

Disturbance and net ecosystem production across three climatically distinct forest landscapes

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[1] Biometric techniques were used to measure net ecosystem production (NEP) across three climatically distinct forest chronosequences in Oregon. NEP was highly negative immediately following stand-replacing disturbance in all forests and recovered to positive values by 10, 20, and 30 years of age for the mild and mesic Coast Range, mesic West Cascades, and semi-arid East Cascades, respectively. The response of stand-level NEP to individual disturbance events is greater than that attributable to edaphoclimatic differences between forest type. However, regional age class distributions are such that the variability in landscape-level NEP attributable to disturbance regimes is equivalent to that attributable to regional edaphoclimatic differences between forest types. Simulations of age class distribution under varying disturbance frequencies suggest that the sensitivity of landscape-level NEP to changes in disturbance regime varies among forest types and is linked to both remnant detritus and photosynthetic recovery rate that are partly a function of edaphoclimatic differences. **INDEX TERMS:** 1615 Global Change: Biogeochemical processes (4805); **KEYWORDS:** disturbance, forest carbon dynamics, net ecosystem production

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1. Introduction

[2] Net ecosystem production (NEP) can be defined as the difference between gross primary production and ecosystem respiration. Forests exhibiting negative NEP are acting as sources of atmospheric carbon, while forests exhibiting positive NEP are acting as sinks. Current concern over atmospheric CO₂ levels and subsequent global warming has brought the issue of forest NEP to the forefront of Earth science and challenged forest ecologists to quantify the impact of climate and disturbance on NEP, not only of individual forest stands but across entire forest landscapes. Climate is known to affect forest NEP by directly controlling the physiology of production and decomposition of organic matter [Woodwell and Whittaker, 1968; Jarvis, 1995].

[3] Conventional theory regarding the successional trends in NEP following disturbance is based on assumptions about the relative proportions of growing and decomposing tissue [Odum, 1969; Sprugel, 1985; Harmon *et al.*, 1990]. According to this theory (Figure 1, top), forests experience a pulse of negative NEP following catastrophic disturbances such as crown fire or clear-cutting, as these events both drastically reduce the amount of photosynthetic tissue and increase pools of respiring detritus. As living vegetation recovers and detrital pools decay, NEP becomes more positive, reaching a peak

when detrital pools are near their lowest and production is near its highest. A subsequent decline in NEP occurs as interdisturbance mortality restocks detrital pools, which may or may not be compounded by declines in gross primary production.

[4] Recent studies suggest that the changes in stand-level NEP that occur as a result of disturbance, even without accounting for losses incurred during the disturbance event, may well exceed that attributable to either interannual variation in climate [Thornton *et al.*, 2002] or among-biome variation in climate [Chapin *et al.*, 2002]. However, when considering landscapes comprising stands in varying stages of regrowth, it is not immediately apparent how much variability in overall NEP is being caused by disturbance or how sensitive landscape NEP is to changes in the frequency of disturbance.

[5] As implied in Figure 1, the NEP of any forested landscape is constrained both by the successional trends in NEP and the age class distribution created by the prevailing disturbance regime [Kurz and Apps, 1999], and perhaps more important than the overall weighting of NEP by age class frequency is just how the amplitude and recovery rate of NEP renders a landscape more or less sensitive to alterations in age class distribution brought on by changes in disturbance regimes. After all, depending on the exact shape of the NEP curve in Figure 1, we would expect there to be age ranges where shifts in relative abundance would have little effect on landscape NEP as well as age ranges where shifts in relative abundance would profoundly alter landscape NEP.

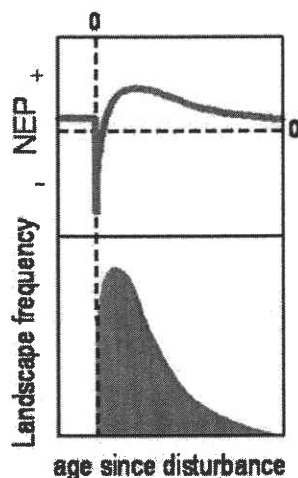


Figure 1. Theorized successional patterns in forest NEP following a stand-replacing disturbance. Disturbance regimes affect landscape-level NEP by defining the relative frequency of forest age classes.

[6] The robust chronosequence studies which aid in quantifying the influence of age class distribution on regional NEP are only now appearing in the literature. *Wirth et al.* [2002], *Bond-Lamberty et al.* [2004], *Howard et al.* [2004], and *Litvak and Miller* [2003] have all quantified age-related trends in NEP for boreal forests, while *Smith and Resh* [1999], *Janisch and Harmon* [2002], and *Law et al.* [2003] have reported age-related trends in temperate systems. Together, these studies help refine theories regarding successional trends in forest carbon exchange and provide valuable information regarding the response of stand-level NEP to disturbance. In this study we present values for NEP measured across multiple, replicated, edaphoclimatically distinct forest chronosequences and assess for each the capacity of disturbance to influence landscape-level NEP through current and alternative age class distributions. Specifically, our goals were to (1) quantify the successional trends in NEP that follow stand-replacing disturbance in each of three edaphoclimatically distinct conifer forests types in Oregon, (2) determine which component carbon fluxes were most responsible for the magnitude of NEP and which were most responsible for the trends in NEP, (3) compare the relative importance of disturbance and edaphoclimatic controls on regulating NEP at both individual stands and across entire landscapes, and (4) assess the sensitivity of landscape level NEP to alterations in disturbance regimes and link this sensitivity to the production biology of each forest type.

