



Inter-annual variability and spatial coherence of net primary productivity across a western Oregon Cascades landscape



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ABSTRACT

Inter-annual variability (IAV) of forest Net Primary Productivity (NPP) is a function of both extrinsic (e.g., climate) and intrinsic (e.g., stand dynamics) drivers. As estimates of NPP in forests are scaled from trees to stands to the landscape, an understanding of the relative effects of these factors on spatial and temporal behavior of NPP is important. Although a high degree of spatial coherence (i.e., the degree of spatial synchrony over time) is often assumed, this inherent behavior is rarely examined. Quantifying this term may improve future predictions as site-level estimates are scaled up spatially. We quantified the spatial coherence of bole biomass production (BBP) within and between trees, and bole-related NPP (NPP_B) between sites of varying age, elevation, moisture, and species composition across a forested landscape in the western Cascade Range of Oregon. Within sites, individual trees with lower than average BBP were the most coherent. IAV of BBP increased as average tree BBP increased and spatial coherence was reduced. Among sites, NPP_B was the most spatially coherent ($r = 0.92$) between young sites, while older sites and comparisons between age classes revealed a much larger range in spatial coherence ($r = -0.18$ to 0.85). Our findings indicate climate variability may be of greater importance for spatial coherence between young sites, and that intrinsic factors could be decreasing spatial coherence between older sites or sites not in close proximity. The wide range in spatial coherence between sites found in this study, coupled with the complex land use history patterns across forested landscapes, has significant implications for modeling and scaling of NPP.

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1. Introduction

Quantifying and modeling the temporal and spatial variability of processes involved in the global carbon cycle is central in the prediction of response to changing global climate and land use patterns, and thus important to management of forests into the future. Net Primary Productivity (NPP) is an integral part of ecosystem carbon balance in terrestrial ecosystems. The balance between NPP and losses of carbon through heterotrophic respiration determines in part whether an ecosystem is a net source or a net sink of carbon from the atmosphere (i.e., Net Ecosystem Production (NEP) and Net Ecosystem Carbon Balance (NECB); e.g., (Janisch and Harmon, 2002; Randerson et al., 2002; Law et al., 2003; Harmon et al., 2004). The inter-annual variability (IAV) of NPP of forests is a func-

tion of both extrinsic (e.g., climate) and intrinsic (e.g., stand structure and composition, small scale disturbance, microclimatic variation created by stand structure, and competition) drivers. Many studies have shown climate in part determines tree growth and site productivity patterns (e.g., Fritts, 1976; Brubaker, 1980; Graumlich et al., 1989; Cook and Kairiukstis, 1990; Gedalof and Smith, 2001; Peterson et al., 2002; Fritts and Swetnam, 1989), while others have reported stand dynamics related to disturbance, mortality, and competition to be key drivers of tree growth as well (e.g., Marks and Bormann, 1972; Swetnam et al., 1985; Fritts and Swetnam, 1989; Cook and Kairiukstis, 1990; Bormann et al., 1995; Piutti and Cescatti, 1997; Lutz and Halpern, 2006).

Predicting ecological change at multiple temporal and spatial scales for ecosystems presents a challenge because of a lack of knowledge of IAV for processes such as NPP (Knapp and Smith, 2001). Factors influencing IAV at the scale of a site (e.g., disturbance and competition) will in part determine the degree IAV is modulated as NPP is scaled to the landscape. Furthermore, spatial location on the landscape affects the response to identical system

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drivers (Kratz et al., 2003). For example, the topographic position of a site (e.g. elevation, slope, and aspect) can affect the variation in climatic patterns influencing that site (Kratz et al., 1991). In addition, site history should be considered as spatial variation associated with the heterogeneity of land use can play an essential role in ecosystem production at the landscape scale (Turner et al., 2003). Recent simulation modeling efforts (Smithwick et al., 2007) have shown decreased IAV (i.e., modulation) and temporal changes in landscape scale carbon balance as more stands with unique histories are simulated. The modulation of NPP over time in response to land use, disturbance regime, and climate change may also determine the magnitude of NEP and NECB. Therefore, the degree to which intrinsic factors occurring at smaller spatial or temporal scales modulate IAV may need to be accounted for to accurately predict future carbon balance.

Biogeochemical (BGC) models (e.g., (Running and Gower, 1991; Running and Hunt, 1993; Running, 1994; White et al., 2000) used for estimating and predicting NPP over large scales (regional to global) are based on physiological processes interacting with climate at very fine temporal resolutions (i.e., days to months). While some parameters and state variables (e.g., leaf area index) in BGC models change with forest age, many (quite logically) assume similar relative responses to climate regardless of age. Moreover, many BGC models do not include what we have described above as intrinsic drivers that could also add IAV. Therefore, the IAV of currently modeled NPP between sites is likely to be highly correlated from year to year (i.e., highly synchronous), at least to the degree that underlying climatic and edaphic drivers are correlated spatially. However, if intrinsic drivers are also important, then it is possible for site to site correlations to be different than expected from IAV caused by climate. This has consequences as model estimates are scaled up spatially because the degree of spatial synchrony of processes such as NPP will determine the degree of modulation at broader spatial scales. For example, as site synchrony decreases in a landscape the degree of modulation at the landscape level increases. Although the temporal variability and spatial correlation of NPP within and between stands will in part shape ecosystem carbon balance across the landscape, the degree to which these behaviors modulate NPP over space and time has generally not been assessed.

