

Modeling landscape net ecosystem productivity (LandNEP) under alternative management regimes

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Abstract

Forests have been considered as a major carbon sink within the global carbon budget. However, a fragmented forest landscape varies significantly in its composition and age structure, and the amount of carbon sequestered at this level remains generally unknown to the scientific community. More precisely, the temporal dynamics and spatial distribution of net ecosystem productivity (NEP) in a mosaic are dependent on ecosystem type and the chronosequence of the ecosystem in the landscape. In this study, we developed a model, LandNEP, to follow the change in NEP by ecosystem and chronosequence. The model creates user-defined hypothetical landscape mosaics of ecosystem and age over a given number of simulation years. It then calculates NEP and biomass for each ecosystem and over the entire landscape based on a distribution function, and any disturbances that have occurred within a landscape at a given year. We simulated three different scenarios and a sensitivity analysis within a hypothetical landscape. Based on these scenarios, we were able to show that theoretically, timber harvest strategies requiring rotations that go beyond the time of an ecosystem's maximum NEP will ultimately yield the greatest cumulative NEP value. Furthermore, the sensitivity analysis demonstrated that increasing the disturbance interval could switch an ecosystem from acting as a net carbon source to acting as a net carbon sink. These results suggest that carbon losses within a managed forested landscape could be mitigated by permitting the ecosystem to reach its maximum as a net carbon sink before harvesting timber. Therefore, alternative management regimes play a leading role in determining to what extent a landscape sequesters carbon. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

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Undisturbed, mature forest ecosystems exhibit a net gain in carbon exchange with the atmo-

sphere while newly created or regenerating forests generally yield a net loss of carbon. These carbon fluxes represent net ecosystem productivity (NEP), and can be calculated by subtracting heterotrophic respiration (R_h) from net primary productivity (NPP; $NEP = NPP - R_h$). The magnitude of NEP of an ecosystem depends on its type, age, physical environment, latitude, and regional climate (Woodwell and Whittaker, 1968; Waring and Running, 1998; Buchmann and Schulze, 1999; Valentini et al., 2000).

Human-induced disturbances, particularly those associated with modifications in land-use, could have equal or more severe effects on ecosystem productivity than those physiological changes associated with climate and atmospheric composition (Tian et al., 1999; Schimel et al., 2000). Land use changes alter the fluxes of energy and materials, community composition, and its environment (Forman, 1995; Chen et al., 1999), and have subsequent impacts on atmospheric CO_2 concentrations if undertaken at sufficient temporal and spatial scales (Houghton et al., 1987; Chen et al., 2002). Likewise, many ecosystem models that focus primarily on physiological processes (e.g. photosynthesis) often exclude the dominant factor governing the rate of carbon loss in forests, namely land-use history (Caspersen et al., 2000).

Most field-based studies of NEP have focused on single-aged, mature or late-successional natural forested ecosystems (Buchmann and Schulze, 1999), and few have examined productivity over the longer term (i.e. centuries) at the landscape level. The CO_2 fluxes of a landscape depend on its composition; a landscape dominated by mature, late successional stands will likely act as a carbon sink, but one composed primarily of young stands (e.g. ≤ 25 years of age) may act as a source of carbon to the atmosphere (Schulze et al., 2000). Extremely low fluxes occur during stand establishment since CO_2 uptake through photosynthesis and CO_2 release from soil respiration (which is relatively high due to the decomposition of coarse woody debris left in the stand from the prior forest) represent fluxes in the opposite directions (Schulze et al., 2000; Valentini et al., 2000).

Understanding and managing productivity at the landscape level plays a vital role in cooperative international science and treaties such as the Kyoto Protocol (IPCC, 1994; IGBP, 1998). The average NEP and biomass accumulation of a landscape will differ under alternative management strategies that change the composition of the landscape. For example, replacing older stands by young stands could cause a significant amount of carbon loss to the atmosphere, and shortening the rotation length of a stand may cause a reduction in the landscape carbon pool (Schulze et al., 2000). Hence, a landscape can be managed for productivity and carbon sequestration from a spatial perspective because one may alter management strategies so that a landscape can sequester varying amounts of carbon.

Field-based studies of the NEP of a chronological sequence or successional pathway for a given ecosystem over time is difficult due to the long lifetime of forest trees, the expensive monitoring equipment required, and the inability of this instrumentation to take into account the spatial heterogeneity of the landscape (Bond and Franklin, 2002). However, with the aid of such tools as remote sensing imagery, the ecosystem composition and age structure of managed landscapes are usually known with good temporal and spatial resolution. In this context, we developed a computer-based model, LandNEP, which incorporates the ecosystem composition and age structure of a hypothetical landscape to illustrate how differing management strategies in space and over time (e.g. disturbance regimes) can result in varying levels of carbon fluxes and storage. We conducted our modeling efforts to demonstrate that:

1. The chronosequences of the ecosystems within a landscape mosaic can be used to determine the role of a landscape (i.e. source/sink) in contributing to atmospheric CO_2 during a given time period.
2. We can regulate the carbon flux of a forested landscape from a spatial perspective based on, (a) the NEP distribution functions followed by the ecosystems through succession; and (b) the management strategies applied to these ecosystems.

2. Model development and parameterization

LandNEP takes a modular, dynamic approach to the analysis of NEP of a chronosequence for each type of ecosystem in the landscape. The three modules of LandNEP consider, (1) spatial heterogeneity at the landscape level; (2) landscape dynamics; and (3) carbon flux. The information flow between modules is minimal to lessen their dependence. This permits the user to modify the landscape configuration variables and management strategies (e.g. proportion and age structure of each ecosystem within the landscape, or disturbance frequency intervals) while holding constant the NEP distribution curve of an ecosystem. The model is dynamic because it examines the effects of disturbance on NEP in the entire landscape over time.

2.1. LandNEP spatial heterogeneity module

The spatial heterogeneity module of LandNEP is developed as an extension of the generic LEE-MATH model, a decision support tool that balances the economic and ecological constraints of forest management (Li et al., 2000). This module creates a landscape mosaic of specified size with different degrees of heterogeneity in two controlling variables: ecosystem type and age. The components of ecosystem type include number of ecosystems and the proportions of each in the landscape. The age components consist of the minimum disturbance interval (i.e. rotation age, or the number of years between timber harvests) by ecosystem type and the mean age of each ecosystem. The output includes two landscape maps: ecosystem types and ages.

2.2. LandNEP landscape dynamics module

The landscape dynamics module takes as input the maps of ecosystem type and age produced by the landscape spatial heterogeneity module. It then creates simple landscape dynamics for NEP analysis with the above two variables. This module provides disturbance (e.g. harvests) under the following constraints: a maximum area to be disturbed (harvested) each year, a minimum age

(specified by ecosystem) where harvest is allowed (mindisturb), a must-disturb ecosystem age by type (defined as mindisturb * 1.2), and a time delay (equals 1 the year after disturbance, i.e. planting following clearcutting). Successional pathways of the ecosystems are not modeled, in part because the forest plantings are controlled, but also in the interest of model simplicity. The landscape mosaic containing the age of each ecosystem is exported to an external file at the end of each model simulation year, and each map is read into the carbon flux module (Section 2.3.2).

2.3. LandNEP carbon flux module

2.3.1. Modeling the NEP of an ecosystem over time

Landscape-level analysis often requires a simplified, parameter-scarce approach to modeling the ecosystems within the landscape (Levin, 1992). Therefore the carbon flux model does not explicitly model the variables that control the dynamics of NEP (e.g. NPP and R_h), but takes an analytical approach to examining the NEP of an ecosystem over a given number of stand development years. We divide the change of NEP over time (Fig. 1) into four phases along a curve:

- (I) $t(\text{NEP}_{\min})$, the time at which the minimum NEP (NEP_{\min}) value is attained
- (II) $t(\text{NEP}_{\min}) + 1$ to $t(\text{NEP}_{\max})$, from the year following NEP_{\min} to the time at which the maximum NEP (NEP_{\max}) value is attained
- (III) $t(\text{NEP}_{\max}) + 1$ to $t(\text{NEP}_{\text{steady}})$, from the year following NEP_{\max} to the time at which the steady-state NEP ($\text{NEP}_{\text{steady}}$) value is attained
- (IV) $t(\text{NEP}_{\text{steady}}) + i$, from the year following $\text{NEP}_{\text{steady}}$ to all i years beyond this point.

