes into and out of the pool over that year, including the effects of disturbance. The general equation is:

$$\text{pool : mass (age)} = \text{pool : mass(age} - 1) + \Sigma\text{input : flux} - \Sigma\text{output : flux}$$

The calculations are based on a set of cascading calculations between pools (Figure 2) and the specific equations are in Smithwick (2002) and Appendix A. Input fluxes are calculated



Pools: FOL=foliage, SW=sapwood, HW=heartwood, HR= heart-rot, BR=branch, CR=coarse root, FR= fine root, ST=stable

Fluxes: D=decay, F=formation, FA= fall, M=mortality, P=prune, R=respiration, TR=transfer, TU=turnover, BGE=bole growth efficiency

Fig. 2 Flows of mass (carbon) between 7 live, 6 dead, and 3 stable soil pools (described in the text). During a simulation, disturbances modify flows between pools by altering inputs to dependent pools, and outputs from donor pools

from the mass of contributing (or donor) pools and rate constants modifying the input to the current pool (i.e., the pool currently being considered in the calculations). Output fluxes are calculated from the mass of the current pool and rate constants modifying the transfer of mass to subsequent pools (transfer rates, mortality rates, formation rates, or pruning rates), and the loss of mass to the atmosphere (respiration rates for live pools, and decay rates for detrital pools). Output fluxes are a function of some combination of these transfers and losses, depending on the pool being calculated. For example, live pools (including heart-rot) do not have a decay loss; so their output fluxes are a function of transfers to dead pools and autotrophic respiration losses only.

Disturbances cause transfers from live to dead pools, and from live bole pools (sapwood, heartwood, and heart-rot) to forest products following harvests (see Appendix B). In addition, there may be combustion losses from live, dead, and stable pools following fires and harvest site preparation. The user specifies the disturbance severity, i.e., the amount transferred to other pools or combusted. The model is capable of simulating many disturbance events including harvest, fire, windthrow, and insect outbreak, although only harvest and fire are simulated here. The effects of the disturbances on C storage occur only in the current model time-step (i.e., year of the disturbance event).

Fluxes and masses of C pools are calculated with rate-constants (Table 1) derived by calibrating the model to StandCarb (Harmon and Domingo 2001; Harmon and Marks 2002) and field data (Smithwick et al. 2002). These rate constants reflect an aggregated set of species and life-forms. Thus, they reflect the general stand dynamics through time, integrating effects of species and life-form. Rates currently reflect parameterization to forest stands in the Pacific

Table 1 Rate constants used to parameterize the simulation experiments (see Smithwick 2002 for derivation)

Variable Name	Value	Units
Production		
Foliage mass maximum (FOL_{MAX})	18.00	Mg ha^{-1}
Bole growth efficiency (BGE)	1.000	unitless
Live Pool Ratios		
Branch to bole ratio (BR:BOLE)	0.480	unitless
Coarse root to bole ratio (CR:BOLE)	0.520	unitless
Fine root to foliage ratio (FR:FOL)	0.770	unitless
Bole Formation		
Heartwood formation (F_{HW})	0.059	yr^{-1}
Heart-rot formation (F_{HR})	0.010	yr^{-1}
Respiration		
Sapwood respiration (R_{SW})	0.017	yr^{-1}
Heart-rot respiration (R_{HR})	0.002	yr^{-1}
Branch respiration (R_{BR})	0.017	yr^{-1}
Coarse root respiration (R_{CR})	0.017	yr^{-1}
Turnover		
Foliage turnover (TU_{FOL})	0.200	yr^{-1}
Fine root turnover (TU_{FR})	0.500	yr^{-1}
Pruning		
Branch pruning (P_{BR})	0.020	yr^{-1}
Coarse root pruning (P_{CR})	0.005	yr^{-1}
Mortality		
Foliage mortality (M_{FOL})	0.021	yr^{-1}
Sapwood mortality (M_{SW})	0.021	yr^{-1}
Heartwood mortality (M_{HW})	0.021	yr^{-1}
Heart-rot mortality (M_{HR})	0.021	yr^{-1}
Branch mortality (M_{BR})	0.021	yr^{-1}
Coarse root mortality (M_{CR})	0.021	yr^{-1}
Fine root mortality (M_{FR})	0.021	yr^{-1}
Percent snags (%Snags)	90, stand age <120	%
	65, stand age ≥ 120	%
Decay		
Dead foliage decay (D_{DEAD}-FOL)	0.220	yr^{-1}
Dead sapwood decay (D_{DEAD}-SW)	0.110	yr^{-1}
Dead heartwood decay (D_{DEAD}-HW)	0.030	yr^{-1}
Dead branch decay (D_{DEAD}-BR)	0.150	yr^{-1}
Dead coarse root decay (D_{DEAD}-CR)	0.100	yr^{-1}
Dead fine root decay (D_{DEAD}-FR)	0.220	yr^{-1}
Stable foliage decay (D_{ST}-FOL)	0.205	yr^{-1}
Stable wood decay (D_{ST}-WOOD)	0.250	yr^{-1}
Stable soil decay (D_{ST}-SOIL)	0.025	yr^{-1}
Transfer		
Dead foliage transfer (TR_{DEAD}-FOL)	0.300	yr^{-1}
Dead sapwood snags fall (FA_{SW})	0.200	yr^{-1}
Dead sapwood logs transfer (TR_{SW}-LOGS)	0.075	yr^{-1}
Dead heartwood snags fall (FA_{HW})	0.200	yr^{-1}
Dead heartwood logs transfer (TR_{HW}-LOGS)	0.037	yr^{-1}
Dead branch transfer (TR_{DEAD}-BR)	0.200	yr^{-1}
Dead coarse roots transfer (TR_{DEAD}-CR)	0.160	yr^{-1}
Dead fine roots transfer (TR_{DEAD}-FR)	0.160	yr^{-1}

Northwest (USA) (Smithwick 2002; Smithwick et al. 2002).

Simulation experiments

Disturbance regimes simulated by the model were defined by the type of disturbance (fire or harvest), the regularity of the disturbance interval (regular or random), the severity of the disturbance (low, moderate, or high levels of removal of dead stores), the interval between disturbance events (ranging from 25 to 250 years, in 25 year intervals), and in the case of harvests the longevity of C stores that were removed from the forest.

We examined two contrasting disturbances, typical of the Pacific Northwest forests: fire and harvest. In all cases, disturbances were catastrophic and all live pools were killed, although harvest transfers live woody pools from the ecosystem to the forest product pool. Fire regimes were defined by either low or high-severity fire events (Table 2). Harvest regimes were defined by the variation in C removal, the severity of site preparation fire and by forest product longevity (Table 3). Thus, these harvest scenarios represent fast-, intermediate-, and slow-turnover of C following harvest events. For example, the ‘‘fast-harvest’’ regime was defined by a high level of tree removal (100% of boles were removed), a severe site-preparation fire, and a forest product loss rate of 4%. There was a large transfer of C to the atmosphere following site preparation fire to forest products pools, and a relatively fast transfer of product pools to the atmosphere. In the ‘‘intermediate harvest’’ regime, only 50% of boles were removed, there was a moderate severity site-preparation fire, and forest products had a moderate longevity, decaying at 2% per year (Harmon et al. 1996). In the ‘‘slow-harvest’’ regimes, only 25% of the boles were removed and a low severity site-preparation fire was used; forest products decayed at 1% per year. We recognize that these disturbance regime characteristics are specific to Pacific Northwest forests, and may not capture the range of silvicultural options that are realized through limiting climatic, geographic, or socio-economic factors. The regimes were chosen to represent hypothetical disturbance scenarios that envelope the range of disturbance regimes for the area. Results should be extrapolated in relative, not absolute, terms when compared to other regions with different forests dynamics and silvicultural prescriptions.