Spatial coherence, defined as the degree to which signals of different sites across space are synchronous (i.e., correlated) through time (definition adapted from Magnuson et al., 1990; Soranno et al., 1999; Baines et al., 2000; Baron and Caine, 2000), can be a useful measure to better understand the degree of correlation of NPP and IAV across space and thus improve NPP modeling and scaling efforts. In addition, an understanding of coherence can be useful when monitoring forests response to climate change, as lower spatial coherence may indicate the need for increased sampling across ecological gradients (Larsen et al., 2001).

We hypothesized that if physiologic responses to climate (extrinsic factors) are the main drivers of NPP IAV at both the individual tree and site scales, then the spatial coherence of this variable would be extremely high regardless of spatial proximity and differences in site characteristics (e.g., xeric versus mesic sites). In addition, NPP would be highly responsive to year to year climatic variation. Conversely, if intrinsic factors exhibit a greater influence on NPP patterns, we would expect to see lower spatial coherence between sites dissimilar in age, proximity, and site characteristics. In addition, IAV of NPP would also be less correlated to year to year climatic variation.

To test this hypothesis annual tree growth increments from long-term permanent plots combined with Monte Carlo methods were used to estimate annual tree bole productivity (Woolley et al., 2007). These estimates were used to quantify the general patterns and behaviors of bole biomass production (BBP) within

and between trees, and bole-related NPP (NPP_B) between sites of varying age, elevation, moisture, and species composition across a forested landscape in the western Cascade Range of Oregon. Using correlation coefficients to estimate spatial coherence, we present estimates of spatial coherence for both annual BBP between individual trees within a site, and for NPP_B between sites across the landscape. We also examine the relationships between NPP_B and climate at the site scale. We conclude by discussing the implications of our findings for forest management as well as modeling and scaling of NPP_B across forested landscapes.

2. Materials and methods

2.1. Study site

Long-term permanent study plots were sampled (Table 1) within the H.J. Andrews Experimental Forest, Long Term Ecological Research (LTER) site. The long-term permanent study plot network was designed to monitor changes in forest composition, structure, and function (Acker et al., 1998). The experimental forest covers a 6400 hectare (ha) drainage located in the western Oregon Cascades, experiencing cool wet winters and warm dry summers. Annual average daily temperatures range from 0.6 °C in January to 17.8 °C in July, and mean annual precipitation ranges from 230 cm (cm) at lower elevations to 355 cm at higher elevations (Bierlmaier and McKee, 1989). Douglas-fir (*Pseudotsuga menziesii* Mirbel Franco), western hemlock (*Tsuga heterophylla* Raf. Sarg.), and western red-cedar (*Thuja plicata* Donn ex D. Don) dominate lower elevations. Douglas-fir and western hemlock dominance decreases, and noble fir (*Abies procera* Rehd.), mountain hemlock (*Tsuga mertensiana* Bong. Carr.), and Pacific silver-fir (*Abies amabilis* Dougl. ex Loud. Dougl. ex Forbes) become dominant as elevation increases.

We chose sites to represent environmental gradients (e.g., elevation; young, mature, and old age classes) and site moisture extremes (mesic riparian and north facing slopes versus xeric ridges and south facing slopes) at a landscape scale (~6400 ha). The differing site classifications (elevation, age, and site moisture) were used to select sites so comparisons of spatial coherence would support a better understanding of the drivers (extrinsic or intrinsic) of spatial coherence. Each site sampled was one of three age classes (young, mature, or old-growth) and occurred at elevations ranging from 460 to 1440 m (Table 1). Young sites are second-growth sites regenerating from clear-cut harvesting less than 50 years of age, while mature and old-growth sites regenerated from stand replacing fire 145–460 years before present. Ten of the eleven sites are within the *T. heterophylla* forest zone (Franklin and Dyrness, 1988), the exception being the highest elevation site within the *A. amabilis* zone. Although these sites were not randomly selected, they represent gradients of age, moisture, and elevation typical of this forested landscape.

2.2. Data collection

Tagged trees ≥ 5 cm diameter at breast height (DBH) within each permanent plot were divided into quartiles based on DBH. Sample trees from each quartile were then randomly selected prior to sampling in the field. Increment cores were taken at breast height, and tag number, species, core number, DBH, and bark thickness were recorded. All linear measurements were recorded to the nearest 0.1 cm. In old-growth and mature sites, trees ≥ 10 cm DBH were cored twice, at approximate right angles (preferentially side-slope and upslope). In the young sites, only 1 core per tree was collected due to small tree sizes. Increment cores were taken to the lab and mounted on routed blocks with wood glue and then

Table 1
Site characteristics for 11 sites sampled in the western Oregon Cascades.