Phase I (NEP_{\min}) occurs in the first year after a disturbance (e.g. timber harvest), which leaves a large amount of woody debris at the site. During this period, the leaf area of a forested stand is at a minimum resulting in little photosynthetic carbon fixation, and a low value of net primary production (NPP; Barnes et al., 1998). Furthermore, there is a high decomposition rate of woody debris, damaged roots, and other organic matter

from the previous ecosystem causing heterotrophic respiration (R_h) to reach a maximum (Waring and Running, 1998). These factors force the ecosystem to act as a net carbon source to the atmosphere (i.e. negative NEP) and attain NEP_{min} (Fig. 1).

Phase II begins the year following $t(NEP_{min})$ and ends at $t(NEP_{max})$. At the beginning of Phase II, the carbon flux remains negative for several years as carbon exports from R_h are continually higher than photosynthetic carbon uptake. However, as the stand ages and Phase II continues, leaf area increases, thereby augmenting photosynthetic carbon uptake and NPP. R_h begins to decrease since much of the organic matter left from the previous ecosystem has become decomposed (Janisch and Harmon 2002; Valentini et al., 2000). Eventually, the ecosystem reaches a point of being neither a sink nor source ($NPP = R_h$; NEP_0 in Fig. 1; Waring and Running 1998; Barnes et al.,

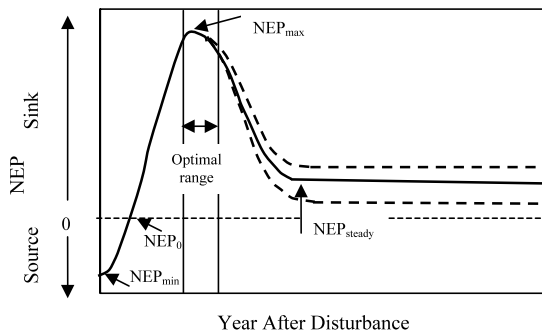


Fig. 1. Four points along a curve (NEP_{min} , NEP_0 , NEP_{max} , and NEP_{steady}) are used to model the four phases of NEP of an ecosystem over a selected number of simulated ecosystem development years. Immediately following a disturbance, the ecosystem attains its minimum value as a carbon source (i.e. negative NEP; NEP_{min}). Eventually, as the system grows towards maturity it switches to a carbon sink (i.e. positive NEP; NEP_0) and reaches a point of maximum carbon sequestration (NEP_{max}). Assuming constant conditions within the ecosystem, a steady-state (NEP_{steady}) is reached. The amount of time it takes to reach this equilibrium depends on the initial amount of carbon released immediately following the disturbance (NEP_{min}). A range of optimal years of productivity can be defined as, for example, those years during which NEP values fall within the 90–100% of the NEP maximum. A sensitivity analysis applied to the quantity ($|NEP_{min}| + NEP_{steady}$) results in a slightly higher or lower steady-state value as indicated by the two dashed curves.

1998). If no further disturbance occurs in the years following NEP_0 , the productivity of the site dramatically increases and the ecosystem switches to a net sink. It rapidly climbs towards a maximum NEP value (NEP_{max}) that is generally reached around the time of canopy closure for most forest ecosystems (Schulze et al., 2000). Thus, to model this second phase of the curve, the NEP is approximated with an exponential distribution function that takes into account the growth characteristics and carbon flux capacity of the ecosystem (Barnes et al., 1998). A modified two parameter exponential function that is bounded by zero and one is used:

$$f(T) = 1 - \exp\left[-\left(\frac{T}{b}\right)^c\right] \quad (1)$$

where $b > 0$ is the scale parameter, $c > 0$ is the shape parameter, and $T = t/10$. This equation is the same as the cumulative Weibull function; its derivative form will be a bell-shape curve (e.g. Fig. 1) with $f'(T) \in (0,1)$. A larger scale parameter will yield a wider range of years where $t_i(NEP) = 90-100\%$ of NEP_{max} . That is, for two ecosystems with the same values of NEP_{min} and NEP_{max} , the ecosystem with a larger scale parameter will remain in a period of high productivity (e.g. $NPP \gg R_h$) for a longer period of time than an ecosystem with a smaller scale parameter ($t_{optimal_yrs}(NEP)$; Fig. 1). The shape parameter determines the stand development stage at which an ecosystem reaches NEP_{max} , and therefore represents the growth rate of the stand. A slower maturing stand will have a larger shape parameter, while a stand that matures quickly will have a smaller shape parameter, providing these two ecosystems have the same values of NEP_{min} and NEP_{max} . Since Eq. (1) is bounded by zero and one, we incorporate the constants NEP_{min} and NEP_{max} and use the following equation to calculate the NEP for Phase II:

$$NEP_{min \text{ to } max}(t) = \left\{ \frac{g(T)}{g(T)_{max}} k_1 \right\} + NEP_{min} \quad (2)$$

where $g(T) = \{f(T) - f(T-1)\}$ for $t = 2 \dots n$ years, $g(T)_{max}$ is the maximum $g(T)$ over all simulated stand development years, and $k_1 = (NEP_{max} - NEP_{min})$. That is, at $t(NEP_{max})$, $g(T)/g(T)_{max} = 1$ so that $(1 \times k_1) + NEP_{min} = NEP_{max}$.

During Phase III, from $t(\text{NEP}_{\max}) + 1$ to $t(\text{NEP}_{\text{steady}})$, the NEP of the fully mature ecosystem declines for a number of years, eventually reaching a steady-state value (Fig. 1; Schulze et al., 2000). During this decline in NEP, the NPP of the aging ecosystem decreases (though the physiological mechanisms for this age-related decline are not well understood; Murty et al., 1996) while rates of R_h remain steady due to continual litter inputs from the overstory (Waring and Running, 1998). Therefore, the NEP of this section of the curve is also a function of Eq. (2), but in addition it is dampened with terms incorporating the value of $\text{NEP}_{\text{steady}}$ and rate constants to determine how quickly the steady state is reached:

$$\begin{aligned} & \text{NEP}_{\max \text{ to steady}}(t) \\ &= \text{NEP}_{\min \text{ to max}}(t) + (|\text{NEP}_{\min}| +) \exp\left(-\frac{h}{z}\right) \quad (3) \end{aligned}$$

where $h > 0$ is a model parameter determining how quickly the NEP approaches a steady state, and z is a model parameter beginning at 1 and increasing by one each year until $\text{NEP}_{\text{steady}}$ is reached (Loucks, 1970; Arneeth et al., 1998; Schulze et al., 2000).

Finally, when $\text{NEP}_{\text{steady}}$ is attained in Phase IV, the NPP is slightly greater than the R_h of the ecosystem, resulting in a value of NEP just above zero. Decreased substrate quality in these older ecosystems causes limited decomposition, and thus low R_h (e.g. Covington and Sackett, 1984; Bauhus et al., 1998). Unless a disturbance occurs, the NEP of the ecosystem will retain this steady state value.

2.3.2. Modeling the NEP of a landscape over time

The NEP of the landscape over time is modeled using simple summations of the ecosystem NEP values obtained from the NEP distribution function described in Section 2.3.1. First, each ecosystem age on the annual age structure maps output from the landscape dynamics module (Section 2.2) is matched to the age on the corresponding NEP distribution function. Thus, each ecosystem within a landscape mosaic has an associated NEP value. The total NEP of an ecosystem for any given simulation year is equal to the sum of the NEP values for that ecosystem:

$$\text{NEP}_{\text{ecosys}} = \sum_{i=1}^p \text{NEP}_i \quad (4)$$

where p is the number of ecosystems of a given type in the landscape. Then, the NEP of the landscape with L ecosystems is:

$$\text{NEP}_{\text{land}} = \sum_{j=1}^L \text{NEP}_{\text{ecosys}_j} \quad (5)$$

and the landscape biomass at the end of the specified simulation period t is:

$$\text{Biomass} = \sum_{k=1}^t \text{NEP}_{\text{land}_k} \quad (6)$$

The NEP values of the same types of ecosystems are weighted by ecosystem by multiplying the non-weighted NEP values by the ecosystem's proportion in the landscape. This weighting accounts for the total area covered by the individual ecosystems of similar types within the landscape.