Scaling from stands to landscapes

Rather than spatially track the stores and fluxes at multiple locations within a landscape for a short period of time, we calculated the stores of C

Table 2 Fire parameters used to define the amount of material transferred from live to dead pools and the amount of live and dead pools remaining after natural and site preparation fires

	Net % transfer to dead			% Remaining		
	High	Moderate	Low	High	Moderate	Low
Foliage	0	10	15	0	0	0
Sapwood	50	50	25	0	0	0
Heartwood	50	50	25	0	0	0
Heart-rot	10	50	25	0	0	0
Branch	50	25	25	0	0	0
Coarse root	50	25	0	0	0	0
Fine root	50	25	5	0	0	0
Dead Foliage	NA	NA	NA	0	50	75
Dead sapwood snags	NA	NA	NA	50	85	100
Dead sapwood logs	NA	NA	NA	10	75	95
Dead heartwood snags	NA	NA	NA	75	95	100
Dead heartwood logs	NA	NA	NA	50	90	100
Dead branch	NA	NA	NA	0	50	75
Dead coarse roots	NA	NA	NA	50	100	100
Dead fine roots	NA	NA	NA	0	75	100
Stable foliage	NA	NA	NA	5	50	100
Stable wood	NA	NA	NA	5	50	100
Stable soil	NA	NA	NA	100	100	100

Table 3 Parameters for harvest regimes defining the amount of aboveground mass taken off-site following harvest, the intensity of site preparation fire, and the longevity (manufacturing efficiency, decay rate) of forest products for fast, intermediate, and slow harvest regimes. Simulations were replicated with these parameters for all disturbance intervals (ranging from 25 to 250 years, in 25 year intervals) and for the regularity of the disturbance interval (random or regulated)

Interval	% Taken	Manufacturing efficiency	Forest Product decay rate	Fire Intensity
‘‘Slow’’ Harvest	25	50	0.01	Low
‘‘Intermediate’’ Harvest	50	50	0.02	Moderate
‘‘Fast’’ Harvest	100	50	0.04	High

within a single ‘‘stand’’ over a long period of time (10,000 years). Since long-term C dynamics exhibit little spatial interaction among stands (Smithwick et al. 2003), we subsampled 100 year segments of this extended time series to produce multiple, unique stand histories that would be present in a landscape. This can be thought of as a substitution of time for space. We allowed the simulations to run for 500 years to equilibrate the model and then used the remaining 9,500 years to provide a time series. We randomly selected multiple 100-year time-segments to represent stand histories within this long time-series. However, in the case of regular disturbance intervals, we also examined the special case in which all age-classes are equally represented in the landscape, i.e., a regulated disturbance regime. The total C store of all stands was averaged each year to determine temporal changes in mean landscape C store. Annual values of landscape NECB were determined from the net change in landscape C stores, and for a given disturbance regime, NECB was the average value over the 100-year period. We also explored how the choice of the number of unique stand histories present in the landscape (1, 5, 10, 50, 100, or 200) affected NECB estimates.

Because landscapes represent a combination of multiple disturbance events, the area of each stand in the landscape need not be of equal size. To assess the influence of the effect of evenness of stand size, we applied several forms of weightings to the multiple 100-year segments: equal, negative exponential or geometric to simulate three general types of hypothetical landscape structures. By definition, forests managed in a ‘‘regulated’’ disturbance regime are represented by an equal distribution of age-classes on the landscape; the same stand area is available for harvest each year and stands are never older than the disturbance interval. Equal weighting represents the simplest case in which stands are equally represented on the landscape. The negative exponential distribution is commonly used in the literature to explore the recurrence of natural disturbance events (i.e., fire) on a landscape (Van Wagner 1978; Johnson and Van Wagner 1985; Johnson and Gutsell 1994). Thus, a Poisson ‘‘random’’ process is used to represent an unregulated disturbance regime. The mean of the randomly selected values represents the disturbance interval that is specified by the user. Therefore, the same mean disturbance interval will result in a different distribution of stand ages for regulated versus random (Poisson) regimes. The Poisson random process will result in lower frequency of larger disturbances; most stands on the landscape will be small in area, although stands may survive past the mean disturbance interval due to the random nature of disturbances. Intermediate between these cases, we also simulated a geometric weighting (by squaring the segment number); in this case, small stands are more common on the landscape than large stands, but the distribution is more evenly distributed compared to the negative exponential distribution. We simulated a total of 300 hypothetical landscape structures resulting from unique disturbance regimes and landscape weighting functions.

Results

Stand level patterns in C storage and NECB over time

Temporal changes at the stand level can be examined by looking at the year-to-year changes in total C storage and NECB. Using harvests as an example, we compared patterns between regular and random disturbance intervals for a 1,000 year segment (Figure 3). For both regular and random harvest regimes, total C storage gradually and monotonically increased through time following a harvest event (Figure 3a). When averaged through the last 9,500 years of the simulation (ignoring the first 500 years for the model to equilibrate), total C storage was higher for the random compared to regular disturbance interval. This is as one would expect since random disturbance regimes modeled with a Poisson frequency distribution allow some stands to persist on the landscape for longer periods of time allowing them to reach higher total C stores for longer periods than regular disturbance intervals. Moreover, random and regular harvest events tended to reduce C stores regardless of the disturbance regularity.

As expected, NECB was negative following harvest events, but the simulated stands quickly transitioned from a net source to a net sink (Figure 3b). Although stands generally persisted as a net C sink until the next harvest event, NECB became less positive through time, approaching zero. In fact, average stand NECB the last 9,500 years of each simulation was not significantly different from zero. Regulated harvests with equal weighting in space and time had no random element in these simulations, thus long-term NECB was essentially zero ($2.1\ e^{-7}$ ± 0.76 Mg C ha^{-1} yr^{-1}). Long-term NECB for random harvests was also not significantly different than zero (–0.017 ± 0.65 Mg C ha^{-1} yr^{-1}).