2. Methods

2.1. Study Design

[7] To assess successional trends in NEP across western Oregon, we selected 36 independent forest plots arranged as three replicates of four age classes in each of three edaphoclimatically distinct forest types. Each study plot encom-

passed 1 ha of structurally homogenous forest determined to be representative of its age and compositional type. The three forest types are located along a wide precipitation and elevation gradient and are best described as hemlock-Sitka spruce in the fog belt of Coast Range near Cascade Head Experimental Forest, Douglas fir in the West Cascade Mountains near H. J. Andrews Experimental Forest, and ponderosa pine in the Metolius basin in the dry east side of the Cascade Mountains. The locations of the study sites are shown in Figure 2, and the climatic, edaphic, and compositional characteristics of each site are given in Table 1. Forest ages range from 10 to 450 years and are subjectively classified as either initiation, young, mature, or old. Structural qualities of these age classes are described in Table 2.

2.2. Estimating NEP

[8] The mass balance approach for estimating NEP from field measurements begins in this study by separating the flow of gross photosynthate into three carbon allocation paths represented by equations (1) through (3).

$$\text{NEP}_{\text{foliage}} = \text{NPP}_{\text{foliage}} - \text{litterfall}, \quad (1)$$

where $\text{NPP}_{\text{foliage}}$ is the net primary production of tree, shrub, and herb foliage and litterfall is assumed to approximate the heterotrophic decomposition of dead leaves.

$$\text{NEP}_{\text{wood}} = \text{NPP}_{\text{wood}} - \text{RH}_{\text{woody debris}}, \quad (2)$$

where NPP_{wood} is the net primary production of the bole branches and bark of trees and shrubs, and $\text{RH}_{\text{woody debris}}$ is the heterotrophic respiration from fine and coarse woody debris.

$$\text{NEP}_{\text{root}} = \Delta \text{ coarse root} + \Delta \text{ fine root}, \quad (3)$$

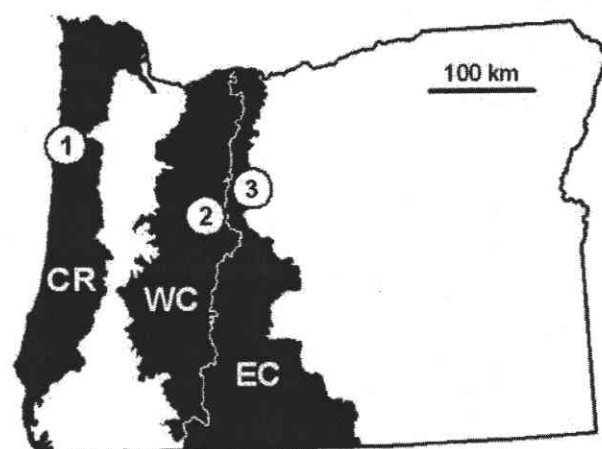


Figure 2. Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1–3. CR, Coast Range; WC, West Cascades; EC, East Cascades.

Table 1. Climatic, Edaphic, and Biological Characteristics of the Three Study Sites

Site Characteristic	Coast Range	West Cascades	East Cascades
Canopy composition (importance by basal area)	western hemlock (0.36)	Douglas fir (0.79)	ponderosa pine (0.95)
	Sitka spruce (0.34)	western red cedar (0.10)	
	Douglas fir (0.27)	western hemlock (0.10)	
Additional indicator species	red alder, vine maple, salmonberry, salal, red huckleberry, sword fern	vine maple, salal, red huckleberry, sword fern, Rhododendron	white fir, incense cedar, antelope bitterbrush, green leaf manzanita, Idaho fescue
Geographic location	Salmon River drainage of Tillamook county Oregon	Blue River drainage of Linn county Oregon	upper Metolius River of Deschutes county Oregon
Map coordinates	45.1°N 123.9°W	44.2°N 122.2°W	44.4°N 121.7°W
Elevation, m	120–300	710–860	890–1230
Precipitation (long-term average mm yr ⁻¹)	2800	2100	500
Mean Summer air temperature (long-term average C°)	14.5	14.1	14.5
Number of frost-free days	333	255	190
Soil description	basaltic colluvium forming well drained silt loams	igneous colluvium and residuum forming well drained stony clay loams	ash over colluvium forming well drained sandy to gravelly loams

where Δ coarse root and Δ fine root are the changes in each of these carbon pools over time, respectively. Total plot-level NEP is then calculated as

$$\text{NEP}_{\text{total}} = \text{NEP}_{\text{foliage}} + \text{NEP}_{\text{wood}} + \text{NEP}_{\text{root}} + \Delta \text{ soil C}, \quad (4)$$

where Δ soil C accounts for any accumulation or depletion of carbon in the mineral soil.

2.3. Vegetation Surveys

[9] All forest vegetation was divided into three classes: trees (woody plants having a stem diameter >5 cm at a height of 1.24 m), understory (woody shrubs and saplings having a stem diameter <5 cm at a height of 1.37 m), and herbs (grasses, forbs, and bryophytes). Vegetation surveys were conducted inside four subplots regularly spaced throughout each of the 1-ha study plots. Subplot sizes ranged from 75 to 700 m² for trees, 5 to 75 m² for understory, and 2 m² for herbs, depending on the density

and homogeneity of the vegetation. The frequency and dimensions of trees and understory in each subplot were converted to tissue mass or volume per unit area using species and site-specific allometric equations obtained from the BIOPAC database [Means *et al.*, 1994; Van Tuyl, 2003]. Herb mass per unit area was determined through the harvest, drying and weighing all aboveground tissue.