3. Simulations

3.1. LandNEP model scenarios and input parameters

To demonstrate the utility of the model, we used LandNEP to describe three hypothetical management regimes (Scenarios 1, 2, and 3 in Table 1) over a landscape comprised of ecosystems with faster (< 80 years) and slower (≥ 80 years) disturbance intervals (e.g. timber harvests). Therefore, our analysis of the model output could be extended from examining the differences in production between the individual ecosystems within a landscape to an overall landscape-level comparison of production between the three scenarios. Although these scenarios are hypothetical, they were chosen to correspond loosely with forest management practices in the upper Great Lakes region of the US where clearcutting (e.g. removal of all trees in a single harvest) at regular intervals is a common practice (e.g. USDA, 1994). In all the scenarios each ecosystem type comprised variable proportions of a 10 000 ha landscape. The model output annual values of NEP, area harvested, biomass, and ecosystem ages over 300 simulated development years.

Table 1
Input parameters applied in LandNEP simulation

Ecosystem type	Scenario 1			Scenario 2				Scenario 3	
	A	B	C	D	E	F	G	H	I
Proportion ^a	0.2	0.4	0.4	0.25	0.25	0.25	0.25	0.7	0.3
MPS ^b	40	40	40	30	30	30	30	60	60
Mean age ^c	20	39	50	12	25	40	50	15	50
Disturbance interval ^d	25	40	80	25	50	80	100	25	100
Year of NEP _{max} ^e	31	35	58	31	35	77	89	44	66
NEP (mg/ha) at disturbance interval	1.4	3.5	2.2	1.9	2.4	4.4	3.6	0.4	3.8
NEP _{max} ^f	1.5	3.7	3.4	2.0	3.7	4.5	3.8	1.5	5.6
90% NEP _{max} ⁱ	1.4	3.3	3.1	1.8	3.3	4.1	3.4	1.4	5.0
NEP _{min} ^f	-0.5	-1.3	-1	-0.5	-1.3	-1.2	-1	-1	-1.5
Weibull scale parameter (c) ^g	4.3	4	6	4.3	3	8	9.5	5	8
Weibull shape parameter (b) ^g	2	3	3	2	4	4	3	3	2
Year of NEP _{steady} ^h	65	97	125	67	89	136	196	66	124
Value of NEP _{steady}	0.2	0.3	1.1	0.4	0.3	1.0	1.2	0.2	2.4
$t_{\text{optimal_yrs}}(\text{NEP})^i$	23–40	30–43	49–69	23–40	30–41	67–87	72–106	38–50	48–84

The landscape size is 100×100 ha, and the ecosystems are randomly dispersed across the landscape. All model scenarios took place over a period of 300 simulation years. Scenario 1 is based on a landscape consisting of three ecosystem types (A, B, C) with each ecosystem type disturbed at a time close to its NEP_{max}. Scenario 2 comprises four ecosystem types (D, E, F, G) with ecosystem types D, F, and G having disturbance intervals within 6 years of the NEP_{max}, but with ecosystem type E having a disturbance interval of 15 years after the NEP_{max}. Scenario 3 consists of two ecosystem types (*H*, *I*) with ecosystem *H* having a disturbance interval of 19 years prior to the NEP_{max} and ecosystem type *I* having a disturbance interval 44 years after the NEP_{max}.

^a Proportion of each hypothetical ecosystem in the landscape.

^b Mean size of each ecosystem in the landscape (ha).

^c Mean age of each ecosystem at the start of the simulation (years).

^d Year at which disturbance occurred for each ecosystem.

^e Year at which the maximum value of NEP occurs for each ecosystem.

^f Maximum/Minimum values of NEP (mg C per ha/year). All minimum values occur at simulation year 1.

^g Values of the shape and scale parameters assigned to the distribution function in Eq. (1) (see text).

^h Year at which a 'steady-state' is attained.

ⁱ Range of ecosystem ages (years) during which 90–100% of the maximum NEP value is obtained. The quantity 90% NEP_{max} represents 90% of the maximum NEP value, e.g. the lower limit of the optimal NEP value for an ecosystem.

Scenario 1 included three different forest ecosystems (A, B, C in Table 1); two of these comprised 60% of the landscape, were routinely harvested within the $t_{\text{optimal_yrs}}(\text{NEP})$ time frame, and had short rotation times (e.g. ≤ 50 years). The third stand had a longer rotation length and a harvesting regime falling outside of the range of $t_{\text{optimal_yrs}}(\text{NEP})$. In Scenario 2, four types of forested ecosystems (D, E, F, G in Table 1) were present in the same proportions, all ecosystems were harvested within the $t_{\text{optimal_yrs}}(\text{NEP})$ range, and two types were fast rotating (intervals of 25 and 50 years) while two types were slower rotating (intervals of 80 and 100 years). Scenario 3

consisted of two different ecosystem types (*H*, *I* in Table 1); ecosystem *H* comprised 70% of the landscape and was routinely harvested every 25 years, while ecosystem *I* was harvested within the optimal time frame and had a long (100 years) rotation length (Table 1; (a) on Figs. 3–5). We applied a sensitivity analysis to this third scenario in order to examine the effect of altering the disturbance interval on the productivity of the ecosystems over the simulation period.

In all three scenarios the change of NEP of the individual ecosystems over time differed; the scale parameter (c) varied from 3 to 9.5 and the shape parameter (b) ranged from 2 to 4. Since the

ecosystems and landscape are hypothetical, the absolute values of NEP used in and obtained from this analysis are of interest only in the sense that they help us to compare the final output between the scenarios. However, to maintain a somewhat realistic perspective we did choose values for NEP_{\min} , NEP_{\max} , and the year of NEP_{\max} based on reported values of net carbon flux for various ecosystems (Canadell et al., 2000; Valentini et al. 2000; Buchmann and Schulze, 1999; Waddington et al., 1998). The minimum NEP values ranged from -1.5 to -0.5 mg C per ha/year, while the maximums ranged from 1.5 to 5.6 mg C per ha/year (Table 1). All of the ecosystems were disturbed prior to the year of NEP_{steady} .

4. Modeling results

4.1. Age structure and disturbance following LandNEP simulation

Over the 300 simulation years, the average ecosystem age ranged from 13.7 years for ecosystem *D* to 58.2 years for ecosystem *I* (Table 2). Although it only comprised 30% of the landscape in Scenario 3, Ecosystem *I* also acted as the highest net carbon sink with an average weighted NEP value of 1.2 mg C per ha/year throughout the simulation period. Ecosystem *H* was the only ecosystem acting as a net carbon source, releasing an average 0.2 mg C per ha/year. The total average area harvested per year ranged from 62 to 310 ha, but the variability of these yearly averages was high (ecosystems *G* and *H*, respectively; Table 2).

At the end of simulation year 1, the ecosystem ages ranged from 19.2 to 47.9 years for Scenario 1, 11.6 to 47.7 years for Scenario 2, and 15.0 to 47.8 years for Scenario 3 ('Year 1' in Table 2). There was no area harvested for Scenarios 2 and 3 during year 1, but in Scenario 1, 1800 ha were harvested. The NEP of 2.6 mg C per ha/year for Scenario 1 was the highest of the three scenarios during year 1 ('Year 1' in Table 2). However, 25 years later, the NEP of Scenario 1 was the lowest (1.2 mg C per ha/year for Scenario 1 vs. 2.1 and 1.5 mg C per ha/year for Scenarios 2 and 3, respectively; 'Year 25' in Table 2). At year 100,

Scenario 1 again had the highest NEP of the three scenarios (2.3 mg C per ha/year for Scenario 1 vs. 1.3 and 0.7 mg C per ha/year for scenarios 2 and 3, respectively; 'Year 100' in Table 2).

By the end of the 300 simulation years, the landscape in Scenario 1 had the greatest overall biomass of the three scenarios (434 mg C per ha for Scenario 2 vs. 419 and 259 mg C per ha, for Scenarios 1 and 3, respectively; Table 2). Ecosystem *I* produced the highest biomass (335 mg C per ha); ecosystem *A* yielded a low value of biomass (42 mg C per ha), and ecosystem *H* acted as a continual carbon source, releasing 76 mg C per ha over the simulation period (Table 2).