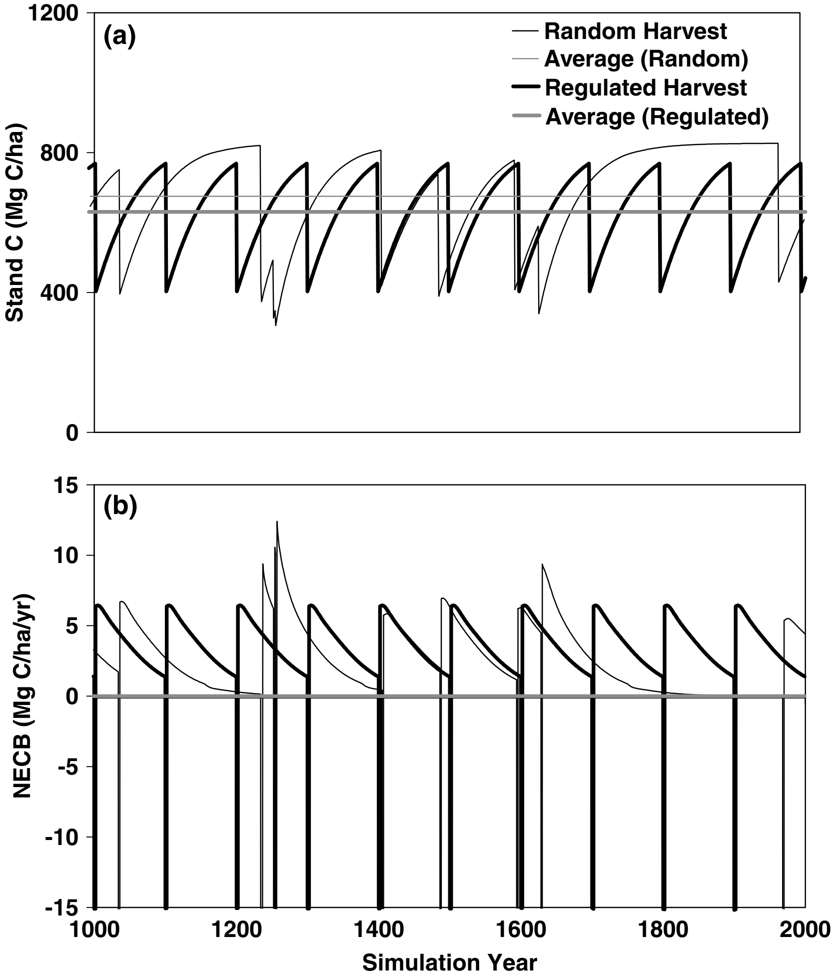


Fig. 3 Annual variation in (**a**) carbon stores (Mg C ha^{-1}) and (**b**) NECB (Mg C ha^{-1} yr^{-1}) for random and regulated harvest disturbances between years 1,000 and 2,000 of the model simulation, plotted with the average values across the entire 9,500 years. Only 1,000 years of the simulation, representative of the entire 10,000 years of simulation results, are presented here for clarity. Results shown are for ''fast'' harvests with a 100-year harvest interval (the *mean* rotation interval for random harvests)

Scaling from stands to landscapes

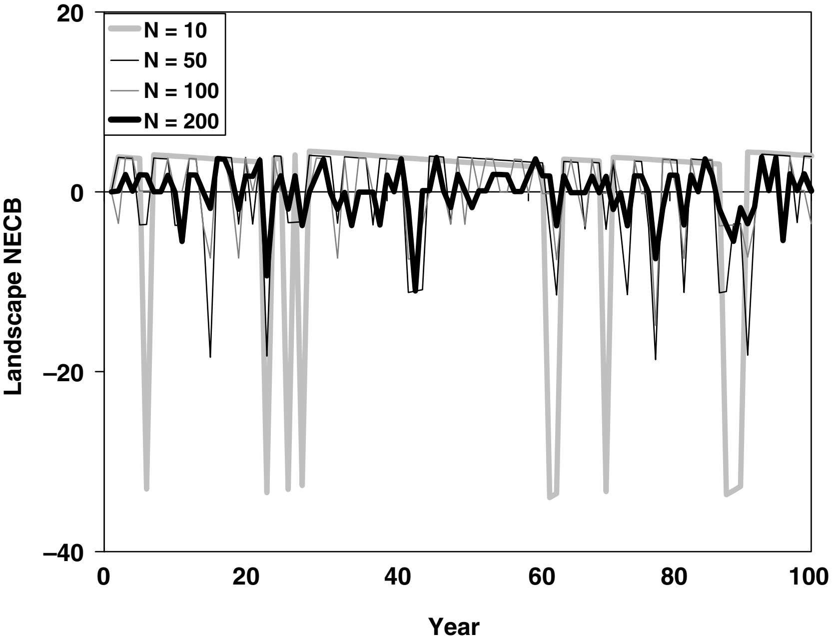
Variability in landscape NECB was strongly affected by the number of stands simulated in the landscape. As the number of stands increased from 10 to 200, the year-to-year variability in landscape NECB decreased (Figure 4). Specifically, for landscapes comprised of 10, 50, 100, and 200 stands the standard error of landscape NECB was 1.13, 0.60, 0.39, and 0.28 Mg C ha^{-1} yr^{-1}, respectively. Thus, as the number of segments (“stands”) in our simulated landscapes increased, variability in landscape NECB decreased.

To compare year-to-year variation of NECB in a stand ($N = 1$) to a landscape comprised of 200 stands ($N = 200$), we randomly selected one 100-year segment from the 9,500-year simulation to represent a typical stand history. Across the 100 years, the range of NECB for the stand was greater than that of the landscape (Figure 5a). Although the long-term average for both the stand and landscape NECB were not significantly different than zero (Figure 5b), the year-to-year variation around the mean was greater for stand NECB than landscape NECB regardless of the type of stand area weightings used to construct landscapes. Specifically, one standard error for stand NECB was 3.7 Mg C ha^{-1} yr^{-1}. In contrast, standard error for landscape NECB ranged from 0.19 Mg C ha^{-1} yr^{-1} for equal landscape structures to 0.31 Mg C ha^{-1} yr^{-1} for negative exponential landscape structures.

Disturbance interval and severity

Average total C storage increased as the interval between disturbances increased in accordance with our initial hypothesis (Figure 6). The increase was monotonic and nonlinear for both fires and harvests at all levels of severity. The highest total C storage (765 Mg C ha^{-1}) was observed in the 250-year rotation. For both regulated and random harvests, the “fast” systems stored >100 Mg C ha^{-1} less than the “slow” systems when harvests occurred with a 25-year interval but the difference was ~10 Mg C ha^{-1} when the disturbance interval was lengthened to 175 years, and was 0 Mg C ha^{-1} at 250-year intervals (Figure 6a). In general, the landscape stored less C when harvests involved high tree removal to forest products and had high severity site preparation fires and when forest product longevities were short. However, these differences in C turnover in harvest regimes were less important as the disturbance interval increased, i.e., C storage in the forest ecosystem increasingly

Fig. 4 Annual variation in NECB (Mg C ha^{-1} yr^{-1}) for a landscape comprised of 10, 50,100, or 200 stands