Site	Age class (years)	Elevation (m)	Record (years)	Dominant tree species	Density (trees/ha)	Basal area (m ² /ha)	Bole biomass (Mg ha ⁻¹)
RS01	Old-growth (460)	510	32	<i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i>	421	62.11	533.74
RS07	Old-growth (460)	520	28	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	372	85.42	771.00
RS12	Old-growth (460)	950	28	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	224	105.0	1080.21
RS22	Old-growth (450)	1440	24	<i>Abies procera</i> <i>Pseudotsuga menziesii</i>	639	59.84	528.89
RS26	Mature (150)	920	26	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	768	102.0	803.51
RS32	Mature (145)	460	32	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	580	24.41	518.99
RS33	Mature (145)	500	22	<i>Tsuga heterophylla</i> <i>Thuja plicata</i>	428	80.54	561.41
RS34	Old-growth (450)	610	21	<i>Thuja plicata</i> <i>Pseudotsuga menziesii</i>	349	82.15	686.05
WS01	Young (40)	480–965	24	<i>Pseudotsuga menziesii</i>	1642	29.87	176.95
WS02	Old-growth (460)	475–1070	22	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	580	69.50	774.04
WS06	Young (25)	900–1020	12	<i>Pseudotsuga menziesii</i>	1277	24.05	117.55

sanded to a readable surface using a belt sander. All cores were then scanned and measured for annual radial growth (cm) using WinDendro™ image analysis software. For old-growth and mature sites, radial growth of the two cores taken were averaged and used for further analyses.

2.3. Tree increment dating accuracy

To ensure dating accuracy of radial growth measurements for mature and old-growth sites a system was used combining two methods of cross-dating. As increments were measured for individual trees, marker years (Yamaguchi, 1991) were recorded. All radial tree growth increment series were then examined using COFECHA (Holmes, 1983; Grissino-Mayer, 2001) and output statistics were compared to marker year records. Discrepancies were inspected visually on the increment core resulting in remeasurement, rejection of increment core for use in further analysis, or the measurements remaining unchanged. This technique was not used for the young watersheds because of large growth rates, complacency, and lack of missing rings in young trees (Fritts, 1976; Schweingruber, 1988), and because the length of each radial growth series was less than 50 years (Swetnam et al., 1985).

2.4. Annual NPP_B and Monte Carlo simulations

Radial growth for non-sampled trees in each site was estimated by applying the mean growth rate, and the variation about that mean, of all sampled trees from within that site in a given year using the simple random model shown in Eq. (1) (Woolley et al., 2007).

$$\hat{G}_{ij} = \mu_j + \epsilon_{ij} \quad (1)$$

The radial growth ($\hat{G}_{ij}$) of a non-sampled tree (*i*) for a given year (*j*) is predicted by adding random variability (ϵ_{ij}) to the mean growth rate (μ_j) of sampled trees for that year. The random variability is based on the mean and variance (σ_j^2) of the sampled distribution in that year.

Annual stem diameters (outside bark) were estimated for each tree using the most recently measured DBH, combined with measured or estimated annual radial growth increment. The estimation

of radial growth for non-sampled trees, assignment of mortality dates, and estimation of individual tree biomass production using annual stem diameters were repeated 10,000 times in a Monte Carlo simulation. The average of those 10,000 iterations was used as an estimate and the standard deviation as the level of uncertainty of annual NPP_B for each site.

Using long-term records of tree mortality (except for WS06 where mortality records were not available), trees that died in the past were accounted for prior to death using the same radial growth estimation process as described above for non-sampled trees. Mortality measurement intervals of three to six years created uncertainty in dates of annual mortality for individual trees. This uncertainty was captured by assigning each tree an equal probability of dying within the years between measurements. The year of death was then randomly chosen for each individual and increments were estimated from the beginning of the time series to that date.

Tree bole (stem wood and bark only) biomass production (BBP; Mg yr⁻¹) was estimated annually using stem diameters for each year with species-specific wood and bark volume equations, wood/bark volume ratios, and wood and bark density values following the methods of (Acker et al., 2002). For *Acer macrophyllum* (Pursh.), *Arbutus menziesii* (Pursh.), and *Castanopsis chrysophylla* (Dougl. ex Hook.) (Hjelmqvist), bole biomass for each year was estimated from volume equations based on height and dbh (Means et al., 1994). Tree height for these three species was estimated from dbh-height relationships (Garman et al., 1995). Biomass estimates for *Alnus rubra* (Bong.), *Prunus emarginata* (Dougl. ex Hook. D. Dietr.), *Cornus nuttallii* (Audubon ex Torr. & Gray), and *Rhamnus purshiana* (DC. Cooper) were derived using dbh based biomass equations (Means et al., 1994). In the two young sites bole biomass for *P. menziesii*, *T. heterophylla*, and *T. plicata* was estimated using dbh-volume equations modified from (Browne, 1962). All other volume equations, and all wood/bark ratios and density values were obtained from the Oregon State University Forest Science Databank (<http://www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TV009&topnav=97>). When volume equations, bark/wood ratios, or density values were not available for the less common species (e.g., *R. purshiana*) equations and values of species with similar growth forms were substituted.

Given that this analysis accounted for trees that had died in the past (and the uncertainty in dates of mortality) through permanent plot records, the change in total tree BBP annually is the Net Primary Production of tree boles (NPP_B; Mg/ha⁻¹ yr⁻¹) for each site. Production of tree boles was used for this analysis because whole tree biomass (stems, leaves, branches, roots, etc.) estimates would have been attained using diameter based allometric equations as well, and therefore would have shown similar patterns. Furthermore estimates of total aboveground NPP would not have been possible without estimates of leaf fall, a process that cannot be directly estimate without modeling leaf longevity and adding substantial uncertainty to the analysis.