2.4. Wood NPP

[10] Live tree wood increment was determined for each plot using stem surveys and increment cores collected in 2001 only (as described by Clark *et al.* [2001]). For each tree in a subplot, the frequency, species, and DBH (stem diameter at 1.37 m) were recorded. For every fifth tree encountered, total height was recorded and two increment cores were taken to determine the average radial growth during the past 5 years. Plot-specific regressions relating height and radial increment to DBH allowed us to estimate the probable height and growth of trees from which no cores

Table 2. Structural Qualities of Each Age-Class Averaged Across Three Replicate Stands^a

	Age	Stem Diameter, cm	Stem Density, ha ⁻¹	Canopy Height, m	Ontogeny
Coast Range					
Initiation	12–14	11	1830	11	crowns closed, suppression not occurring, large shrub component suppression and self-thinning occurring, understory absent self-thinning nearly complete, understory reestablishing multistory canopy, gap formation, well-developed understory
Young	22–40	20	1440	20	
Mature	45–52	38	600	38	
Old	170–190	51	340	51	
West Cascades					
Initiation	13–20	10	1120	10	crowns closing, large shrub component self-thinning occurring, shade-tolerant understory developing. self-thinning complete, well-developed understory multistory canopy, gap formation, well-developed understory
Young	40–70	22	740	22	
Mature	140–170	38	340	38	
Old	400–450	32	510	32	
East Cascades					
Initiation	9–20	10	320	10	tree crowns widely spaced, understory establishing crowns expanded (not closed), well-developed understory some thinning occurring, some new cohort establishment open multistory canopy, understory often burned.
Young	56–89	27	300	27	
Mature	93–106	21	980	21	
Old	190–316	30	470	30	

^aStand age defined as the ninetieth percentile of the tree stem age distribution. Stem diameter is average DBH of stems >5.0 cm DBH. Stem density is number of stems >5.0 cm DBH per ha. Height is average maximum. Sample size is three replicate plots per age class.

Table 3. Measurement Errors Associated With Each Component of NEP^a

Component of NEP	Source of Largest Measurement Error	Average Standard Error, gC m ⁻² yr ⁻¹	Average Coefficient of Variation, %	Average Resulting Error in NEP, %
Tree wood production	prediction of radial growth based on stem diameter for the portion of trees from which no increment cores were taken	58	20	20
Tree foliage production	spatial sampling error associated with optical estimates of leaf area within each plot	36	26	16
Understory wood production	predicting mass from stem diameter using non-site-specific allometry	20	317	7
Understory foliage production	uncertainty in estimates of leaf retention	8	35	2
Woody debris decomposition	spatial sampling error in field estimates of debris volume	17	25	5
Litterfall	spatial sampling error in field estimates of litterfall mass	45	33	18
Δ coarse roots	prediction of radial growth based on stem diameter for the portion of trees from which no increment cores were taken	33	57	13
Δ fine roots	standard error of a linear slope (not different from zero) fit to the change in fine root mass across the chronosequence	<1	NA	<1
Δ soil carbon	standard error of a linear slope (not different from zero) fit to the change in soil carbon across the chronosequence	5	NA	1

^aAverage SE and CV computed across all 36 plots. In the case of Δ fine root and Δ soil C, mean values were zero, and therefore a CV is not computable.

were taken. DBH and height were combined with site and species-specific allometric equations to determine the past and present volume of stemwood, branches, and bark for each tree. Tree wood volume was converted to mass using site and species-specific wood densities determined from the increment core samples. Strictly speaking, live tree wood increment as determined in this manner underestimates tree wood NPP by the live growth that any dead trees experienced in the measurement interval before dying [see *Bond-Lamberty et al.*, 2004]. However, since estimates of tree wood mortality in the Pacific Northwest are around 2% [*Harcombe*, 1986; *Grier and Logan*, 1977], we assume our estimate of live tree wood increment to equate to tree wood NPP. Understory wood production was not directly measured; rather, we assumed it to approximate 0.06 of the estimated understory wood mass [*Grier and Logan*, 1977].

2.5. Foliage NPP

[11] Overstory foliage NPP was calculated as the product of total overstory leaf mass and the canopy-average leaf retention time. Total overstory leaf mass was calculated as the product of leaf area index (LAI, expressed as hemispherical leaf area per unit ground area) and canopy-wide estimate of leaf mass per unit area. LAI for each plot was determined optically using a LAI2000 plant canopy analyzer (LICOR, Lincoln, Nebraska) as the average of 30 sample points per plot. Corrections for crown clumping were obtained using a TRAC crown gap analyzer (3rd Wave Engineering, Canada), while corrections for shoot clumping and wood interception were made as by *Law et al.* [2001a]. Canopy-wide leaf retention time and leaf mass per unit area (LMA) were determined by weighting plot and species-specific values by the frequency of overstory species in each plot, which were determined from 7–20 representative shoot samples collected in each plot. Understory foliage NPP was calculated as the understory foliage mass divided by leaf retention time, which varied from 1 year for deciduous species to 6 years for certain evergreen shrubs. Herbaceous production was assumed to

be all foliage and equal to the aboveground biomass. All foliage tissue mass was converted to carbon mass by multiplying by 0.45.