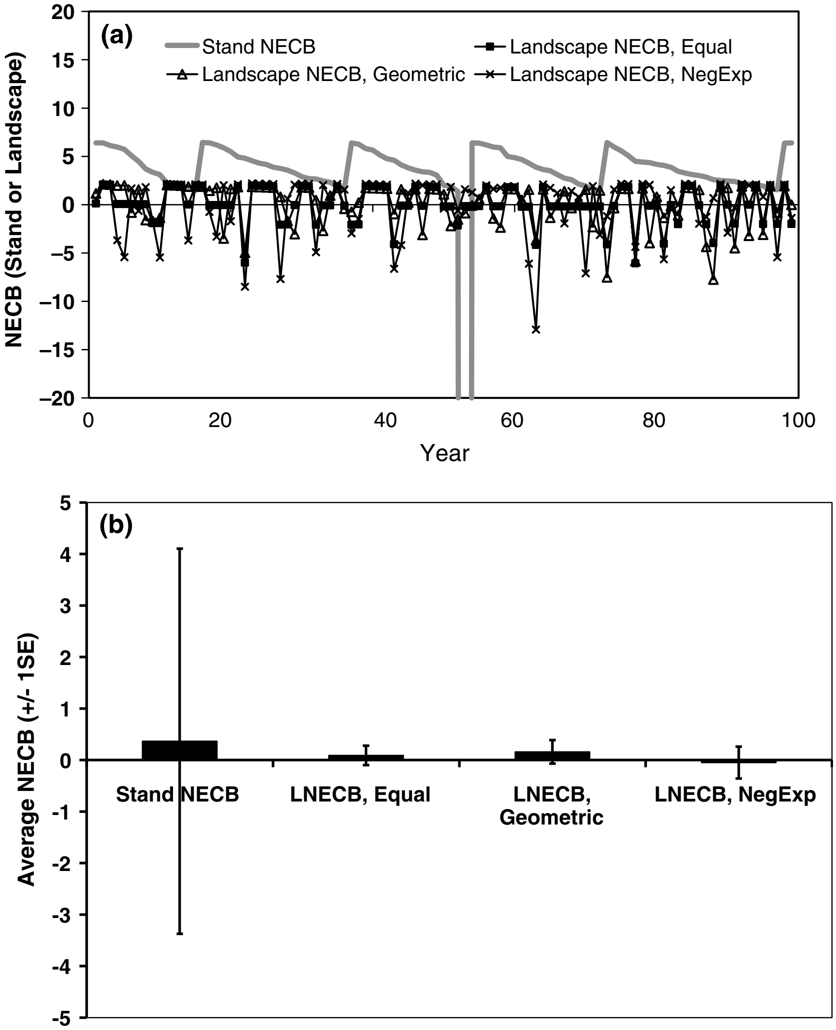


Fig. 5 (**a**) Annual variation in NECB (Mg C ha^{-1} yr^{-1}) for a stand and landscape (LNECB). Stand NECB values represent one 100-year segment from the last 9,500 years of the model simulation whereas LNECB values represent the average of 200 100-year segments, with equal weighting. (**b**) Average stand NECB (for the last 9,500 years of the simulation) and LNECB (equal, geometric, and negative exponential stand area weighting) ± one standard error. Results shown are for "fast" harvests with a 100-year harvest interval (the *mean* rotation interval for random harvests)

compensated for the differential effects of harvest severities. Not surprisingly, the difference between hot and light fires was less for harvests since the latter also included the fate of forest products. However, the differences ranged from 5 to 24 Mg C ha^{-1} for random fires and from 5 to 40 Mg C ha^{-1} for regulated fires. As for harvests, these differences decreased as disturbance intervals were lengthened.

Given our parameterization, the maximum total C stores would be 826 Mg C ha^{-1} in the absence of fires and harvests; thus disturbance intervals longer than 250 years would result in further increases in total C stores. The reduction in total C stores decreased from the maximum as a negative exponential function of mean disturbance interval (Figure 7). The largest reduction in C storage from the maximum was with the shortest return interval (25 years), when C storage for regulated, low-severity fire regimes was only 58% that of the maximum (Figure 7a). As the average interval between disturbances exceeded 100 years, the reductions in total C storage, expressed as a fraction maximum, was less than 25%. Even beyond 100 years, reductions in C storage were generally 10% lower than maximum C storage for a non-disturbance scenario. Although the reductions were small in relative terms, a 10% change in total C storage translates into a net loss of ~83 Mg C ha^{-1}. Thus, even relatively small relative reductions may translate into substantial decreases in absolute total C storage. Generally, regulated disturbances showed greater sensitivities to changes in the

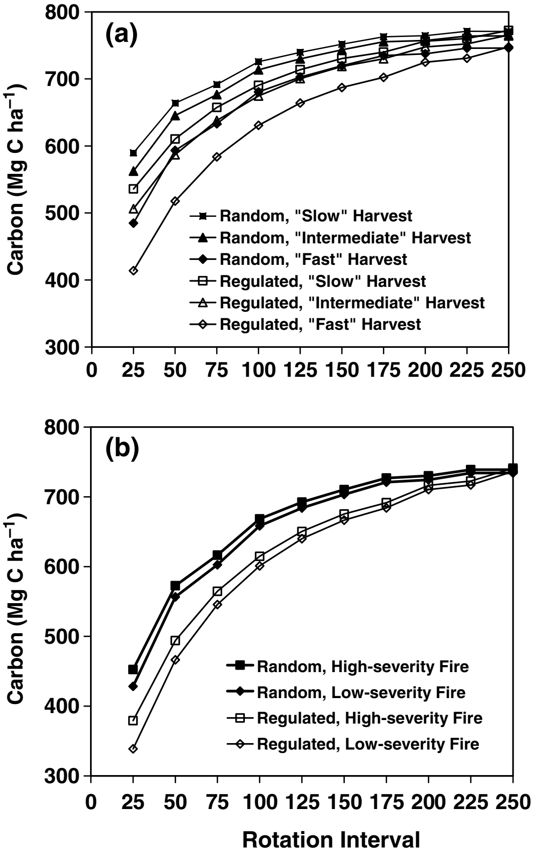


Fig. 6 Average landscape total carbon storage (Mg C ha^{-1}) for disturbance intervals between 25 and 250 years for (**a**) harvests (“fast”, “intermediate” and “slow” harvests, random or regular) and (**b**) fires (high and low severity, random or regular)

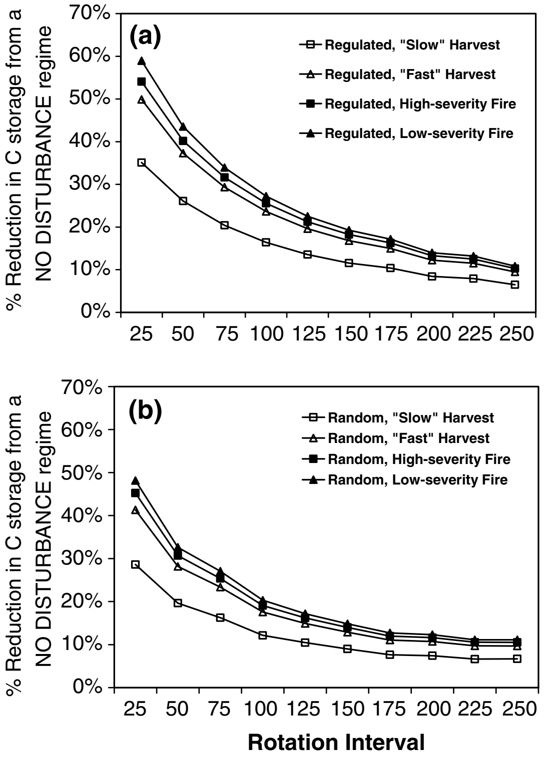


Fig. 7 Percent reduction in total landscape C storage from landscapes with a no-disturbance scenario (maximum C storage) to landscapes with disturbance intervals ranging from 25 to 250 years for (**a**) regulated fire and harvest regimes, and (**b**) random fire and harvest regimes

rotation interval, with greater reductions in total C storage from the maximum compared to random disturbance intervals (Figure 7b).

In contrast to total C storage, average landscape NECB was not statistically different from the theoretical value of zero for any of the simulated disturbance regimes and did not show consistent changes with disturbance interval length, regularity, or severity. However, variability of NECB (measured as the standard deviation around the mean) varied with disturbance interval and severity. For all simulations, year-to-year variability in landscape NECB decreased with increasing disturbance intervals (i.e., decreasing disturbance frequency) (Figure 8). Disturbance severity also affected the year-to-year variability of NECB but was different for harvests and fires. “Fast” harvest systems had greater overall variability than “slow” harvest systems. There was also greater reduction in variability with increasing interval for “fast” compared to “slow” harvest systems (Figure 8a). In contrast, high- and low-severity fires were similar to each other, but high-severity fires were less variable than low-intensity fires (Figure 8b).