2.5. Statistical analyses

Annual bole biomass production (BBP) patterns of individual sampled trees were visually examined for each site, and simple linear regression was used to examine the relationship between the long-term mean BBP and the IAV of BBP. Spatial coherence of annual BBP between individual trees within each site and spatial coherence of annual NPP_B over the study period between all sites was estimated using Pearson's product-moment correlation coefficient (r). Simple linear regressions of NPP_B over time at each site were conducted to determine if any long term trend existed in site level NPP_B. Autocorrelation within each time series was considered and was accounted for when present by using an autoregressive model with a 1 year lag (AR1).

Annual site level NPP_B (Mg ha⁻¹ yr⁻¹) was compared with annual precipitation (mm), annual average temperature (°C), monthly precipitation (mm), monthly mean temperature, summer (June–July–August) average Palmer Drought Severity index (PDSI; (Palmer, 1965), and average monthly snow depth from January through April using Pearson's product-moment correlation coefficient (r). All temperature and precipitation data was obtained from the Climate and Hydrology Database (<http://www.fsl.orst.edu/climdb/>). Data was used from the primary meteorological station at the H.J. Andrews Experimental Forest (430 m elevation), with the exception of snow depth which was collected from the central meteorological station (1018 m elevation). PDSI values were obtained from the PDSI grid developed by Cook (2004), downloaded from the National Climatic Data Center and National Oceanic and Atmospheric Administration website (<http://www.ncdc.noaa.gov/paleo/pdsidata.html>).

Young sites exhibited a trend of increasing NPP_B over time to an asymptote, and several mature and old-growth sites displayed a slight increase or decrease of NPP_B over time. Therefore, to solely evaluate IAV of NPP_B between sites and not long-term trends, a smoothing function was applied to the time series of NPP_B for all sites. This function used a local mean with a rectangular kernel and a smoothing parameter of five years. This technique resulted in unstandardized residuals of NPP_B which was used for analysis of spatial coherence between sites. Monte Carlo procedures, estimation of NPP_B, and statistical analyses were conducted using SAS v9.1 (SAS, 2002).

3. Results

3.1. BBP

Mean annual BBP (annual BBP averaged over all years) of individual trees over the study period ranged from 0.00035 to 36.69 (young), 0.0385 to 72.99 (mature), and 0.0797 to 120.31 (old-growth) kg yr⁻¹, indicating a large degree of variability between trees for all three age classes. The IAV of BBP for individual trees within sites was highly variable, with some trees expressing much

less variation than others. The range of IAV for individual trees (within tree variation over all the years expressed as %CV) was comparable for young (1–102%), old-growth (6–113%), and mature (9–146%) sites. Linear regressions (Fig. 1) of three sites (young, mature, and old-growth) showed a significant ($p < 0.001$) positive relationship between mean BBP for individual trees and the IAV (standard deviation of mean BBP) for individual trees within each sites ($r^2 = 0.72$ – 0.91).

3.2. BBP and spatial coherence

Trees whose BBP was lower than the overall mean in a site tended to be much less variable, and the observed patterns are more coherent through time than those trees accruing biomass more rapidly than the overall mean (Fig. 2). These patterns were consistent across all sites, regardless of age class. Comparisons between trees within each site yielded statistically significant correlations (r) ranging from -0.97 to 0.98 . However, only 30–40% of comparisons were statistically significant ($p \leq 0.05$) within each site, indicating a wide range of spatial coherence from high synchrony to complete asynchrony of BBP between trees.

3.3. NPP_B

Across all sites the highest mean annual NPP_B (i.e., annual NPP_B averaged over all the years; Table 2) was for a mature site (6.05 Mg ha⁻¹ yr⁻¹), while old-growth sites exhibited the largest range of mean annual NPP_B within an age class (3.63–5.85 Mg ha⁻¹ yr⁻¹). In contrast, mean annual NPP_B only varied from 4.69 to 4.84 Mg ha⁻¹ yr⁻¹ between the two young sites. Mean annual NPP_B of all the sites examined over the study period was 4.90 Mg ha⁻¹ yr⁻¹. Of the 9 mature and old-growth sites sampled, the majority experienced no directional change (increasing or decreasing) of NPP_B over time (Fig. 3). One mature site (Fig. 3c) was found to have decreasing NPP_B over the study period ($p = 0.03$) of 0.05 Mg ha⁻¹ yr⁻¹. In contrast, one old-growth site (Fig. 3a) had a slightly significant ($p = 0.052$) increase in NPP_B of 0.02 Mg ha⁻¹ yr⁻¹ over the study period.

A wide range of values of annual NPP_B occurred between sites within each age class, with mature sites being the least variable (4.37–7.92 Mg ha⁻¹ yr⁻¹). A young site (WS01) expressed the greatest range in NPP_B within a site (1.34–6.46 Mg ha⁻¹ yr⁻¹) due to increasing leaf area in the first 30–40 years following clear-cut harvesting. With the exception of the two young sites, both the highest and lowest rates of NPP_B occurred at low elevation old-growth sites, with annual NPP_B ranging from as low as 2.83 to as high as 7.62 Mg ha⁻¹ yr⁻¹.

A young site had the highest IAV of NPP_B (1.57 Mg ha⁻¹ yr⁻¹) due to the increase in live biomass from stand initiation (Table 2; Figs. 4 and 5). Among the remaining sites the highest IAV of NPP_B was exhibited by an old-growth site (0.78 Mg ha⁻¹ yr⁻¹). The IAV for NPP_B for the average of all the sites was 0.42 Mg ha⁻¹ yr⁻¹ and the CV of 8.5% were much lower than that for many of the individual sites (11–33%; Table 2).