2.6. Respiration From Woody Debris

[12] The volume, species, and decay class (one of five) of woody debris in each study plot was estimated using line intercept transects (four 100-m transects for woody debris >10 cm diameter and four 25-m transects for woody debris <10 and >2 cm diameter). For each piece of debris encountered in the surveys, diameter was converted to volume per unit area (using probabilistic geometry), then to mass per unit area (using a species-specific density), then to mass loss per unit time (using site, species, or diameter-specific decay constants), and finally to carbon loss per unit time (assuming 0.50 g C/g debris). Scaling constants were provided by M. Harmon (personal communication, 2001), and the details regarding the scaling of woody debris transects are given by *Harmon and Sexton* [1996].

2.7. Δ Coarse Root

[13] The annual change in coarse root (roots >2 cm diameter) was calculated as the difference between live coarse root growth minus the decomposition of dead roots attached to stumps and snags. Live coarse root growth was estimated from tree radial increment, a single region-wide allometric equation relating coarse root volume to tree diameter and species-specific wood density values (*Santantonio and Hermann* [1985] and *Van Tuyl* [2003], respectively). The decomposition of dead coarse roots was computed as volume of coarse roots attached to stumps and snags (determined, using the same allometric equations used for live trees) multiplied by decay class-specific densities and site and species-specific decomposition constants [*Janisch and Harmon*, 2002].

2.8. Δ Fine Root and Soil Carbon

[14] Measurement inaccuracies make it very difficult to directly assess a single year's change in either fine root mass

or mineral soil carbon. Consequently, we used the variation in these carbon pools across the chronosequence to estimate how much these pools may change over the course of a single year. Using this approach, neither the change in fine root mass or mineral soil carbon was discernibly different from zero. Especially notable was fine root mass that was no higher in mature forests than in the youngest age classes. Recognizing that this conclusion is subject to type II statistical error [Davidson *et al.*, 2000], we assigned an uncertainty to these zero values based on the site-wide range of pool size (see Table 3).

2.9. Ecosystem Heterotrophic Respiration

[15] Because we are more confident in our ability to estimate the components of NEP contained in equations (1) through (4) than our ability to estimate belowground heterotrophic respiration, we made estimates of total ecosystem heterotrophic respiration (HR_{total}) by subtraction according to equation (5).

$$HR_{\text{total}} = NPP_{\text{total}} - NEP_{\text{total}}, \quad (5)$$

where NPP_{total} is the sum of NPP of foliage wood and roots. HR_{total} was then further partitioned into fluxes from mineral soil, forest floor, and woody debris based on the relative magnitude of these fluxes estimated independently on each plot. Heterotrophic respiration from the mineral soil and forest floor were approximated by multiplying estimates of annual soil respiration on each study plot [Campbell and Law, 2004] by forest type-specific fractions representing the portion of soil respiration attributable to live roots, mineral soil, and forest floor based on in situ root separation measurements which averaged 40, 44, and 16% for root, mineral soil, and forest floor, respectively (B. E. Law, unpublished data, 2000; methods given by Law *et al.* [2001b]).

2.10. Back-Calculated C Losses

[16] An equation describing annual NEP as a function of age must include a zero point representing carbon lost to the atmosphere during the initiation disturbance if it is to be applied to a population of stands, some of which may experience such disturbances in the NEP measurement interval. Accordingly, estimates of carbon combusted as a result of slash burning following harvest were back-calculated for the youngest stands in each forest type. Without specific knowledge of what percentage of post-harvest debris actually combusted in site preparation and believing that among-site variation in debris combustion is more a function of detritus volume than the fraction combusted, we assumed that 80% of harvest debris was combusted in each plot (M. Harmon, personal communication, 2001). Consequently, NEP at age zero (NEP_0) was computed as negative 0.80 of the preharvest carbon stocks in foliage, tree branch, and understory wood, which in turn was estimated from stump inventories and site-specific allometric relationships between basal area and biomass pools.

[17] Another NEP, reflecting the heterotrophic losses occurring immediately following disturbance but prior to the re-establishment of vegetation (NEP_1), was also back-calculated for each of the youngest stands. Maximum NEP_1 at this stage was estimated as the sum of woody debris decomposition (set equal to that of the initiation stand) and soil and litter heterotrophic respiration (set equal to the average of total soil respiration among old stands on the site). Minimum NEP_1 was estimated as the sum of respiration from woody debris decomposition (recalculated from the initiation stand as if all volume was of the freshest decay class) and soil heterotrophic respiration (equal to the total soil respiration measured on the initiation stand multiplied by the site-wide fraction attributable to heterotrophic sources). The methods and values for soil respiration and separation of heterotrophic fraction are given by Campbell and Law [2004] and Law *et al.* [2001b], respectively.

[18] NEP_0 was located on the chronosequence at year zero, while NEP_1 was located on the chronosequence at the end of the first year following disturbance. By not including the export and fate of carbon as forest products, we limit our definition of NEP to the on-site exchange of carbon between the forest and atmosphere apart from a regional mass balance. It is important to recognize that by adopting this flux perspective, landscape NEP may be positive despite reductions in storage due to harvest.