Discussion

NEP is calculated as the balance of gross primary productivity minus ecosystem respiration. Over the short-term, physiological controls may directly affect NEP. However, this strictly physiological perspective of C dynamics limits the ability to directly account for land use changes on the C budget (Pacala et al. 2001), which may be between 40% and 98% of the C sink in Northern

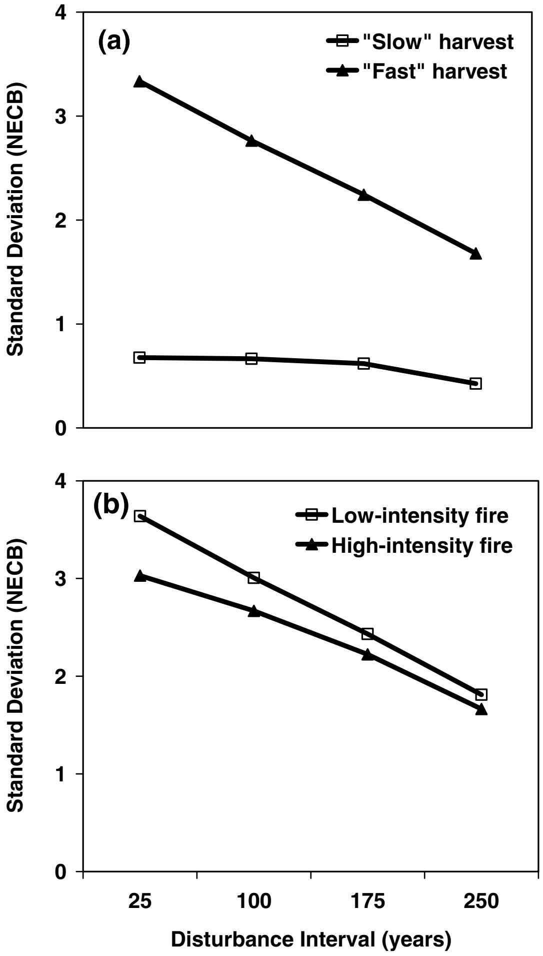


Fig. 8 Standard deviation of landscape NECB (± 1 standard deviation from the mean) for (**a**) harvest ("fast" or "slow") and (**b**) fire (high or low severity) regimes. Results shown are for regulated regimes with equal stand weighting

latitudes (Houghton 2003). When other fluxes, such as export and import, are considered then NECB is the preferred concept to use (Chapin III et al. in press). Changes in land use and the effects of disturbances are best examined at regional scales over long time periods, necessitating the use of ecosystem simulation models to assess their importance (Schimel et al. 1997). In this paper, we developed a model that can explicitly track changes in total C storage and NECB in a hypothetical landscape. In so doing, we were able to systematically explore the importance of different elements of disturbance regimes (frequency, severity, type) on landscape C dynamics.

There are several obvious limitations to our model simulations. First, growth, respiration, non-disturbance mortality and decomposition rate-constants were not changed by disturbances and were assumed constant over succession. While our approach is similar to many others, these parameters can change over succession affecting NECB at the stand level (Law et al. 2000; Wirth et al. 2002; Bond-Lamberty et al. 2004). However, this assumption is unlikely to influence our general conclusions concerning differences in C dynamics introduced by spatial scale, specifically the change in behavior as one transitions from stands to a landscape. Second, we did not estimate charcoal or other related long-term C sinks following fire, which might have contributed to a positive NECB over a stand's history (Kuhlbusch et al. 1996; Zackrisson et al. 2003). While, our approach overestimated the C loss caused by fire, charcoal represents a very small fraction of total C stores in most forests. Third, nutrient dynamics were not included in our model. Losses of nitrogen and other nutrients by severe fires (Raison 1979; Smithwick et al. 2005) could decrease productivity and potentially decrease long-term total C storage (Sun et al. 2004), although increased frequency of fires could shift the proportion of younger stands on the landscape potentially increasing nutrient availability and productivity (Peng and Apps 1999). Thus, the balance of severity versus frequency may alter mean landscape C stores in ways that we were unable to predict. Finally, we modeled very simple theoretical landscapes that had one disturbance regime, whereas in reality landscapes may be a combination of different disturbance regimes and types. Given the very local spatial interaction of stands regarding long-term C dynamics (Smithwick et al. 2003), it is likely that total C stores in mixed disturbance regimes can be approximated by a linear combination of the regimes present in the landscape. Spatial interactions among patches are likely to be important for patch sizes that are very small (< 100 m) but may result in potential errors of < 5% for typical patch sizes of harvests and fires (Smithwick et al. 2003). Thus, we expect our assumption of limited spatial interaction is reasonable across broad spatial scales. Moreover, it is likely that if each disturbance regime is repeated, the overall NECB would be approximately zero for any combination.

In a recent paper, Euskirchen et al. (2002) showed that landscape NECB varies with ecosystem type and ages within a landscape. Our paper is similar to that of Euskirchen et al. (2002) in that we provide one of the first estimates of landscape NECB as a function of disturbance regimes and stand age. However, Euskirchen et al. (2002) approximated temporal trends in stand-level NECB using a predefined function. Predictions of this function are summed for individual stands with landscapes to provide an overall estimate of NECB for a variety of ecosystem mosaics within landscapes. A shortcoming of this approach is that variation in NECB with stand age is often not known a priori. In contrast, we do not constrain NECB a priori, but NECB is calculated from our model from the net change in C stores between years which allows for a more flexible approach to simulating stand-level NECB. In our study, as more and more stands were included in the landscape, NECB approached zero, consistent with our initial hypothesis. Thus, in contrast to the results of Euskirchen et al. (2002), we conclude that disturbance regimes do not result in landscape-scale NECB different than zero as long as there are sufficient number of stands in the landscape to capture the ''equilibrium'' dynamics of a disturbance regime over the long term. Several factors might lead to the consistent positive values of NECB predicted by (Euskirchen et al. 2002), but the most likely is that the C gain phases of succession were not offset by the loss phases of succession. In our simulations, these two phases of NECB balanced over the long-term even for disturbances with random disturbance intervals. The cyclical temporal pattern predicted by (Euskirchen et al. 2002) is also puzzling, but could occur if a few stand histories influence the overall landscape or if there is an alternation between disturbance regimes.

The increase in total C stores as the mean disturbance interval increased has been found in other studies (Kurz et al. 1997–1998; Harmon and Marks 2002; Thornley and Cannell 2004). Thornley and Cannell (2004) showed that reductions in fire intervals from 500 to 100 years halved C storage. Our simulations showed a slightly less severe effect, as we would need to reduce the interval to 25 years to see a 50% reduction in C stores. Harmon and Marks (2002) also found that total C stores increased as the interval between regulated disturbances increased and as the removal of dead C by fire following harvest decreased. The shape of these curves are generally the complement to a negative exponential function of disturbance interval, with an asymptotic value approaching the average C stores found in old forest stands as the disturbance interval approaches infinity. This asymptotic value is the same regardless of disturbance severity, regularity of the disturbance interval, or the type of disturbance and can be thought of as being defined by the physiological limits of the ecosystem type. Disturbances therefore reduce the C store below what would be predicted from strictly physiological controls.

Although our results indicate that over the long-term NECB will approximate zero if a disturbance regime is relatively constant, it does not mean that NECB is always zero for all landscapes. NECB should be consistently positive for a period if a disturbance regime with a short interval is replaced by one with a longer mean disturbance interval. An example of this change would be fire exclusion in the western United States. Conversely shortening the mean interval between disturbances should lead to a consistently negative NECB for a period. This might also be typical of a region undergoing conversion of native forests to short-rotation forestry or agriculture (e.g., Apps et al. 2000). Kurz et al. (1997–1998) showed that conversion from a natural to managed disturbance regime resulted in a reduction of 58–101% of C stores. A similar change will occur if the disturbance interval remains constant and severity increases. Regardless of the change in disturbance regime, our simulations indicate that eventually the NECB will approach zero as long as the new disturbance regime becomes relatively stable in terms of severity and mean interval between disturbances. Further examination of the time required to reach the new mean landscape C stores needs to be undertaken for theoretical as well as real landscapes. This will increase our ability to predict how long regions undergoing changes in disturbance regime will remain C sources or sinks.