A similar relationship to that of individual tree BBP and IAV was found for NPP_B of sites (Fig. 4). Specifically, as annual NPP_B increased, the IAV in NPP_B increased ($p = 0.019$). This relationship was not as robust ($r^2 = 0.52$) as that of individual trees ($r^2 = 0.72$ – 0.91) within old-growth sites.

3.4. NPP_B and climate

The strength of the relationship between annual NPP_B and climate varied among sites. NPP_B for individual sites was correlated with either temperature or precipitation variables, but not both (Table 2), indicating different climatic variables may be influencing

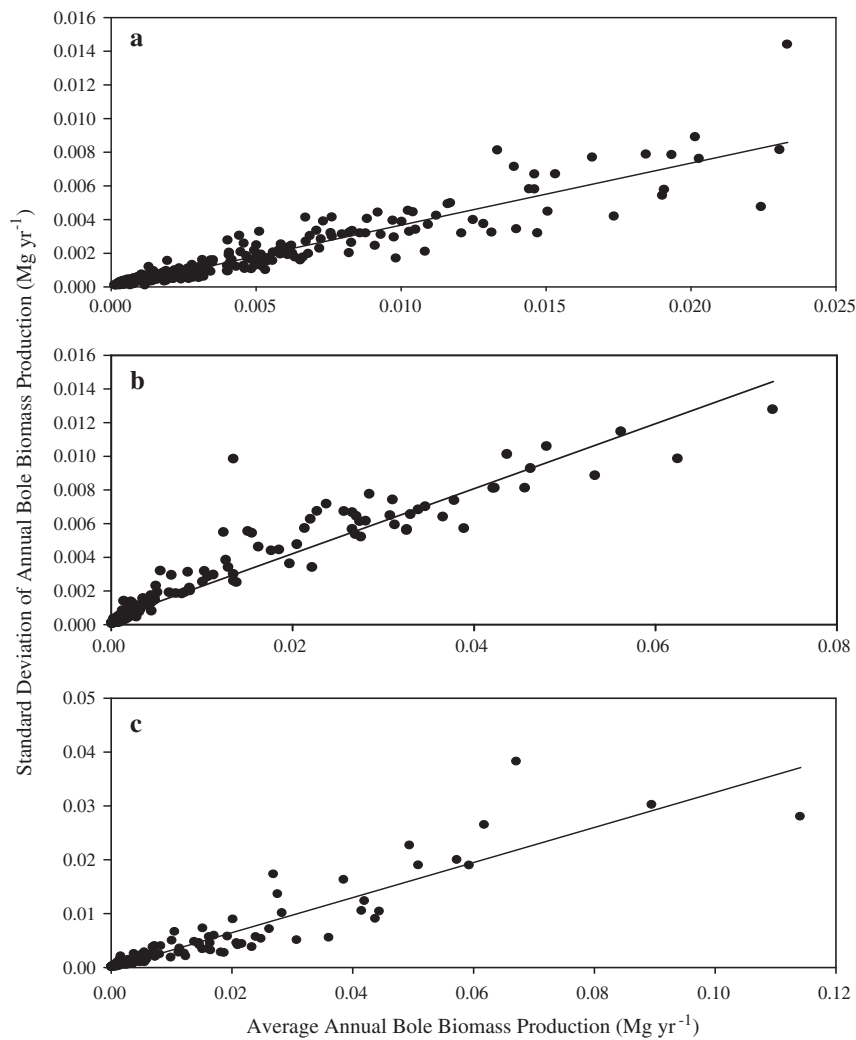


Fig. 1. Linear regressions illustrating the relationship of increasing inter-annual variability (indicated by the standard deviation) of annual bole biomass production as mean bole biomass production increases. Each panel is a simple linear regression of trees from one site (**a** = young, **b** = mature, and **c** = old-growth).

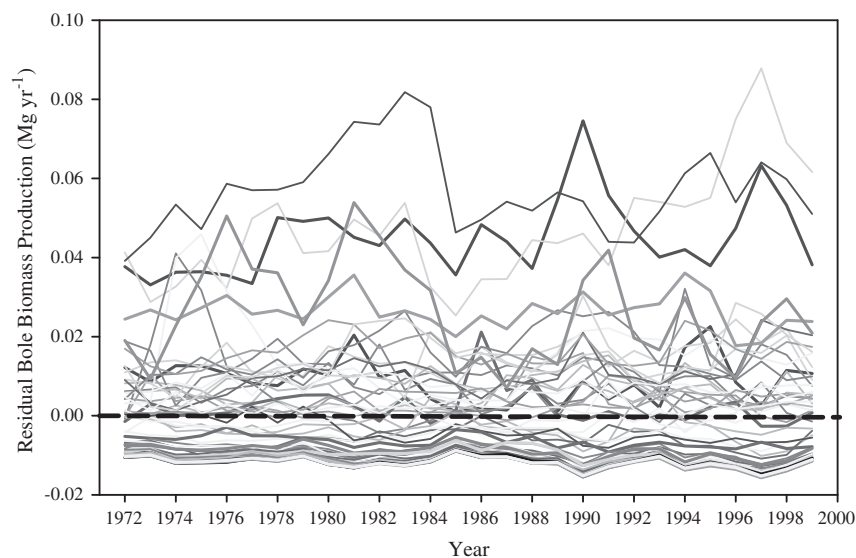


Fig. 2. Residual annual bole biomass production (annual bole biomass production – average annual growth increment) for 56 trees in an old-growth site. Dashed line (0.0) indicates the mean growth rate of all trees over time. As growth rate increases spatial coherence decreases and inter-annual variability increases.