4.2. Age structure and NEP of the landscape

The cyclical age structure pattern of the landscape over time caused by the disturbance schedules included years where a substantial number of ecosystems fell within the range of $t_{\text{optimal_yrs}}(\text{NEP})$, followed by years where most ecosystems lay outside of this range. This altered the amount of carbon sequestered over time within a given area and over the entire landscape (Fig. 2 and Table 2). For example, during simulation year 100, ecosystems *B* and *C* in Scenario 1 had average ages 28 and 58 years, respectively (Table 2). These ages fell within the range of $t_{\text{optimal_yrs}}(\text{NEP})$, and consequently the landscape-level value of NEP was relatively high for this year (Tables 1 and 2). However, during year 300, none of the ecosystems in Scenario 1 fell within this $t_{\text{optimal_yrs}}(\text{NEP})$ time frame, and the overall value of NEP for this landscape was substantially lower (0.9 mg C per ha/year; Tables 1 and 2).

4.3. Cumulative NEP over time

For Scenario 1 the landscape-level NEP value (NEP_{land}) reached its highest point at the beginning of the simulation period (70 mg C in year 1; (d) in Fig. 3). For Scenario 2, the highest value for NEP_{land} was attained at year 120 (96 mg C; (d) in Fig. 4), and for Scenario 3, the highest value for NEP_{land} was reached at year 17 (52 mg C; (d) in Fig. 5). The contribution of each ecosystem to the landscape-level NEP depended on its propor-

Table 2
Average ecosystem ages, weighted NEP, weighted biomass, and total harvest area by ecosystem type in six of the 300 simulation years, and averages (S.D.) of ecosystem age, weighted NEP, and harvest area over all 300 simulation years

Ecosystem type	Scenario 1						Scenario 2						Scenario 3							
	Ecosystem age (years)	NEP (mg C per ha/year)	Biomass (mg C)	Harvest Area (ha)	Ecosystem Type	Ecosystem Age (years)	NEP (mg C per ha/year)	Biomass (mg C)	Harvest Area (ha)	Ecosystem Type	Ecosystem age (years)	NEP (mg C per ha/year)	Biomass (mg C)	Harvest Area (ha)	Ecosystem type	Ecosystem age (years)	NEP (mg C per ha/year)	Biomass (mg C)	Harvest Area (ha)	
Year 1																				
A	19.2	0.2	0.2	1000	D	11.6	0.2	0.2	0	H	15.0	-0.3	-0.3	0						
B	37.8	1.4	1.4	400	E	24.5	0.6	0.6	0	I	47.8	1.4	1.4	0						
C	47.9	1.0	1.0	400	F	37.7	0.1	0.1	0	-	-	-	-	-						
-	-	-	-	-	G	47.7	0.3	0.3	0	-	-	-	-	-						
Year 25																				
A	15.5	0.2	3.4	0	D	8.0	0.1	6.5	1000	H	16.3	-0.1	-1.8	0						
B	19.1	0.0	17.3	2300	E	32.9	0.5	17.3	3100	I	71.5	1.6	38.0	0						
C	62.1	1.0	27.2	1600	F	57.9	0.7	10.3	1000	-	-	-	-	-						
-	-	-	-	-	G	69.2	0.8	14.0	300	-	-	-	-	-						
Year 50																				
A	11.5	0.1	7.0	100	D	11.1	0.2	13.5	1900	H	14.5	-0.1	-3.4	2100						
B	31.2	1.2	30.3	0	E	21.4	0.4	20.6	100	I	76.3	1.1	70.9	500						
C	21.0	0.0	37.4	2200	F	43.8	0.4	25.5	1400	-	-	-	-	-						
-	-	-	-	-	G	67.6	0.6	31.9	600	-	-	-	-	-						
Year 100																				
A	9.3	0.1	14.3	2100	D	14.6	0.3	26.1	3800	H	17.5	-0.1	-17.6	0						
B	27.6	1.0	62.6	0	E	18.0	0.3	42.5	0	I	40.9	0.8	111.8	0						
C	58.1	1.2	67.5	400	F	52.1	0.5	28.9	100	-	-	-	-	-						
-	-	-	-	-	G	42.8	0.2	39.3	0	-	-	-	-	-						
Year 200																				
A	17.8	0.2	28.6	1400	D	14.3	0.3	50.0	200	H	14.7	-0.3	-42.4	3100						
B	18.1	0.4	131.6	400	E	14.7	0.0	87.8	2700	I	59.2	1.0	225.6	700						
C	43.6	0.7	130.5	3000	F	51.2	0.6	63.5	1400	-	-	-	-	-						
-	-	-	-	-	G	39.3	0.2	78.3	100	-	-	-	-	-						
Year 300																				
A	11.4	0.1	42.3	800	D	12.4	0.2	74.9	2200	H	14.4	-0.3	-76.0	3500						
B	23.9	0.4	202.8	3500	E	25.6	0.3	132.1	2300	I	57.6	1.1	335.2	1100						
C	43.5	0.4	189.3	400	F	43.0	0.4	94.8	1100	-	-	-	-	-						
-	-	-	-	-	G	36.9	0.1	117.4	0	-	-	-	-	-						
Values averaged over 300 simulation years																				
A	13.8 (3.1)	0.1 (0.1)	-	146 (116)	D	13.7 (2.7)	0.3 (0.1)	-	200 (134)	H	15.2 (3.1)	-0.2 (0.1)	-	310 (234)						
B	27.2 (6.6)	0.7 (0.4)	-	167 (140)	E	26.8 (7.5)	0.4 (0.3)	-	113 (111)	I	58.2 (8.3)	1.2 (0.2)	-	830 (80)						
C	43.4 (10.6)	0.6 (0.3)	-	107 (104)	F	42.6 (10.5)	0.3 (0.3)	-	73 (71)	-	-	-	-	-						
-	-	-	-	-	G	51.5 (16.5)	0.4 (0.3)	-	62 (71)	-	-	-	-	-						

Ecosystem types are listed according to their alphabetic character values given in Table 1.

tion within the landscape, disturbance interval, and the time at which each ecosystem reached its maximum NEP. For example, ecosystems *A* and *B* were at their peak NEP values and ecosystem *C* was nearly at a peak in year 1 of Scenario 1 (Fig. 3c). However, ecosystems *B* and *C* had relatively high values of NEP_{max} (3.7 and 3.4 mg C per ha/year, respectively; Table 1) and comprised 80% of the landscape. Therefore, they contributed much more to this peak than ecosystem *A* (Fig. 3c and d). In Scenario 2, a low cumulative NEP was reached at year 80, caused primarily by ecosystems *G* and *E* since they both approached their minimum NEP values during this year (Fig. 4c and d). For all scenarios, the ecosystems accumulated carbon between disturbance intervals at a rate indicated by ‘increasing waves’, an indication of long-term variability (Fig. 3b, Fig. 4b and Fig. 5b).

4.4. Sensitivity analysis of Scenario 3

The sensitivity analysis applied to Scenario 3 demonstrated that an increase or decrease in the disturbance interval played a significant role in determining the carbon flux of ecosystems *H* and *I*. By increasing the disturbance interval of ecosystem *H* from 25 to 50 years, the total biomass at the end of the 300 simulation years increased by nearly 150 mg C, and ecosystem *H* switched from acting as a net carbon source to acting as a net carbon sink (‘Year 300’ in Table 3). However, when the disturbance interval for ecosystem *H* was again increased from 50 to 75 years, the total biomass at the end of the simulation period remained the same (‘Year 300’ in Table 3). Notably, for ecosystem *H*, a decrease in the disturbance interval of just 6 years, from 50 years to 44 years, caused a significant ($P < 0.001$) decrease of 25 mg