It has long been recognized that concepts of landscape equilibrium must incorporate disturbance (Turner et al. 1993). Concepts of patch mosaics (Watt 1947) or shifting mosaic steady-state (Bormann and Likens 1979) were developed to incorporate disturbances into general ideas of landscape stability. Further work showed that the degree of stability is dependent on the spatial extent of the landscape relative to the size of the disturbance event (Shugart and West 1981; Romme and Knight 1982; Baker 1989). The ratio of these terms was used by Turner et al. (1993) to define a spatial parameter controlling landscape stability. Our results are consistent with the Turner et al. (1993) analysis of the spatial parameter in that NECB for landscapes comprised of at least 50 stands was close to zero. Here we showed that predictions of average landscape C storage were more stable when more segments (stand histories) were selected. Moreover, the year-to-year variability in NECB decreased as the number of stands present in a landscape increased. Turner et al. (1993) further proposed that landscape stability depends on a temporal parameter, defined as the ratio of disturbance interval to recovery time. Although we did not vary the time of recovery in our simulations, the observation that variation in NECB decreased as mean disturbance interval increased is consistent with the Turner et al. (1993) analysis of the temporal parameter. Over short temporal scales, one would expect fluctuations in NECB due to changes in C stores, but if the landscape is in equilibrium with its disturbance regime and climate, these variations should average out over longer temporal scales. It follows, then, that if there is a consistent drift with NECB over time, or if NECB shows consistent dynamics (e.g., cyclic patterns), the landscape may be experiencing non-equilibrium conditions, making general predictions difficult.

Despite these conceptual foundations, there exists considerable uncertainty about the temporal and spatial variability of regional C storage and NECB, particularly about the role of land use change and natural disturbances (Schimel et al. 2001). Many broad-scale models include physiologically-based controls, but due the local nature of most disturbances the latter is usually not included. This is particularly challenging if the effects of individual disturbances are to be estimated. Importantly, our results show that by using the concept of a disturbance regime, it is possible to predict changes in C storage and/or its variability in disturbed landscapes. This would allow one to efficiently include disturbance effects at a broad-scale by adjusting physiologically based estimates of C stores downward (given that physiologically based models tacitly assume an infinitely long disturbance interval). The ability to implement this new strategy will depend on decreasing uncertainties in disturbance regime characteristics for many regions, especially the spatial distribution and frequency of disturbance events and rates of recovery (Houghton 2003).

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Appendix A

Equations in the disturbance model to calculate the C pool size of live, dead, and stable pools.

In general, C pools equal input minus output fluxes at each time-step:

$$\mathrm{C_{POOL}}(t) = \mathrm{C_{POOL}}(t-1) + \Sigma\ \mathrm{Input_{POOL}}(t) - \Sigma\ \mathrm{Output_{POOL}}(t) \tag{1}$$

a. $\Sigma\mathrm{Output_{POOL}}(t) = \Sigma\mathrm{Loss_{POOL}}(t) + \Sigma\ \mathrm{TR_{POOL}}(t)$

b. $\Sigma\ \mathrm{Input_{POOL}}(t) = \Sigma\ \mathrm{TR_{POOL}}(t)$

Live Pools

An exception to Eq. (1) is the calculation of foliage C ($\mathrm{C_{FOL}}$):

$$\mathrm{C_{FR}}(t) = \mathrm{C_{FOL}}(t)^{*}\mathbf{FR : FOL} \tag{2}$$

All live pools transfer C to their corresponding dead pool because of tree mortality:

$$\mathrm{M}_{\mathrm{LIVE\ POOL}}(\mathrm{t}) = \mathrm{C}_{\mathrm{LIVE\ POOL}}(t-1)^{*}\mathbf{M}_{\mathbf{LIVE\ POOL}} \tag{3}$$

Additionally, fine root and foliage pools transfer C to dead pools via turnover:

$$\Sigma\ \mathrm{TR}_{\mathrm{POOL}}(t) =\ \mathrm{TU}_{\mathrm{POOL}}(t) + \mathrm{M}_{\mathrm{POOL}}(t) \tag{4}$$

a. $\mathrm{TU}_{\mathrm{POOL}}(t) = \mathrm{C}_{\mathrm{POOL}}(t)^{*}\mathbf{TU}_{\mathbf{POOL}}$

The SW, HR, BR, and CR pools lose C via respiration:

$$\Sigma\ \mathrm{Loss}_{\mathrm{POOL}}(t) = \mathrm{R}_{\mathrm{POOL}}(t) \tag{5}$$

a. $\mathrm{R}_{\mathrm{POOL}}(t) = \mathrm{C}_{\mathrm{POOL}}(t-1)^{*}\mathbf{R}_{\mathbf{POOL}}$

Allocation of C to sapwood is proportional to foliage C:

$$\Sigma\ \mathrm{Input}_{\mathrm{SW}}(t) = \mathrm{C}_{\mathrm{FOL}}(t)^{*}\mathbf{BGE}, \tag{6}$$

Sapwood transfers C to heartwood via mortality and HW formation:

$$\Sigma\ \mathrm{TR}_{\mathrm{SW}}(t) = \mathrm{F}_{\mathrm{HW}}(t) + \mathrm{M}_{\mathrm{SW}}(t) \tag{7}$$

a. $\mathrm{F}_{\mathrm{HW}}(t) = \mathrm{C}_{\mathrm{SW}}(t-1)^{*}\mathbf{F}_{\mathbf{HW}}$

$$\Sigma \mathrm{Input}_{\mathrm{HW}}(t) = \mathrm{F}_{\mathrm{HW}}(t) \tag{8}$$

Heartwood transfers C to heart rot via mortality and HR formation:

$$\Sigma\ \mathrm{TR}_{\mathrm{HW}}(t) = \mathrm{F}_{\mathrm{HR}}(t) + \mathrm{M}_{\mathrm{HW}}(t) \tag{9}$$

a. $\mathrm{F}_{\mathrm{HR}}(t) = \mathrm{C}_{\mathrm{HW}}(t-1)^{*}\mathbf{F}_{\mathbf{HR}}$

$$\Sigma\ \mathrm{Input}_{\mathrm{HR}}(t) = \mathrm{F}_{\mathrm{HR}}(t) \tag{10}$$

BR and CR input is proportional to SW input:

$$\Sigma\ \mathrm{Input}_{POOL}(t) = \Sigma\ \mathrm{Input}_{\mathrm{SW}}(t)^{*}\mathbf{POOL : BOLE} \tag{11}$$

CR and BR transfers C to dead pools via mortality and pruning:

$$\Sigma \mathrm{Output}_{\mathrm{POOL}}(t) = \mathrm{M}_{\mathrm{POOL}}(t) + \mathrm{P}_{\mathrm{POOL}}(t) \tag{12}$$

a. $\mathrm{P}_{\mathrm{POOL}}(t) = \mathrm{C}_{\mathrm{POOL}}(t-1)^{*}\mathbf{P}_{\mathbf{POOL}}$

Dead Pools

Dead pools (except dead HW) receive C from their corresponding live pool:

$$\Sigma\ \mathrm{Input}_{\mathrm{DEAD-POOL}}(t) = \Sigma\ \mathrm{TR}_{\mathrm{POOL}}(t) \tag{13}$$

Dead HW receives C from HW and HR:

$$\Sigma \mathrm{Input}_{\mathrm{DEAD-HW}}(t) = \Sigma\ \mathrm{TR}_{\mathrm{HW}}(t) + \Sigma \mathrm{TR}_{\mathrm{HR}}(t) \tag{14}$$