Table 2
Estimates of NPP_B and climatic correlations (*r*) for the sites sampled.

Site	Mean annual NPP _B (Mg ha ⁻¹ yr ⁻¹)	Inter-annual variability ^a (Mg ha ⁻¹ yr ⁻¹)	CV (%)	Climate variable	<i>r</i>
RS01	3.95	0.72	18.3	PDSI	0.47
				June precipitation	0.44
RS07	3.63	0.41	11.4	September temperature	0.63
				November temperature	0.46
				January temperature	0.46
				January precipitation	0.51
RS12	3.86	0.43	11.1	September temperature	0.43
				January temperature	0.43
RS22	5.11	0.60	11.8	October precipitation	0.49
				April snow depth	−0.65
RS26	6.05	0.75	12.4	PDSI	0.49
				June precipitation	0.44
RS32	5.02	0.70	13.9	October precipitation	0.42
RS33	4.06	0.66	16.2	June precipitation	0.48
RS34	5.60	0.71	12.7	August temperature	0.45
				Mean annual temp.	0.52
WS01	4.69	1.57	33.5	September temperature	0.48
WS02	5.85	0.78	13.3	October precipitation	0.59
WS06	4.84	0.64	13.3	March snow depth	−0.82
				Total annual precip.	0.51
Average	4.90	0.422	8.6	January precipitation	0.51
				January temperature	0.63
				August temperature	0.49
				October precipitation	0.57
				March snow depth	−0.76

^a Inter-annual variability is the standard deviation of mean annual NPP_B over the study period.

different sites. A number of sites responded positively to early growing season precipitation (June precipitation $r = 0.44$ – 0.47), while several others responded positively to late growing season precipitation (October precipitation $r = 0.39$ – 0.59), and others to mean temperature (September and August mean temperature $r = 0.42$ – 0.63). Xeric sites also responded positively to higher PDSI values ($r = 0.47$), indicating drought as a factor affecting NPP_B of drier sites. High elevation sites were negatively correlated with early to mid-spring snow depth (March and April snow depth; $r = -0.82$ and -0.65 , respectively), presumably due to a prolonged growing season with decreased snow depth in late spring.

Many of the significant relationships between climatic variables and NPP_B found at the site scale were also significant for the average of the sites (Table 2). Specifically, temperature and precipitation variables were consistently correlated to NPP_B at most sites, and this pattern was evident for the average of sites as well. Furthermore, the degree to which the average of sites NPP_B was correlated with these climatic variables was similar to or higher than those observed at the site scale.

3.5. NPP_B and spatial coherence

An analysis of spatial coherence of residual NPP_B between sites resulted in a wide range of correlations ($r = -0.18$ to 0.92). Of the 55 comparisons between sites, 12 were not significant ($p > 0.05$), indicating no spatial coherence between these sites. All but one of the comparisons between sites was positive. The negative correlation ($r = -0.18$), between an old-growth and young site, was not significant ($p = 0.7663$) and thus the correlation was considered zero.

The highest degree of spatial coherence of all comparisons occurred between the two young sites ($r = 0.92$ $p = 0.0013$) of contrasting elevations. Comparisons of young and old-growth sites

comprised the greatest degree of variability in spatial coherence between age classes, ($r = 0.0$ – 0.64). In contrast, old-growth sites had the largest range in spatial coherence ($r = 0.57$ – 0.85) of any within age class comparison. Xeric and mesic comparisons fell at the lower end of this range ($r = 0.57$) and sites with similar site moisture characteristics had higher correlations ($r = 0.60$ – 0.80) than those that did not. Comparisons along the elevation gradient showed no consistent pattern within or between age classes ($r = 0.49$ – 0.92).

The variability in spatial coherence produced complex temporal patterns in the average response of the 11 sites. In some years NPP_B was in synchrony; for example, in 1990 all sites (Fig. 4) showed a significant increase in NPP_B. While in other years (e.g., 1984 and 1992) there was either a complete lack of spatial coherence among sites, lags between sites, or a lack of spatial coherence between some sites. There were several possible lags evident between sites as well (Fig. 5), in which a decrease in one site was not seen until the following year in another site (e.g. 1992–1993, 1996–1997, and 2001–2002).