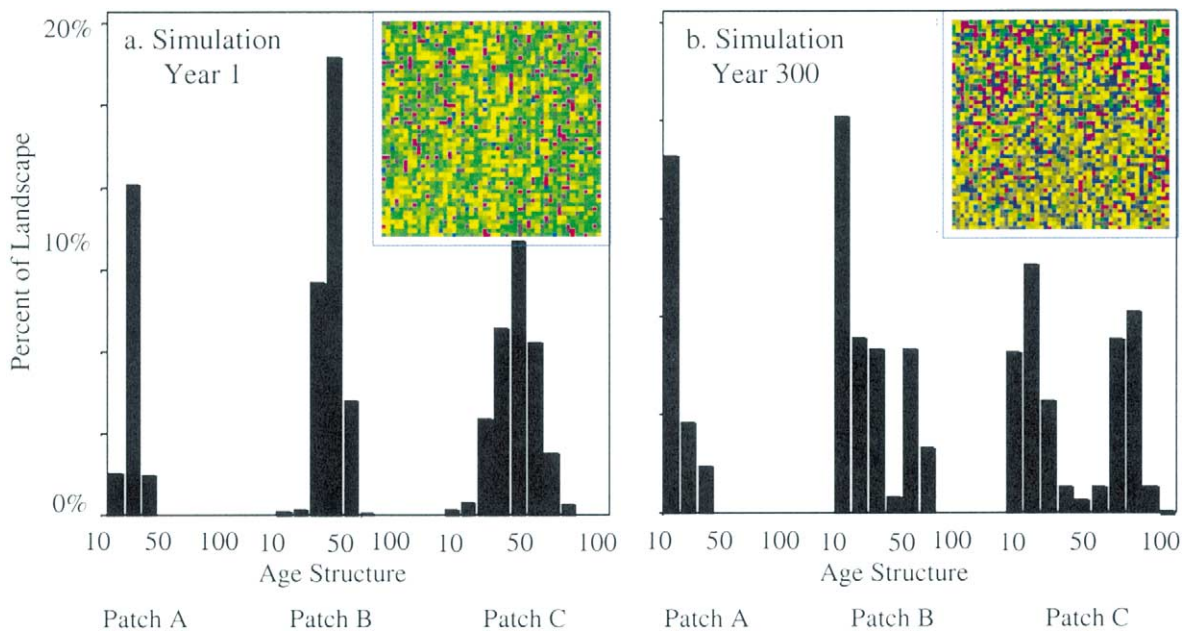


Fig. 2. Age frequencies and spatial distribution (inset) for the three patch types of Scenario 1 at simulation years 1 and 300. The age structure of the landscape, and hence, carbon sequestration, changes over time based on disturbance intervals and the time at which a patch type reaches its NEP_{max} . For example, at simulation year 1 (a), ecosystems B and C are dominated by stands that are close to their NEP_{max} , representing a high net carbon sink (1.4 and 1.0 mg C per ha/year, respectively; Table 2). However, at simulation year 300 (e) the age distributions of ecosystems B and C are dominated by stands further from their NEP_{max} , representing less carbon sequestration (0.4 mg C per ha/year for both B and C; Table 2). Younger stands (0–29 years) are represented by yellow, middle-aged stands (30–59 years) are represented by greens, and older stands (60–100 years) are represented by dark blues and reds.

Table 3
Average (S.D.) ecosystem ages, weighted NEP, weighted biomass, and total harvest area by ecosystem type following a sensitivity analysis applied to scenario 3
Disturbance Intervals (years) applied to ecosystem types *H* and *I*

Ecosystem type	Analysis 1 (<i>H</i> = 25, <i>I</i> = 100)						Analysis 2 (<i>H</i> = 50, <i>I</i> = 84)						Analysis 3 (<i>H</i> = 75, <i>I</i> = 100)						Analysis 4 (<i>H</i> = 44, <i>I</i> = 66)					
	Ecosystem age (years)	NEP C /ha/year	NEP (mg C /ha per year)	Biomass (mg C)	Harvest Area (ha)	Harvest area (ha)	Ecosystem age (years)	NEP C /ha per year	NEP (mg C /ha per year)	Biomass (mg C)	Harvest area (ha)	Harvest Area (ha)	Ecosystem age (years)	NEP C /ha per year	NEP (mg C /ha per year)	Biomass (mg C)	Harvest Area (ha)	Harvest area (ha)	Ecosystem age (years)	NEP C /ha per year	NEP (mg C /ha per year)	Biomass (mg C)	Harvest area (ha)	
<i>Year 1</i>																								
<i>H</i>	15.0	-0.3	-0.3	-0.3	0	600	14.5	-0.3	-0.3	-0.3	600	34.0	0.6	0.6	0.6	0	0	33.5	0.7	0.7	0.7	3200		
<i>I</i>	47.8	1.4	1.4	1.4	0	0	48.2	1.4	1.4	1.4	0	47.8	1.4	1.4	1.4	0	0	46.8	1.4	1.4	1.4	2300		
<i>Year 25</i>																								
<i>H</i>	16.3	-0.1	-1.8	8.1	0	900	36.9	0.8	0.8	8.1	900	54.9	0.5	17.4	17.4	900	900	19.0	-0.1	-0.1	8.2	0		
<i>I</i>	71.5	1.6	38.0	37.4	0	1300	58.5	1.4	37.4	37.4	1300	69.4	1.5	37.9	37.9	400	400	53.8	1.3	1.3	34.3	0		
<i>Year 50</i>																								
<i>H</i>	14.5	-0.1	-3.4	17.4	2100	2600	21.0	-0.1	17.4	2600	2600	32.2	-0.2	19.8	19.8	4500	4500	30.1	0.5	0.5	11.7	3000		
<i>I</i>	76.3	1.1	70.9	64.3	500	300	53.1	0.9	64.3	300	300	62.1	1.0	69.7	69.7	1700	1700	21.5	0.5	0.5	50.5	0		
<i>Year 100</i>																								
<i>H</i>	17.5	-0.1	-17.6	30.9	0	5700	21.2	0.0	30.9	5700	5700	53.0	0.6	37.6	37.6	700	700	29.5	0.5	0.5	21.0	2700		
<i>I</i>	40.9	0.8	111.8	112.2	0	500	53.7	1.4	112.2	500	500	43.6	1.3	109.6	109.6	0	0	41.0	1.0	1.0	105.7	3500		
<i>Year 200</i>																								
<i>H</i>	14.7	-0.3	-42.4	57.1	3100	3200	27.8	0.3	57.1	3200	3200	38.0	-0.1	64.8	64.8	500	500	25.1	0.3	0.3	40.3	4300		
<i>I</i>	59.2	1.0	225.6	223.4	700	1900	51.5	1.3	223.4	1900	1900	40.9	1.2	219.6	219.6	0	0	30.1	0.8	0.8	193.0	0		
<i>Year 300</i>																								
<i>H</i>	14.4	-0.3	-76.0	81.5	3500	3100	29.3	0.4	81.5	3100	3100	22.7	0.1	84.4	84.4	700	700	23.7	0.2	0.2	57.0	4100		
<i>I</i>	57.6	1.1	335.2	331.4	1100	1600	46.0	1.1	331.4	1600	1600	38.1	1.1	329.8	329.8	100	100	41.1	1.2	1.2	290.3	2100		
<i>Values averaged over 300 simulation years</i>																								
<i>H</i>	15.2 (3.1)	-0.2 (0.1)	-	-	310 (234)	255 (197)	26.3 (5.6)	0.3 (0.3)	-	255 (197)	255 (197)	38.9 (11.2)	0.3 (0.3)	-	-	207 (188)	207 (188)	23.7 (3.8)	0.2 (0.2)	0.2 (0.2)	-	207 (188)		
<i>I</i>	58.2 (8.3)	1.2 (0.2)	-	-	830 (80)	98 (84)	45.0 (9.0)	1.1 (0.3)	-	98 (84)	98 (84)	51.2 (14.7)	1.1 (0.3)	-	-	94 (88)	94 (88)	36.0 (8.1)	1.0 (0.3)	1.0 (0.3)	-	94 (88)		

In each analysis, the disturbance intervals of each ecosystem type were changed while all other parameters retained the original values shown in Table 1. Ecosystem types are listed according to their alphabetic character values given in Table 1. Analysis 1 represents the original Scenario 3 (Table 2), and is shown again here for ease in comparison. In Analysis 2, the disturbance interval of ecosystem type *H* is 25 years longer than that in Analysis 1 while that for ecosystem *I* is 16 years shorter. In Analysis 3, the disturbance interval for ecosystem type *H* is 50 years greater than that in Analysis 1, while that of ecosystem type *I* is the same. In Analysis 4, ecosystem types *H* and *I* are disturbed exactly at the year of NEP_{max}. The highest total biomass values are achieved for ecosystem type *H* when the disturbance interval of ecosystem *I* is set at 75 years and that of ecosystem *I* is set at 100 years (or more). The total biomass in Year 300 of Analyses 2 and 3 are not significantly different, but the total biomass of Analyses 2 and 3 are significantly higher than Analysis 4 ($P < 0.001$).