2.11. Uncertainty Propagation

[19] We recognize that there is a great deal of uncertainty associated with each of the above-mentioned field measurements. In reporting field estimates of NEP, we believe it is more important to define the range of possible NEP values than to report a single "best estimate." When quantifying the behavior exhibited by a certain condition class (forest type and age in this study), the most useful measure of uncertainty is the variance among condition replicates. We refer to this as experimental uncertainty and calculate it for all measured parameters, including NEP, as the standard deviation among each of the three plot replicates. It is important to realize that computing this experimental uncertainty is possible only when there is true plot replication [Hurlbert, 1984]. When quantifying the structure of an individual study plot, the most useful measure of uncertainty is that stemming from measurement inaccuracy. We refer to this as measurement uncertainty. The measurement uncertainty associated with each component of the NEP equation was propagated through to NEP, using a Monte Carlo stochastic uncertainty estimation (M. Harmon, <http://carbon-model.forestry.oregonstate.edu>). In this approach, values for each component of NEP are randomly selected from a probability distribution defined by the mean and uncertainty of that component as well as the estimated covariance among components. We simulated NEP in this manner 1000 times for each plot and reported measurement uncertainty as the range in which 90% of the outcomes occurred. The sources of error assigned to each component of NEP are shown in Table 2. While these are not the sole sources of error for each parameter, our experi-

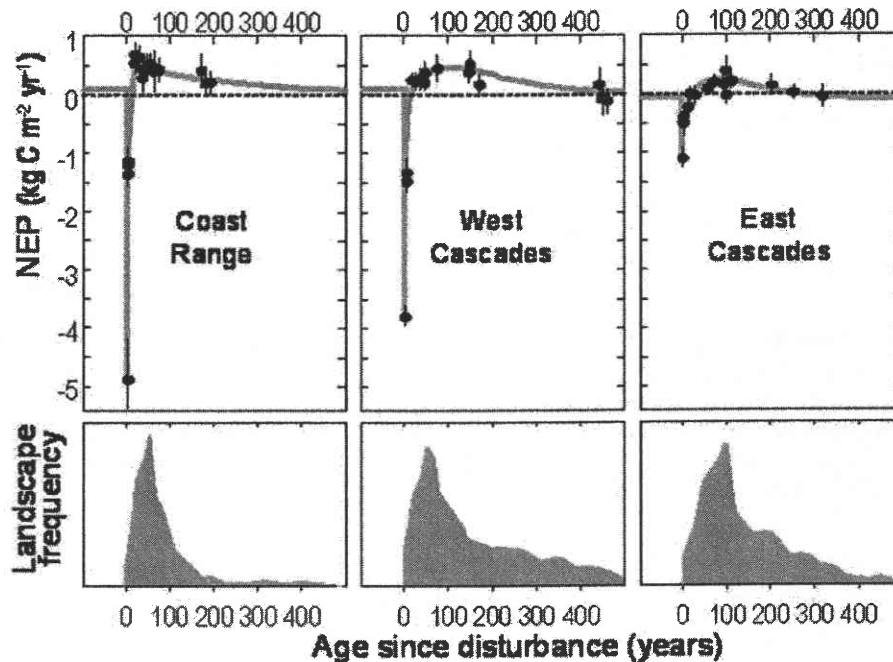


Figure 3. Successional trends in NEP measured in three climatically distinct forest types in Oregon and the current distribution of forest ages in forest type. Error bars represent measurement error expressed as 90% confidence intervals.

ence suggests that they dominate the uncertainty of each parameter estimate.

2.12. Regional Age Class Distribution

[20] To assess the importance of age class distribution in weighting landscape level NEP, equations of the following form were fit to each chronosequence,

$$y = y_0 + a \cdot \exp\left(-0.5(\ln(x/x_0)/b)^2\right), \quad (6)$$

where y is NEP and x is age since stand-replacing disturbance for each of the 12 study plots plus the back-calculated NEP_0 and NEP_1 . This three-parameter lognormal function was the simplest equation that captured the biologically relevant trends in NEP and produced an R^2 of greater than 0.94 for each chronosequence. Current age class distributions for each of the forest types are shown in Figure 3 and were determined from a combination of Forest Inventory Analysis (FIA) and Current Vegetation Survey (CVS) field surveys (comprehensive USDA forest inventories of Forest Service and privately owned lands, respectively). For each of the 4500 survey locations, forest age was calculated as the ninetieth percentile of the distribution of tree ages [Spies and Franklin, 1991].

[21] The landscape-level variability in NEP resulting from a given age class distribution was determined by counting the NEP predicted for each 1-year age class as many times as that age class would probabilistically occur in a 1000-cell landscape and then computing the standard deviation among all counts. The same approach was used to determine the variability in NEP experienced in the life of a

single stand following a disturbance event, except that in this case, all age classes were counted evenly since a single stand spends an even amount of time at each age.

3. Results and Discussion

3.1. Successional Trends in NEP

[22] As shown in the top panels of Figure 3, successional patterns in NEP are remarkably similar to that theorized by Odum [1969]. That is, disturbance initiates a large spike of negative NEP (driven in this case by the combustion of harvest residue) followed by a recovery to positive, then maximum NEP, with some decline thereafter.

[23] In the Coast Range, positive NEP is reached in less than 10 years following disturbance. In the West Cascades, positive NEP is achieved as early as 20 years following disturbance. The ponderosa pine forests growing in the East Cascades first attain positive NEP about 30 years following disturbance, which is similar to values reported for jack pine forests in Saskatchewan [Howard *et al.*, 2004] and lodgepole pine forests in Colorado [Smith and Resh, 1999].

[24] Generally speaking, maximum NEP corresponds to the time when stands first reach the maximum leaf area for the site, that is, about 10, 60, and 90 years following disturbance for the Coast Range, West Cascades, and East Cascades respectively [Sun *et al.*, 2004].