4. Discussion

4.1. NPP_B

The estimates of annual NPP_B presented in this paper are comparable to those found in many other studies in the area (Gholz, 1982; Acker et al., 2002; Campbell et al., 2004) and forests in the Pacific Northwest (Graumlich et al., 1989). However, our estimates of annual NPP_B for old-growth are up to three times higher than those reported by Grier and Logan (1977), Harmon et al. (2004). Both Grier and Logan (1977) and Harmon et al. (2004) reported long-term averages, while our estimates were derived from data collected at an annual scale. Estimates of NPP_B for all age classes

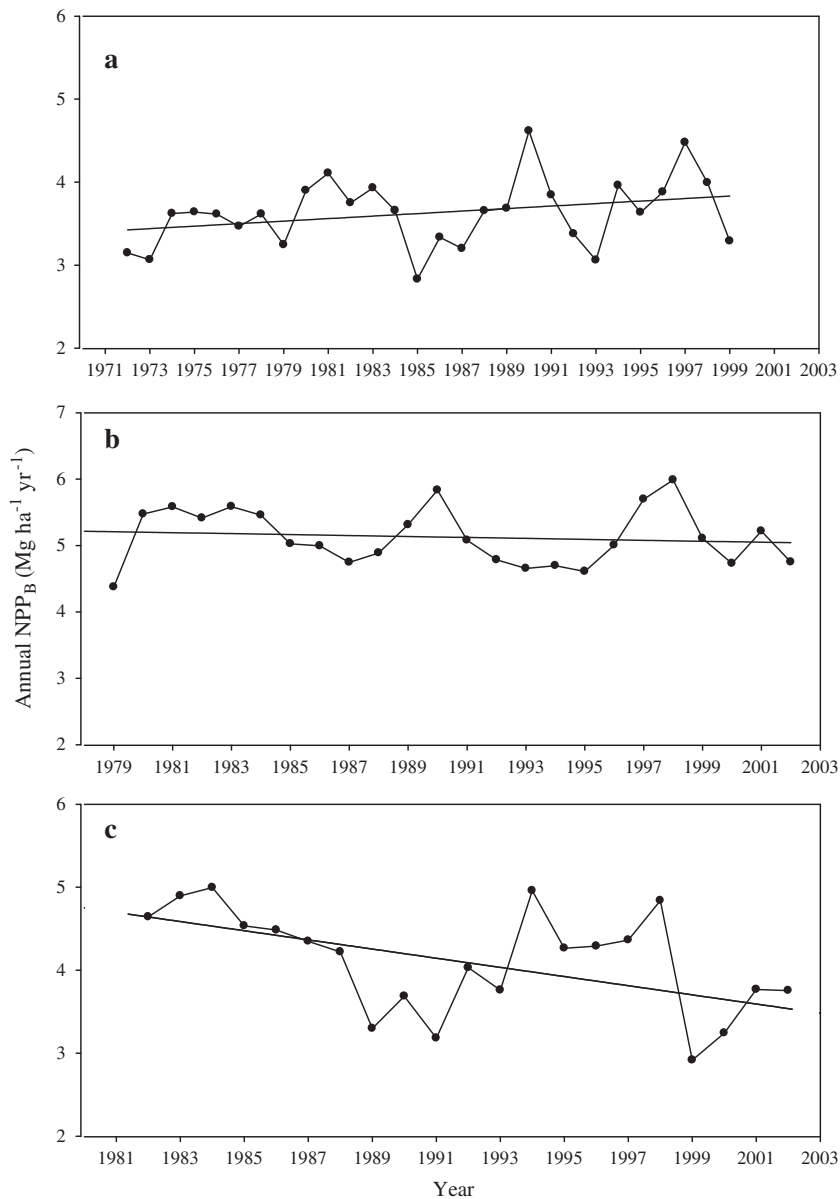


Fig. 3. Annual NPP_B (Mg ha⁻¹ yr⁻¹) over time for three sites illustrating examples of the long-term change in productivity. Panels a and c were the only mature and old-growth sites found to have a significant long-term pattern in NPP_B. Panel b is an example of the long-term trends found in the remaining 7 sites showing no change in NPP_B over the study period. Note that the time series are of different lengths for the 3 sites.

are up to 60% lower than reported by Van Tuyl et al. (2005). However, the plots used to derive the latter estimates covered the entire western Oregon Cascades, included branch, foliage, and both coarse and fine roots (which could add substantially to NPP), and exhibited a much wider range of variability NPP_B within age classes (approximately 3.2–9.4 Mg ha⁻¹ yr⁻¹) than our estimates.

The inclusion of mortality estimates in our calculation of NPP_B is more realistic for most forests across the Pacific Northwest, and should improve our estimates of spatial coherence between sites as temporal variability of annual mortality patterns is site specific (Franklin et al., 1987; Lutz and Halpern, 2006). If not accounted for, a loss in biomass annually due to mortality of up to 1% (Franklin et al., 1987; Grier and Logan, 1977; Clark et al., 2001) will compound error in NPP estimates over long periods, and in small sample plots the death of one large tree could result in a severe underestimate of biomass increment (Clark et al., 2001).

Mean annual NPP_B estimates were comparable between young sites, but varied more widely for mature and old-growth sites. Both

young sites displayed an increasing trend of NPP_B. The similarity in means of younger sites is likely driven by the successional trend of monotonically increasing leaf area as stand development progresses following stand establishment (Turner and Long, 1975). Whereas, in older mature and old-growth stands differences in structure and disturbance history between sites are likely factors increasing the variability in mean annual NPP_B. Interestingly, the 2 young sites did not have the highest NPP_B of all sites, and were superseded in NPP_B by 5 of the remaining 9 sites. Presumably these sites will continue to accumulate biomass over time, although at a slower rate given recent trends in our data suggesting declines of NPP_B towards the end of the study period for young sites (Fig. 5).