Dead boles are separated into snags and logs. Logs receive C from snags due to snag fall:

$$\begin{aligned}&\Sigma \mathrm{Input}_{\mathrm{POOL-SNAGS}}(t)\\ &\quad = \Sigma \mathrm{Input}_{\mathrm{DEAD-POOL}}(t)^{*}\%\mathbf{Snags}\end{aligned} \tag{15}$$

$$\begin{aligned}&\Sigma\ \mathrm{Input}_{\mathrm{POOL-LOGS}}(t)\\ &\quad = (\Sigma\ \mathrm{Input}_{\mathrm{DEAD-POOL}}(t)\\ &\qquad - \Sigma\ \mathrm{Input}_{\mathrm{POOL-SNAGS}}(t))\\ &\qquad + \Sigma\ \mathrm{TR}_{\mathrm{POOL-SNAGS}}(t)\end{aligned} \tag{16}$$

a. $\Sigma \mathrm{TR}_{\mathrm{POOL-SNAGS}}(t)$
$\quad = \mathrm{C}_{\mathrm{POOL-SNAGS}}(t-1)^{*}\mathbf{FA}_{POOL}$

C lost via decomposition $(\mathrm{D}_{\text{DEAD-POOL}})_{t}$ is calculated from the pool's decay rate, a weighted average of the pool's existing decay rate and the decay rate associated with its input flux (**D**).

$$\Sigma\ \mathrm{Loss}_{\mathrm{DEAD-POOL}}(t) = \mathrm{D}_{\mathrm{DEAD-POOL}}(t) \tag{17}$$

a. $\mathrm{D}_{\mathrm{DEAD-POOL}}(t)$
$\quad = \mathrm{C}_{\mathrm{DEAD-POOL}}(t-1)^{*}\mathrm{DR}_{\mathrm{DEAD-POOL}}(t)$

b. $\mathrm{DR}_{\mathrm{DEAD-POOL}}(t)$
$= \text{weighted-avg}(\mathrm{DR}_{\mathrm{DEAD-POOL}}(t-1),$
$\quad \mathrm{C}_{\mathrm{DEAD-POOL}}(t-1),$
$\quad \mathbf{D}_{\mathbf{DEAD-POOL}}, \Sigma\ \mathrm{Input}_{\mathrm{DEAD-POOL}}(t))$

c. $\text{weighted-avg}(\text{rate}_1, \text{mass}_1, \text{rate}_2, \text{mass}_2) = (\text{rate}_1^{*}\text{mass}_1 + \text{rate}_2^{*}\text{mass}_2)/(\text{mass}_1 + \text{mass}_2)$

The input decay rate of SW or HW is used for snag and log pools:

$$\mathbf{D}_{\mathbf{POOL-SNAGS}} = \mathbf{D}_{\mathbf{POOL-LOGS}} = \mathbf{D}_{\mathbf{DEAD-POOL}} \tag{18}$$

The non-bole dead pools and the log pools transfer C to the stable pools:

$$\Sigma \mathrm{TR}_{\mathrm{DEAD-POOL}}(t) = \mathrm{C}_{\mathrm{DEAD-POOL}}(t-1)^{*}\mathbf{TR}_{\mathrm{DEAD-POOL}}. \tag{19}$$

Stable Pools

Stable pools receive C from corresponding dead pools:

$$\Sigma \mathrm{Input}_{\mathrm{ST-FOL}}(t) = \Sigma\ \mathrm{TR}_{\mathrm{DEAD-FOL}}(t) \tag{20}$$

$$\Sigma\ \mathrm{Input}_{\mathrm{ST-WOOD}}(t) = \Sigma\ \mathrm{TR}_{\mathrm{SW-LOGS}}(t) + \Sigma\ \mathrm{TR}_{\mathrm{HW-LOGS}}(t) + \Sigma\ \mathrm{TR}_{\mathrm{DEAD-BR}}(t) \tag{21}$$

$$\Sigma\ \mathrm{Input}_{\mathrm{ST-SOIL}}(t) = \Sigma\ \mathrm{TR}_{\mathrm{DEAD-CR}}(t) + \Sigma\ \mathrm{TR}_{\mathrm{DEAD-FR}}(t) \tag{22}$$

and they lose C via decomposition:

$$\Sigma\ \mathrm{Loss}_{\mathrm{ST-POOL}}(t) = \mathrm{C}_{\mathrm{ST-POOL}}(t-1)^{*}\mathbf{D}_{\mathbf{ST-POOL}} \tag{23}$$

Appendix B

Pools are adjusted for disturbance after the annual calculations (Appendix A).

Harvest

Harvest events are catastrophic:

$$\mathrm{C}_{\mathrm{LIVE-POOL}}(t_{\mathrm{POST-HARVEST}}) = 0 \tag{1}$$

Live non-bole pools transfer C to dead pools:

$$\mathrm{C}_{\mathrm{DEAD-POOL}}(t_{\mathrm{POST-HARVEST}}) = \mathrm{C}_{\mathrm{DEAD-POOL}}(t) + \mathrm{CUT\_TR}_{\mathrm{POOL}}(t) \tag{2}$$

a. $\mathrm{CUT\_TR\_POOL}(t) = \mathrm{C}_{\mathrm{POOL}}(t).$

A user-specified portion of bole C is taken off site:

$$\mathrm{CUT\_TR}_{\mathrm{BOLE-POOL}}(t) = \mathrm{C}_{\mathrm{BOLE-POOL}}(t) - \mathrm{HARVEST\_TR}_{\mathrm{BOLE-POOL}}(t) \tag{3}$$

a. $\mathrm{HARVEST\_TR}_{\mathrm{BOLE-POOL}}(t) = \mathrm{C}_{\mathrm{BOLE-POOL}}(t)^{*}\%\mathbf{taken}.$

The portion remaining is transferred into the log pools:

$$\mathrm{C}_{\mathrm{SW-LOGS}}(t_{\mathrm{POST-HARVEST}}) = \mathrm{C}_{\mathrm{SW-LOGS}}(t) + \mathrm{CUT\_TR}_{\mathrm{SW}}(t) \tag{4}$$

$$\mathrm{C}_{\mathrm{HW-LOGS}}(t_{\mathrm{POST-HARVEST}}) = \mathrm{C}_{\mathrm{HW-LOGS}}(t) + \mathrm{CUT\_TR}_{\mathrm{HW}}(t) + \mathrm{CUT\_TR}_{\mathrm{HR}}(t) \tag{5}$$

Fire

If there is no harvest before the fire, then:

$$\mathrm{C}_{\mathrm{POOL}}(t_{\mathrm{PRE-FIRE}}) = \mathrm{C}_{\mathrm{POOL}}(t) \tag{6}$$

With harvest:

$$\mathrm{C}_{\mathrm{POOL}}(t_{\mathrm{PRE-FIRE}}) = \mathrm{C}_{\mathrm{POOL}}(t_{\mathrm{POST-HARVEST}}). \tag{7}$$

Fire events are catastrophic:

$$\mathrm{C}_{\mathrm{LIVE-POOL}}(t_{\mathrm{POST-FIRE}}) = 0 \tag{8}$$

Live pools transfer C to dead pools depending on fire intensity (low, moderate, or high).

$$\mathrm{BURN\_TR}_{\mathrm{LIVE-POOL}}(t) = \mathrm{C}_{\mathrm{LIVE-POOL}}(t_{\mathrm{PRE-FIRE}})^{*}\%\mathbf{transfer}_{\mathbf{fireintensity}} \tag{9}$$

The remaining amount is combusted:

$$\mathrm{BURN\_LOSS}_{\mathrm{LIVE-POOL}}(t) = C_{\mathrm{LIVE-POOL}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_TR}_{\mathrm{LIVE-POOL}}(t) \tag{10}$$

The amount of dead and stable pool C that remains is:

$$\mathrm{BURN\_LOSS}_{\mathrm{POOL}}(t) = C_{\mathrm{POOL}}(t_{\mathrm{PRE-FIRE}})^{*} (100\% - \textbf{\%remaining}_{\textbf{fire intensity}}). \tag{11}$$