3.2. Component Fluxes of NEP

[25] To understand which factors are most important in driving successional trends in NEP, it is necessary to consider the component fluxes separately. NEP immediately follow-

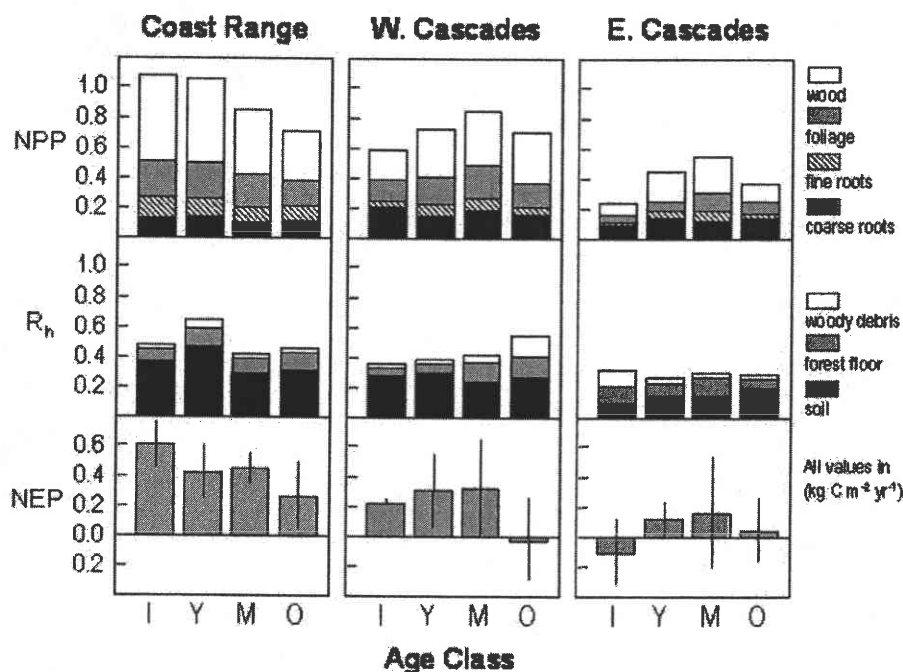


Figure 4. Component fluxes of NEP by age class and forest type. NPP, net primary production; R_h , heterotrophic respiration. Values are all reported as $\text{Kg C m}^{-2} \text{yr}^{-1}$ and represent the average of three replicate stands in each age class (I, initiation; Y, young; M, mature; O, old). Error bars are the SD among the three replicate stands.

ing disturbance is driven almost entirely by the mass of combusted or decomposing detritus, which in turn reflects the biomass of the site prior to harvest. The subsequent trajectory in NEP includes also the contribution of plant production. In Figure 4, the NEP for each age class is broken first into total net primary production and heterotrophic respiration and further into carbon accumulation by wood, foliage, coarse roots, and fine roots as well as carbon release by woody debris, forest floor, and mineral soil.

[26] The decline in NEP with age at the Coast Range is the result of a decline in NPP balanced against substantial yet relatively stable heterotrophic respiration. The production of foliage and fine roots remains surprisingly consistent across all age classes in the Coast Range such that the age-related decline in total production among these forests can be attributed almost entirely to declines in wood and coarse root production. Substantial rates of heterotrophic respiration in all age classes offset nearly half of the net production but do not appear to contribute as much as NPP to successional trends in NEP. Because the Coast Range forests recover more quickly from stand-replacing disturbance and we did not have stands less than 10 years of age, we missed the pattern of increasing NPP and NEP soon after disturbance, which is seen at the other sites.

[27] Age-related trends in wood and coarse root production are largely responsible for successional trends in NEP in the West Cascades, too. In these forests, however, maximum production is not reached until the mature age

classes (~100–200 years following disturbance). Furthermore, an increase in respiration from woody debris and the forest floor in the oldest age class compounds the effects of late successional decline in production and plays a key role in lower NEP in these old forests.

[28] The most pronounced successional trends in NPP occur at the East Cascade site where wood, coarse root, and foliage all contribute to a doubling of NPP between the initiation and mature age classes. At this site, a decline in woody debris respiration over time is somewhat compensated by an increase in soil and forest floor respiration, leaving total heterotrophic respiration remarkably consistent across the entire chronosequence such that the trend in NPP is the primary driver of the trend in NEP.

[29] Excluding detritus combusted as a result of disturbance itself, aboveground and belowground wood production and the heterotrophic respiration of mineral soil are the fluxes that contribute most to magnitude of NEP in all three forests. However, owing to the lack of consistent trends in heterotrophic respiration over the chronosequences, it appears that successional trends in NEP across all sites are driven chiefly by the net production of wood. Generally speaking, the age class at which NEP first declines corresponds to the age class at which wood production first declines. The decline in stand-level wood production following crown closure is a nearly universal phenomena [Ryan *et al.*, 2004]. This pattern was originally attributed to age- and/or size-related increases in autotrophic respiration