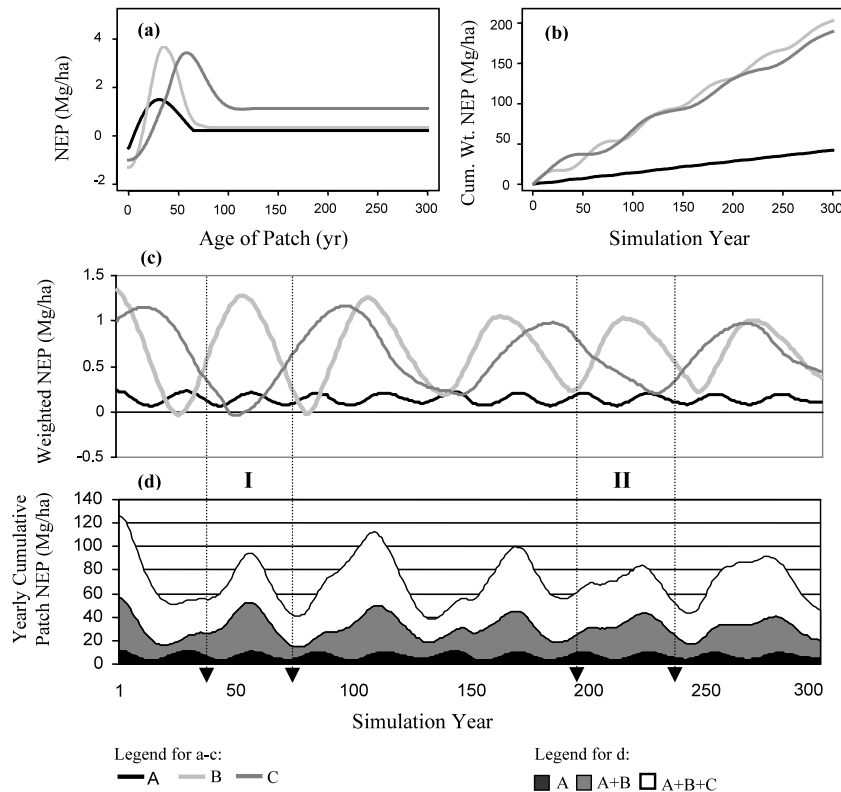


Fig. 3. Changes in NEP with successional age simulated by LandNEP (Scenario 1). A modified two parameter exponential distribution function with varying shape and scale parameters was assigned to three ecosystems (A–C) within a hypothetical landscape (a). The three ecosystems accumulate carbon between disturbance intervals at a rate indicated by the increasing ‘wavy’ graphs in (b). The contribution of each ecosystem to the cumulative depended on its proportion in the landscape, disturbance interval, and its maximum NEP (c, d). For example, the high cumulative NEP in I and II (d) was caused primarily by ecosystems B and C (c).

C per ha in the total biomass. A similar significant ($P < 0.001$) decrease in total biomass was noted when the disturbance interval of ecosystem I was switched from 84 to 66 years (‘Year 300’ in Table 3).

5. Discussion

5.1. NEP dynamics and disturbance intervals

Our model scenarios demonstrated that management practices incorporating regular disturbance regimes can influence the cumulative productivity of a landscape. However, the landscape productivity is also dependent on the com-

position, age structure, and changes of NEP over the successional process of the ecosystems within the landscape (e.g. Fig. 1). Large differences in productivity were noted in comparisons between ecosystems all having 25 year disturbance intervals, but different NEP curves. The mis-timing of a regular disturbance in an ecosystem with NEP_{max} occurring at a later stand developmental stage and lower values of NEP_{max} and NEP_{min} could result in that ecosystem becoming a net carbon source. This implies that land managers should be careful to avoid a short disturbance frequency in those ecosystems with a ‘low’ NEP curve. For instance, ecosystem *H* was marked by a ‘low’ NEP curve, and when it was disturbed every 25 years it acted as a net carbon source. It

switched to a net carbon sink when the disturbance interval was increased (Tables 1 and 3; Fig. 5). Similarly, managers have more leeway in timing the disturbance interval of an ecosystem with an earlier achievement of NEP_{max} and higher values of NEP_{max} and NEP_{min} . For example, ecosystem *D* was also routinely disturbed every 25 years, but remained a net carbon sink due to its 'high' NEP curve (Tables 1 and 2; Fig. 4). Field-based studies have also demonstrated large differences in NEP among ecosystems ≤ 25 years old (Buchmann and Schulze, 1999).

Furthermore, our model scenarios support the hypotheses of Schulze et al. (2000) that a landscape dominated by unmanaged old-growth forest will ultimately have a greater sink capacity than one dominated by younger, faster rotating stands. We documented a similar occurrence when the disturbance interval of ecosystem *I* was increased from 66 to 100 years, resulting in a 10% increase in total biomass. For ecosystem *H* this increase was even more dramatic, yielding an increase of more than 100% when the disturbance interval was changed from 25 to 50 or 75 years (Table 3).

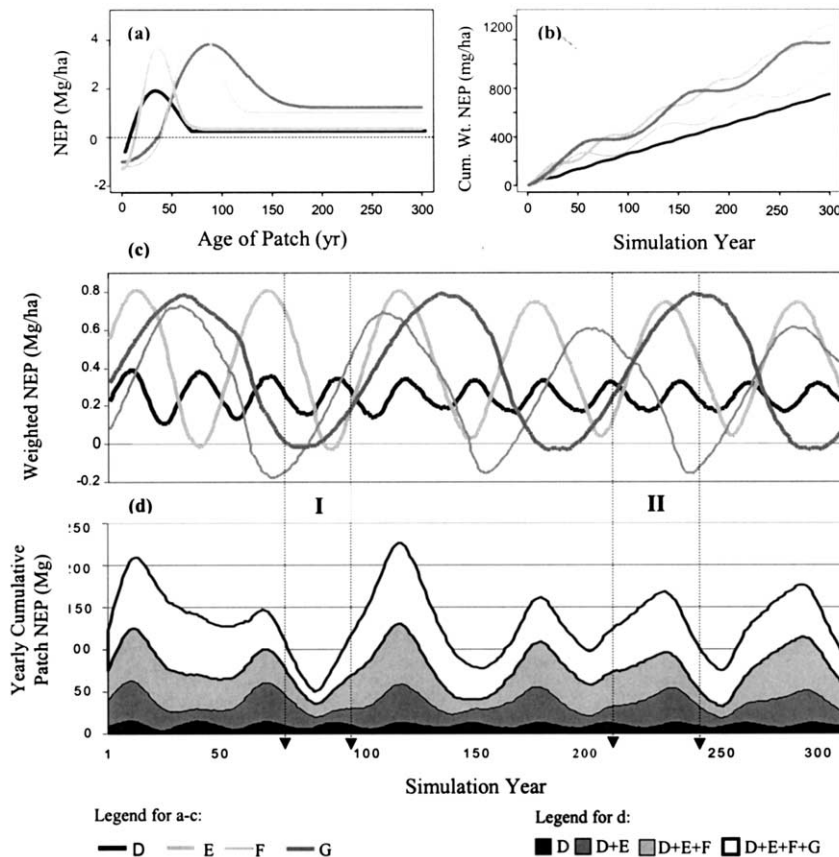


Fig. 4. Changes in NEP with successional age simulated by LandNEP (Scenario 2). A modified two parameter exponential distribution function with varying shape and scale parameters was assigned to four ecosystems (D–G) within a hypothetical landscape (a). The four ecosystems accumulate carbon between disturbance intervals at a rate indicated by the increasing 'wavy' graphs in (b). The contribution of each ecosystem to the cumulative depended on its proportion in the landscape, disturbance interval, and its maximum NEP (c, d). For example, the low cumulative NEP in I (year 80; d) was caused by a combination of a low NEP in ecosystems D, F, and G, and less so by ecosystem E (c). The high cumulative NEP in II (year 225; d) was caused primarily by ecosystems E and G (c).