Non-bole dead C is adjusted for the burn loss and transfer from the live pool:

$$C_{\mathrm{DEAD-POOL}}(t_{\mathrm{POST-FIRE}}) = C_{\mathrm{DEAD-POOL}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_LOSS}_{\mathrm{DEAD-POOL}}(t) + \mathrm{BURN\_TR}_{\mathrm{LIVE-POOL}}(t). \tag{12}$$

Transfers from live pools are added to dead bole pools:

$$C_{\mathrm{SW-SNAGS}}(t_{\mathrm{POST-FIRE}}) = C_{\mathrm{SW-SNAGS}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_LOSS}_{\mathrm{SW-SNAGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{SW-SNAGS}}(t) \tag{13}$$

$$C_{\mathrm{HW-SNAGS}}(t_{\mathrm{POST-FIRE}}) = C_{\mathrm{HW-SNAGS}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_LOSS}_{\mathrm{HW-SNAGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{HW-SNAGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{HR}}(t) \tag{14}$$

$$C_{\mathrm{SW-LOGS}}(t_{\mathrm{POST-FIRE}}) = C_{\mathrm{SW-LOGS}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_LOSS}_{\mathrm{SW-LOGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{SW-LOGS}}(t) \tag{15}$$

$$C_{\mathrm{HW-LOGS}}(t_{\mathrm{POST-FIRE}}) = C_{\mathrm{HW-LOGS}}(t_{\mathrm{PRE-FIRE}}) - \mathrm{BURN\_LOSS}_{\mathrm{HW-LOGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{HW-LOGS}}(t) + \mathrm{BURN\_TR}_{\mathrm{HR}}(t). \tag{16}$$

References

Apps MJ, Bhatti JS, Halliwell DH, Jiang H, Peng CH (2000) Simulated carbon dynamics in the boreal forest of central Canada under uniform and random disturbance regimes. In: Lal R, Kimble JM, Stewart BA (eds) Global climate change and cold regions ecosystems. Lewis Publishers, New York, pp 107–122

Baker WL (1989) Effect of scale and spatial heterogeneity on fire-interval distributions. Can J Forest Res 19:700–706

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Global Change Biol 10:473–487

Bormann FH, Likens GE (1979) Catastrophic disturbance and the steady state in northern hardwood forest. Am Sci 67:660–669

Chapin III FS, Woodwell GM, Randerson JT, Lovett GM, Rastetter EB, Baldocchi DD, Clark DA, Harmon ME, Schimel DS, Valentini R, Wirth C, Aber JD, Cole JJ, Goulden ML, Harden JW, Heimann M, Howarth RW, Matson PA, McGuire AD, Melillo JM, Mooney HA, Neff JC, Houghton RA, Pace ML, Ryan MG, Running SW, Sala OE, Schlesinger WH, Schulze E-D (in press) Reconciling carbon cycle terminology: a search for consensus. Ecosystems

Euskirchen ES, Chen J, Li H, Gustafson EJ, Crow TR (2002) Modeling landscape net ecosystem productivity (LandNEP) under alternate management regimes. Ecol Model 154:75–91

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biol 2:169–182

Harmon ME (2001) Carbon sequestration in forests. J Forest 99:24–29

Harmon ME, Domingo JB (2001) A user's guide to STANDCARB version 2.0: a model to simulate the carbon stores in forest stands. Department of Forest Science, Oregon State University, Corvallis, Oregon

Harmon ME, Harmon JM, Ferrell WK, Brooks D (1996) Modeling carbon stores in Oregon and Washington forest products: 1900–1992. Climatic Change 33:521–550

Harmon ME, Marks B (2002) Effects of silvicultural treatments on carbon stores in forest stands. Can J Forest Res 32:863–877

Houghton RA (1999) The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. Tellus 51B:298–313

Houghton RA (2003) Why are estimates of the terrestrial carbon balance so different? Global Change Biol 9:500–509

Janisch JE, Harmon ME (2002) Successional changes in live and dead wood stores: Implications for net ecosystem productivity. Tree Physiol 22:77–89

Johnson EA, Gutsell SL (1994) Fire frequency models, methods and interpretations. Adv Ecol Res 25:239–287

Johnson EA, Van Wagner CE (1985) The theory and use of two fire history models. Can J Forest Res 15:214–220

Kuhlbusch TAJ, Andreae MO, Cachier H, Goldammer JG, Lacaux J-P, Shea R, Crutzen PJ (1996) Black carbon formation by savanna fires: measurements and implications for the global carbon cycle. J Geophys Res 101:23, 651–623, 666

Kurz WA, Beukema SJ, Apps MJ (1997–1998) Carbon budget implications of the transition from natural to managed disturbance regimes in forest landscapes. Mitigat Adap Strat Global Change 2:405–421

Law BE, Turner D, Campbell J, Sun OJ, Van Tuyl S, Ritts WD, Cohen WB (2004) Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA. Global Change Biol 10:1429–1444

Law BE, Waring RH, Anthoni PM, Aber JD (2000) Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. Global Change Biol 6:155–168

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath LS, Sundquist E, Stallard R, Ciais P, Moorcroft PR, Casperson JP, Shevliakova E, Moore B, Kohlmaier G, Holland EA, Gloor M, Harmon ME, Fan S-M, Sarmiento J, Goodale CL, Schimel D, Field CB (2001) Consistent land- and atmosphere-based U.S. carbon sink estimates. Science 292:2316–2319

Peng C, Apps MJ (1999) Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. Ecol Model 122:175–193

Raison RJ (1979) Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51:73–108

Romme WH, Knight DH (1982) Landscape diversity: the concept applied to Yellowstone Park. Bioscience 32:664–670

Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore III B, Murdiyarso D, Noble I, Pacala SW, Prentice IC, Raupach MR, Rayner PJ, Scholes RJ, Steffen WL, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414:169–172

Schimel DS, VEMAP Participants, Braswell BH (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol Monogr 67:251–271

Shugart HH, West DC (1981) Long-term dynamics of forest ecosystems. Am Sci 69:647–652

Smithwick EAH (2002) Potential carbon storage at the landscape scale in the Pacific Northwest, USA Ph.D. Oregon State University, Corvallis, OR

Smithwick EAH, Harmon ME, Domingo JB (2003) Modeling multiscale effects of light limitations and edge-induced mortality on carbon stores in forest landscapes. Landscape Ecol 18:701–721

Smithwick EAH, Harmon ME, Remillard SM, Acker SA, Franklin JF (2002) Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecol Appl 12:1303–1317

Smithwick EAH, Turner MG, Mack MC, Chapin III FS (2005) Post-fire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems 8:163–181

Sun OJ, Campbell J, Law BE, Wolf V (2004) Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Global Change Biol 10:1470–1481

Tans PP, Fung IY, Takahashi T (1990) Observational constraints on the global atmospheric CO_2 budget. Science 247:1431–1438

Thornley JHM, Cannell MGR (2004) Long-term effects of fire frequency on carbon storage and productivity of boreal forests: a modeling study. Tree Physiol 24:765–773

Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK (1993) A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landscape Ecol 8:213–227

Van Wagner CE (1978) Age-class distribution and the forest fire cycle. Can J Forest Res 8:220–227

Watt AS (1947) Pattern and process in the plant community. J Ecol 35:1–22

Wirth C, Schulze E-D, Luhker B, Grigoriev S, Siry M, Hardes G, Ziegler W, Backor M, Bauer G, Vygodskaya NN (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. Plant Soil 242:41–63

Zackrisson O, Nilsson M-C, Wardle DA (2003) Key ecological function of charcoal from wildfire in the Boreal forest. Oikos 77:10–19