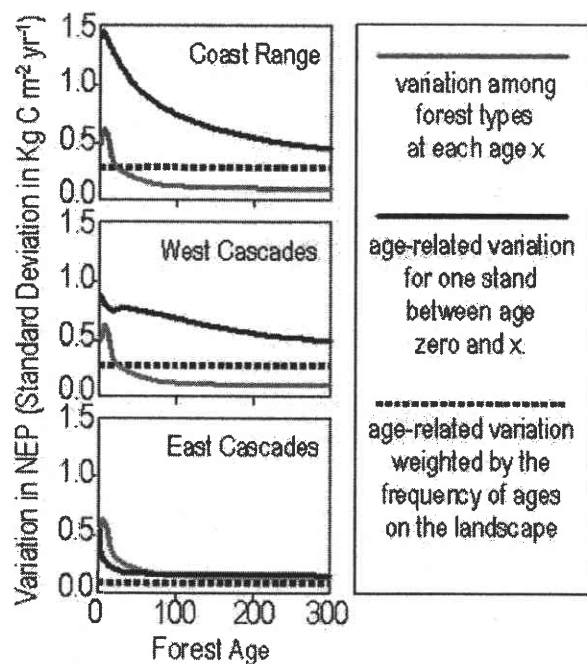


Figure 5. A comparison of the variation in NEP attributable to (1) the edaphoclimatic differences among forest types (variation among forest types at each age x), (2) disturbance events acting on a single stand (age related variation amortized up to age x), and (3) disturbance regimes acting on the whole landscape (age related variation weighted by the frequency of stand ages on the landscape).

[Odum, 1956; Yoda *et al.*, 1965]. Subsequent studies on individual trees, however, suggest decreases in gross primary production as the cause, brought on by either height-related hydraulic constraints [Yoder *et al.*, 1994; Magnani *et al.*, 2000] or by nutrient immobilization [Gower *et al.*, 1996]. We may never identify a single physiological explanation for age-related decline in wood NPP that can be applied across sites [Weiner and Thomas, 2001], but even empirical relationships between tree height, canopy position, and resource-use efficiency can be useful in describing the changes in stand-level production that occur over stand development [Binkley, 2004]. The NEP of old forests in this study is influenced by a decrease in wood production relative to younger forests in all three sites. Unfortunately, the decline in wood production observed after age 40 in the Coast Range, after age 200 in the West Cascades, and after age 100 in the East Cascades does not consistently correspond to either changes in canopy height or the dominance structure of the stand (see Table 2). Consequently, we cannot rule out any of the above-mentioned hypothesis regarding the declining wood production. Declining NPP with stand age should not be ignored when considering age-related change in annual rates of NEP.

3.3. Disturbance Versus Edaphoclimatic Forces

[30] Because the stands in these chronosequences were harvested at or near their maximum branch, foliage, and

root mass, among-site variation in the pulse of negative NEP following disturbance can be attributed largely to differences in the production capacity among sites. Considering this, and the degree to which disturbance history in the region has been dominated by the clear-cutting of mature forests, it is possible to assess the relative importance of disturbance and edaphoclimatic forces in shaping the spatial patterns of NEP by comparing the successional variability in NEP within a forest type to the variability in NEP among forest types of the same age.

[31] From the perspective of an individual stand, the variability in NEP attributable to forest succession is typically 1 to 10 times higher than the variability among forest types of the same age, regardless of the period over which NEP is amortized (Figure 5). The one exception to this is the East Cascades, where low total biomass minimizes the amount of carbon lost following disturbance and reduces the successional variability in NEP to levels equivalent to the variability observed among forest types of the same age. In other words, where the potential to gain and therefore lose carbon is high (e.g., the Coast Range and West Cascades), a harvest disturbance has more influence on stand-level NEP than does Oregon's edaphoclimatic gradient, even when amortized over 300 years.

[32] If weighting successional trends evenly over the life of a stand can be used to assess the influence of disturbance on the NEP of an individual stand, then weighting successional trends by the age-class distribution on the landscape can be used to assess the influence of disturbance on the spatial patterns of NEP. Figure 5 shows that once the effect of stand age on NEP is weighted by the distribution of age classes in each landscape, its influence on NEP becomes one half to one fifth less than the effect of age on a single stand.

[33] It should be noted that this approach to separating the influence disturbance and edaphoclimatic forces on stand-to-stand variation in NEP is limited to landscapes where stands mature to some site-specific biomass before being stand replaced. While such may have been the dominant mode of forest replacement in the last century, shifts in management toward selective harvest and fuels reduction on federal lands and shorter harvest rotations on industrial lands are such that the production capacity of the site and disturbance type are confounded in their influence on initial conditions following disturbance [see Harmon, 2001; Li *et al.*, 2003].

3.4. Sensitivity of Landscape NEP to Disturbance

[34] Any single disturbance regime (i.e., a fixed probability of stand replacement) will eventually lead to an age class steady stasis where landscape NEP equals zero plus any soil carbon accumulation. Assuming the limitations on production and decomposition remain constant, positive or negative landscape NEP is a response to the disequilibria imposed by alterations in disturbance frequency [Kurz *et al.*, 1998; Harmon and Marks, 2002]. As is the case for many landscapes, the disturbance history of Oregon forests has been one of shifting disturbance frequencies, the most notable of which were the anthropogenic increase in stand replacement that began nearly a century ago and the abrupt decrease in harvest that has occurred on federal lands a

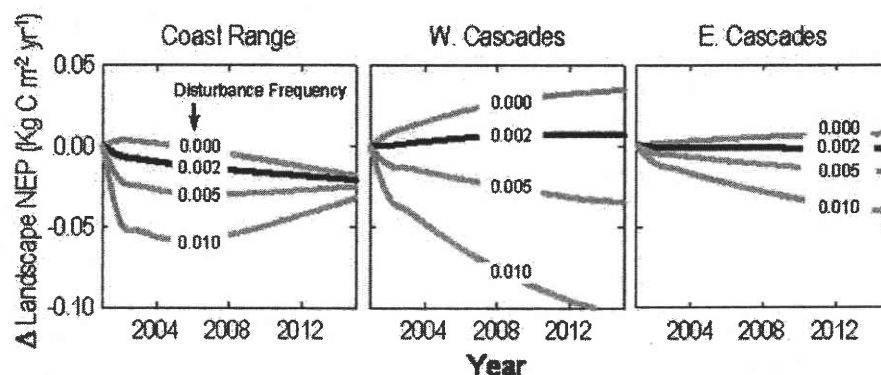


Figure 6. Sensitivity of landscape NEP to short-term changes in disturbance frequency. Shaded lines represent either an increase or decrease in disturbance frequency. The black line approximates current disturbance frequency. The steepness of the curves represents the relative sensitivity of each forest type to shifts in the age class distributions resulting from changes in disturbance frequency.