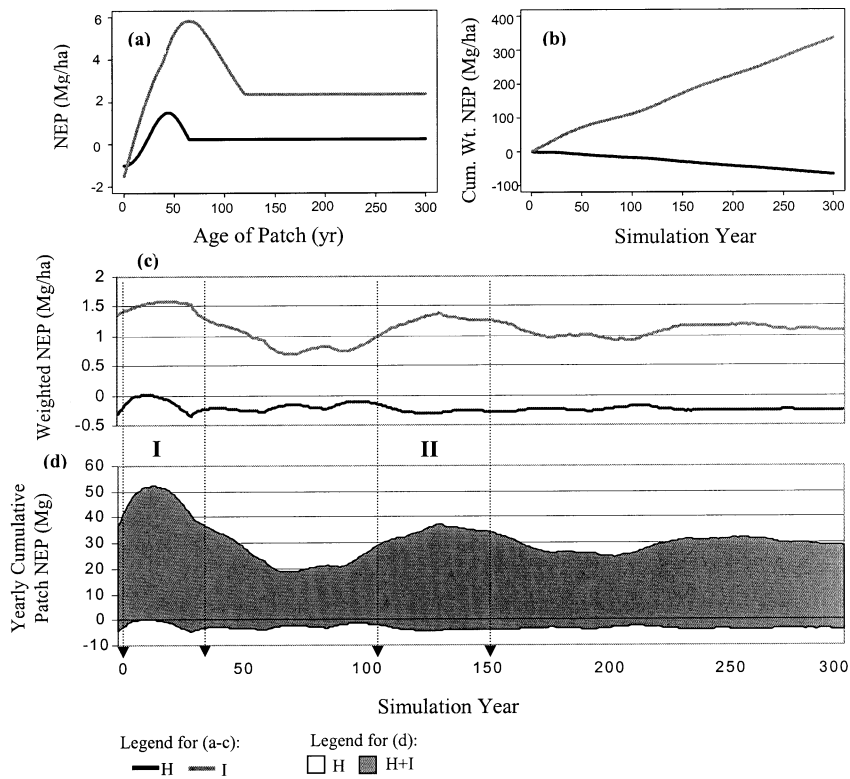


Fig. 5. Changes in NEP with successional age simulated by LandNEP (Scenario 3). A modified two parameter exponential distribution function with varying shape and scale parameters was assigned to two ecosystems ($H-I$) within a hypothetical landscape (a). The two ecosystems accumulate carbon between disturbance intervals at a rate indicated by the increasing 'wavy' graphs in (b). The contribution of each ecosystem to the cumulative depended on its proportion in the landscape, disturbance interval, and its maximum NEP (c, d). For example, the high cumulative NEP in I (year 17; c and d) was caused by a combination of a high NEP in ecosystems H and I . However, the high cumulative NEP in II (year 120; c and d) was caused by a high NEP for ecosystem I , not by type H .

Older, less frequently disturbed stands will allow more carbon to enter the permanent carbon pool, often referred to as net biome production (NBP). NBP represents only a small portion of NEP and is critical in assessing long-term (e.g. decades to centuries) carbon storage (IPCC, 1994; IGBP, 1998).

5.2. Variability in NEP

Many of the ecosystems were poorly constrained, as indicated by their high variability in average NEP over the 300 simulation years. For example, ecosystems A and F had standard deviations (S.D.) equal to their average weighted NEP values (Table 2), and could therefore switch from

being a carbon sink with a positive NEP value to acting as neither a sink nor source, with an NEP value equal to zero. Many modeling and field-based studies have also reported a high interannual variability of ecosystem CO_2 sources and sinks (Woofsy et al., 1993; Goulden et al., 1996; Chen et al., 2002). Researchers conducting field-based eddy covariance studies have noted that in some instances a warm winter can switch a boreal forest from becoming a carbon sink to a source due to an increase in ecosystem respiration (Lindroth et al., 1998; Goulden et al., 1998). This has been attributed to climatic variability and the correlation between temperature and ecosystem respiration (Valentini et al., 2000).

Furthermore, an estimate of the sink strength

of an ecosystem obtained from data over a short time interval (e.g. < 10 years) may not represent an adequate picture of the sink/source strength of an ecosystem due to the cyclical nature of NEP (e.g. (c) in Figs. 3–5; Potter and Klooster, 1999; Fan et al., 1998). That is, two estimates of NEP obtained from the same landscape or region in different years will generally not agree, but both will be correct (Fan et al., 1998). These high interannual climatic variations can make it difficult to predict when a landscape will switch from acting as net carbon sink to acting as a net carbon source, largely due to the complex interactions among landscape composition, NEP dynamics over ecosystem succession, disturbances in time and space, and future climate variability.

5.3. Applications

Physiological processes or random disturbances could be incorporated into the LandNEP distribution function (e.g. Eq. (1)) in the carbon flux model (Fig. 1) to alter the NEP versus ecosystem age relationship over the shorter or longer term. For example, to assess the sensitivity of landscape NEP to transient changes in physiological processes, a section of the NEP distribution curve (Fig. 1) could be shifted up or down to simulate the effect of manipulations applied to an ecosystem (e.g. modifications of nutrients, water, temperature, or CO₂ concentrations over the course of one or several growing seasons; Shaver et al., 2000; Arneth et al., 1998; Goulden et al., 1996). Similarly, a random disturbance (such as a wildfire) could also be included in the LandNEP simulations by shifting a portion of the NEP distribution curve up or down. This would assess how these short-term ecosystem modifications might affect the long-term NEP estimates, and their importance in the cumulative NEP of the entire landscape at broader temporal scales.

Long-term modifications in atmospheric CO₂, soil warming, or ambient O₃ induced by climate change may cause a more dramatic alteration in the general NEP curve (Fig. 1) than the short term changes. The effects of elevated atmospheric CO₂ on NEP are complex and ecosystem-dependent; this phenomenon may increase NPP in the

short term, but over the long-term this increase in NPP could be offset by other factors such as nutrient depletion, water stress, or acclimation (Mickler et al., 2000; Amthor, 1995). This may cause the NEP curve to level at the NEP_{max} value for several years in Phase II, but gradually fall and reach a steady-state slightly below zero in Phase IV. Depending on ecosystem type, soil warming may bring about changes such as decreased soil moisture, shifts in vegetation from more productive to less productive shrubs, increased plant cover, or increased nitrogen uptake (Mickler et al., 2000; Shaver et al., 2000). These changes may mean, for example, that the ecosystem maintains a steady state at a point below or at zero, or that the NEP drops below zero for a period of time during phase III, but rises above zero again in phase IV (see Fig. 3 in Shaver et al., 2000). O₃ tends to decrease biomass growth (Mickler et al., 2000), and may therefore cause the NEP of an ecosystem to decline before actually reaching its NEP_{max}, and to maintain a lower steady state value.

Although our main focus in this research was to demonstrate the utility of this model in strictly forested ecosystems, LandNEP could also be used to model non-forested landscapes. Recently, interest has intensified in quantifying the sink/source capacity of a landscape with any combination of croplands, rangelands, grasslands, or forests under alternative management strategies (Knapp and Smith, 2001; Kaiser, 2000; Mickler et al., 2000). This may provide a more adequate picture of large-scale atmospheric fluxes and the uncertainties associated with certain carbon sinks. For example, management strategies within a cropland may consist of differing crop types and till versus no-till strategies. The carbon pool within these ecosystems may change extremely slowly over time or show large variations at small spatial scales (e.g. between different crop types in a field; Kaiser, 2000) which may not be significant at the landscape level. Furthermore, although none of the model scenarios were chosen to correspond with any specific forest management plan, this model could be implemented by forest managers to investigate the effect of alternative management strategies on NEP. Finally, an even more realistic picture of alternative management strategies could

be provided by incorporating remotely sensed data combined with historical statistics over a landscape consisting of a combination of forested and non-forested ecosystems.

5.4. Comparison of LandNEP to other models of net ecosystem productivity

Although several models exist to examine productivity at the scales of an ecosystem (e.g. 0.25 km²), a region (e.g. 100 km²), or globally, a careful review of the available literature revealed no previous studies of NEP at the landscape scale (e.g. 10 km²). Furthermore, due to the difficulty in measuring belowground processes such as those comprising R_h (e.g. Raich and Nadelhoffer, 1989; Nadelhoffer and Raich, 1992; Gower et al., 1996), some of the existing productivity models focus primarily on NPP or gross primary productivity (GPP, e.g. canopy photosynthesis), and not NEP (e.g. Jenkins et al., 1999).

However, lessons learned from previous ecosystem, region, or global productivity modeling efforts can aid in our understanding of NEP at a landscape scale. For example, Alexandrov et al. (1999) merged global carbon cycle modeling with forest inventory at a Japanese site, and reached a conclusion similar to ours: forest age structure acts as a key variable in projecting the NEP of the world's forests. Huntingford et al. (2000) developed an ecosystem-level model that examined NEP responses to increases in atmospheric CO₂ concentration and temperature. They documented three categories of response causing either a rapid positive pulse of NEP, a large pulse of negative NEP, or a gradual switch to a weakly negative NEP. Jenkins et al. (1999) compared regional NPP predictions for two models (Pnet-II and TEM 4.0) and found that at both fine and coarse resolutions the percent coverage of low- versus high-productivity forests was a critical variable in assessing NPP. Therefore, to ensure more accurate predictions of NPP, the land cover input data sets should preserve the fine-resolution forest type variability.

6. Future directions and conclusions

In this first version of LandNEP, our goal was to demonstrate how, in a deliberately simple context, landscape-level carbon sequestration could be managed from a spatial perspective. LandNEP offers unique features, including the ability to take into account the age structure and differing disturbance regimes within a landscape. Currently, our model does not follow the successional pathways of the ecosystems within the landscape, nor does it examine how edge effects, ecosystem interactions, or ecosystem shape affect carbon sequestration. Further, LandNEP does not track the fate of carbon removed following each disturbance. It is hoped that this model, and our hypothetical scenarios, will provide a structure on which to build more complex models of landscape-level productivity either within a forested or non-forested landscape. Additionally, as more long-term eddy flux measurements (e.g. Ameriflux, Euroflux) are collected, scientists should gain valuable information to estimate the parameters for our carbon flux model.

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References

- Alexandrov, G.A., Yamagata, Y., Oikawa, T., 1999. Towards a model for projecting net ecosystem production of the world forests. *Ecol. Modell.* 123, 183–191.
- Amthor, J.S., 1995. Terrestrial higher-plant response to increasing atmospheric [CO₂] in relation to the global carbon cycle. *Glob. Change Biol.* 1, 243–274.

- Arnell, A., Kelliher, F.M., McSeveny, T.M., Byers, J.N., 1998. Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Phys.* 18, 785–793.
- Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H., 1998. *Forest Ecology, Carbon Balance of Trees and Ecosystems*. Wiley, New York, pp. 514–516 chapter 18.
- Bauhus, J.D., Pare, D., Cote, L., 1998. Effects of tree species, stand age, and soil type on soil microbial biomass and its activity in a southern boreal forest. *Soil Biol. Biochem.* 30, 1077–1089.
- Bond, B.J., Franklin, J.F., 2002. Aging in Pacific Northwest forests: a selection of recent research. *Tree Phys.* 22, 73–76.
- Buchmann, N., Schulze, E.D., 1999. Net CO₂ and H₂O fluxes of terrestrial ecosystems. *Glob. Biogeochem. Cycles* 13, 751–760.
- Canadell, J.G., Mooney, H.A., Baldocchi, D.D., Berry, J.A., Ehleringer, J.A., Field, C.B., Gower, S.T., Hollinger, D.Y., Hunt, J.E., Jackson, R.B., Running, S.W., Shaver, G.R., Steffen, W., Trumbore, S.E., Valentini, R., Bond, B.Y., 2000. Carbon metabolism of the terrestrial biosphere: a multitechnique approach for improved understanding. *Ecosystems* 3, 115–130.
- Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., Birdsey, R.A., 2000. Contributions of land-use history to carbon accumulation in US forests. *Science* 290, 1148–1151.
- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosfokske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. *Bioscience* 49, 288–297.
- Chen, J., Falk, M., Euskirchen, E.S., Paw, U.K., Suchanek, K., Ustin, S., Bond, B.J., Brosfokske, K.D., Phillips, N., Bi, R., 2002. Biophysical controls of carbon flows in three successional Douglas-fir stands based upon eddy-covariance measurements. *Tree Phys.* 22, 171–180.
- Covington, W.W., Sackett, S.S., 1984. The effect of a prescribed burn southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* 30, 183–192.
- Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., Tans, P., 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* 282, 442–446.
- Forman, R.T., 1995. *Land Mosaics*. Cambridge University Press, Cambridge, UK.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Woofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Glob. Change Biol.* 2, 169–182.
- Goulden, M.L., Woofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., 1998. Sensitivity of a boreal forest carbon balance to soil thaw. *Science* 279, 214–217.
- Gower, S.T., Pongracic, S., Landsberg, J.J., 1996. A global trend in belowground carbon allocation: can we use the relationship at smaller scales. *Ecology* 77, 1750–1755.
- Houghton, R.A., Boone, R.D., Fruci, J.R., Hobbie, J.E., Melillo, J.M., Palm, C.A., Peterson, B.J., Shaver, G.R., Woodwell, G.M., Moore, B., Skole, D.L., Meyers, N., 1987. The flux of carbon from terrestrial ecosystems to the atmosphere in 1980 due to changes in land use: geographic distribution of the global flux. *Tellus* 39B, 122–139.
- Huntingford, C., Cox, P.M., Lenton, T.M., 2000. Contrasting responses of a simple terrestrial ecosystem model to global change. *Ecol. Model.* 134, 41–58.
- Chau, K., 1994. [IPCC] Intergovernmental Panel on Climate Change. *Climate Change 1994: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission Scenarios*. Cambridge University Press, Cambridge, UK.
- Chau, K., 1998. [IGBP] International Geosphere Biosphere Programme Terrestrial Carbon Working Group. The terrestrial carbon cycle: implications for the Kyoto Protocol. *Science* 280, 1393–1394.
- Janisch, J.E., Harmon, M.E., 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Phys.* 22, 77–90.
- Jenkins, J.C., Kicklighter, D.W., Ollinger, S.V., Aber, J.D., Melillo, J.M., 1999. Sources of variability in net primary production predictions at a regional scale: a comparison using Pnet-II and TEM 4.0 in northeastern US forests. *Ecosystems* 2, 555–570.
- Kaiser, J., 2000. Soaking up carbon in forest and fields. *Science* 290, 922.
- Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291, 481–484.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Li, H., Gartner, D.I., Mou, P., Trettin, C.C., 2000. A landscape model (LEEMATH) to evaluate effects of management impacts on timber and wildlife habitat. *Comp. Electron. Agric.* 27, 263–292.
- Lindroth, A., Grelle, A., Morén, A.-S., 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Glob. Change Biol.* 4, 443–450.
- Loucks, O.L., 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* 10, 17–25.
- Mickler, R.A., Birdsey, R.A., Hom, J. (Eds.), 2000. *Responses of northern US forests to environmental climate change*. Springer, New York, NY.
- Murty, D., McMurtrie, R.E., Ryan, M.G., 1996. Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses. *Tree Phys.* 16, 187–200.
- Nadelhoffer, K.J., Raich, J.W., 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* 73, 1139–1147.
- Potter, C.S., Klooster, S.A., 1999. Detecting a terrestrial biosphere sink for carbon dioxide: interannual ecosystem modeling for the mid-1980s. *Climatic Change* 42, 489–503.

- Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70, 1346–1354.
- Schimel, D., Melillo, J., Tian, H., McGuire, A.D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* 287, 2004–2006.
- Schulze, E.D., Wirth, C., Heimann, M., 2000. Managing forests after Kyoto. *Science* 289, 2058–2059.
- Shaver, G.R., Canadell, J.C., Chapin, F.S. III, Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bio-science* 50, 871–882.
- Tian, H., Melillo, J.M., Kicklighter, D.W., McGuire, A.D., Helfrich, J., 1999. The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO₂ in the United States. *Tellus* 51B, 414–452.
- USDA Forest Service, 1994. Landscape level analysis: desired future vegetative condition. Washburn Ranger District, Chequamegon National Forest, Washburn, WI.
- Waddington, J.M., Griffis, T.J., Rouse, W.R., 1998. Northern Canadian wetlands: net ecosystem CO₂ exchange and climatic change. *Climatic Change* 40, 267–275.
- Waring, R.H., Running, S.W., 1998. Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, CA.
- Woodwell, G.M., Whittaker, R.H., 1968. Primary production in terrestrial communities. *Am. Zool.* 8, 19–30.
- Woofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bawkin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260, 1314–1317.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–865.