decade ago [Spies *et al.*, 2003]. The resulting disequilibria in age class distribution is apparent in Figure 3. If, as these distributions suggest, the median stand age is over 50 years and NEP is relatively consistent between the age of 50 and 150 years in all three forest types, the current age class distributions should be able to mature with only minimal influence on the rate at which these landscapes remove carbon from the atmosphere. However, even a small change in the number of stands in the early, steep portion of the NEP curve (0–10 years) could greatly increase both the magnitude and spatial variability of landscape carbon fluxes. For example, the shortening of rotation cycles on Oregon's privately owned land may have substantial effects on landscape level NEP.

[35] To more closely examine how site-specific differences in the successional trends of NEP affect the sensitivity of landscape NEP to alterations in disturbance frequency, we conducted a sensitivity analysis where landscape NEP was calculated by weighting age-dependent NEP by various hypothetical age class distributions simulated by allowing the current age class distribution to advance 20 years into the future, recruiting new stands at frequencies ranging from 0 (no stand replacing disturbances) to 0.01 (approximately 10 times the current disturbance frequency). The results of this simulation are shown in Figure 6.

[36] For all forest types, an increase in disturbance frequency led to a decrease in landscape NEP as a larger number of stands experience very negative NEP. The relatively flat response of East Cascades forests suggests that these forests are the least sensitive to changes in disturbance frequency in terms of the absolute amount of carbon uptake relative to the other forest types. The landscape NEP of the West Cascades is by comparison very sensitive to alterations in disturbance frequency. The response of Coast Range forests suggests an intermediate sensitivity to disturbance regime changes. The different sensitivity these landscapes exhibit toward changes in disturbance frequency can be traced, in large part, to the successional trends in NEP reported in Figure 3. For instance, the 20 years required for NEP to level out in the

West Cascades means that a sudden recruitment of young stands will depress NEP for 2 decades. The response of landscape NEP to disturbance in the West Cascades is further compounded by the magnitude of the negative NEP spike, which results from the ability of these forests to accumulate large biomass pools that become respiring detritus following disturbance. The forests in the Coast Range are left with similarly large detritus pools following disturbance; however, high early production rates shorten the number of age classes contributing to negative NEP.

[37] Strictly speaking, some of the differences in sensitivity these landscapes exhibit toward changes in disturbance frequency stem from differences in the current age class distribution. However, in a modified analysis where the age class distributions of each site were imposed on the successional patterns of NEP from each of the other sites (data not shown), the relative sensitivity of each site to changes in disturbance frequency was preserved. In other words, the sensitivity to short-term changes in disturbance regime among these sites is determined chiefly by the ratio of recovery rate to harvest residue and is highest in the West Cascades, lowest in the East Cascades, and intermediate in the Coast Range.

[38] Because these simulations contain no feedback between harvest intensity and any preharvest conditions such as biomass or nutrient status, they are not useful in predicting long-term responses to various disturbance regimes. To accurately model long-term responses to disturbance, one must consider the interaction of initial and time-dependent conditions [Apps, 2003]. Nevertheless, the simulations presented here do illustrate how differences in growth rate and biomass potential among Oregon forest types influence the sensitivity of landscape-level NEP to decadal scale alterations in disturbance frequencies, all else being equal.

4. Conclusions

[39] From the results reported in this and other studies, it is clear that forest NEP varies widely and characteristically as a function of age since disturbance. It is also clear that the

distribution of forest ages is playing a key role in defining landscape-level NEP at any given time. By weighting forest type-specific successional patterns in NEP by the distribution of age classes in that forest type, we made two observations about how disturbance history is shaping current rates of NEP.

[40] First, by concentrating the age class distribution into a range where NEP is relatively stable over time, regional disturbance histories in Oregon are functioning to moderate the spatial variation in NEP attributable to disturbance to levels equal to or less than that attributable to Oregon's edaphoclimatic gradient, despite the fact that an individual stand experiences more variation in NEP as a result of disturbance than that observed among similar aged forests growing in different edaphoclimatic regions in Oregon. These results emphasize the difference between a disturbance event acting on a given forest stand and a disturbance regime acting on a forest landscape. Second, the site-specific biology of Oregon forests renders them differently sensitive to short-term changes in disturbance regimes.

[41] In the last decade, concerns over biodiversity and wildfire in western forests has led to a shift in management objectives on federal forest land from wood products production to fuel reduction and the creation of structural habitat. Lower harvest intensity has already led to a shift in age class distribution toward older stands [Spies et al., 2003]. By increasing the regional biomass, these changes in disturbance regime will lead to increased carbon storage on the landscape [Harmon et al., 1990]. However, considering that the median stand age in each of the three forest types already lies at or near the period of maximum NEP, the rate at which this landscape draws carbon from the atmosphere is expected to decrease from their current levels.

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