We did not find any consistent long-term trends in NPP_B over time for many of the older sites we sampled. NPP_B tended to remain relatively stable over the study period, with the exception of one old-growth site with increasing NPP_B and one mature site with decreasing NPP_B. This finding is similar to that of studies that indicate both positive and negative growth responses to climate

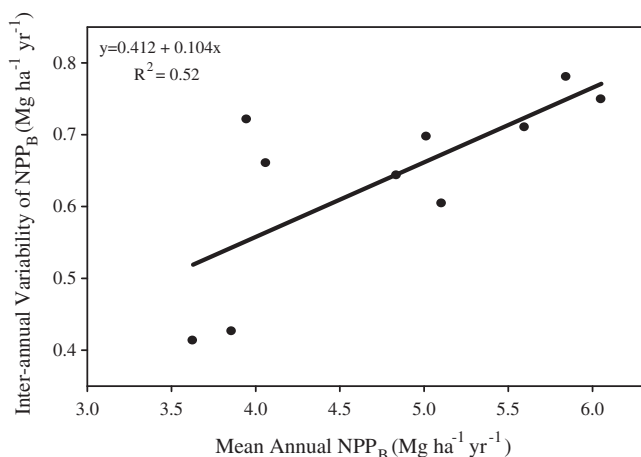


Fig. 4. Linear regression illustrating the relationship of increasing inter-annual variability (IAV) of annual NPP_B (Mg ha⁻¹ yr⁻¹) as mean annual NPP_B (Mg ha⁻¹ yr⁻¹) increases across sites on the landscape. IAV calculated as the SD of mean annual NPP_B.

warming (e.g., Wilmking et al., 2004), but conflicts with studies that report broad scale increases in productivity with warming (e.g., Myneni et al., 1997). Given that at fine spatial scales sites may be limited by different climatic and edaphic (temperature versus moisture) factors there is no reason to expect identical responses within a landscape. Additionally, it may be that for mature and old-growth age classes, the length of our time series (18–30 yrs) was not adequate to detect a consistent trend.

4.2. NPP_B and climate

Greenland et al. (2003) point out that year to year fluctuations in precipitation in the Pacific Northwest are responsible for variation in NPP, but the authors also indicate that the sign of a given ecosystem response could differ, and that further examination of the causes of fluctuations in NPP and NEP are warranted. Although some climate variables were correlated with NPP_B at individual sites in this study, we did not find consistent correlations between NPP_B and climate variables across all sites. Moreover, given the variability of spatial coherence in NPP_B it appears that climate is only responsible for a portion of the IAV found in NPP_B. Future analyses may want to focus on climatic variables that integrate multiple climate signals used in dendroclimatology studies (e.g., water balance deficit; Littell et al., 2008). For example, it is well known that tree growth for many conifer species is correlated with growing season temperature and precipitation (e.g., Case and Peterson, 2005; Peterson et al., 2002) as well as snowpack and growing season length (e.g., Peterson and Peterson, 2001). However, these studies often apply detrending procedures that remove much of the growth signal not related to climate. We chose to leave that non-climatic noise to better understand the other underlying variation in growth patterns, and may be why we are seeing less of a correlation with climatic variables.

Regardless of age, sites exhibiting the highest spatial coherence ($r > 0.50$) were either responding to similar climatic parameters such as PDSI, monthly and annual precipitation, or were in close proximity on the landscape (with the exception of the two young sites). In addition, the high degree of spatial coherence of all sites in individual years would have potentially led to an amplified landscape response in those years. Therefore, sites that are generally out of synchrony may become more synchronous when climate drivers influence the landscape as a whole. For example, one year with a particularly high degree of spatial coherence between sites

(1990) had one of the wetter and warmer spring months (April) of the study period. This may have increased early season growth of lower elevations sites and induced a longer overall growing season for higher elevation sites through early snow melt. An increase in growth across all sites indicates that climate patterns that influence larger spatial scale annually may potentially overcome finer scale processes to produce synchrony in certain years. This year was also a transition period between El Niño/Southern Oscillation (ENSO) cycles (Wolter and Timlin, 1993), shifting from a cooler and wetter to a warmer and drier trend, providing both higher levels of moisture for increased growth at lower elevations, and longer, warmer growing season at higher elevations. Climate variability did seem to be driving IAV of NPP_B between sites that were more spatially coherent, specifically the relationship between NPP_B and October precipitation and PDSI. The positive relationship of some sites with monthly mean temperature in summer months and precipitation later in the growing season was somewhat surprising, although Graumlich et al. (1989) found that in high elevation forests, summer temperature as a significant factor in annual NPP and annual precipitation less so.

Correlations of some sites with early growing season precipitation indicate that timing of precipitation is of importance, but the timing and what climatic feature is significant appears to vary from place to place. The relationship between snow pack in mid to late spring and NPP_B at higher elevations is further evidence of the possible importance of the timing of climatic factors. This is similar to findings of Peterson et al., (2002), who also found negative correlations of growth with winter precipitation for high elevation systems. Therefore, when predictions are made regarding effects of future climate change scenarios on ecosystem processes, the focus may need to shift from average changes in climate (e.g., annual precipitation) to changes in the variability and timing of annual precipitation and other factors such as increased temperature and shifts in decadal trends that affect inter-annual fluctuations of ecosystem responses.

4.3. Spatial coherence

Our analyses indicate that patterns of spatial coherence are influenced primarily by intrinsic factors, but that extrinsic factors also play a role depending on the age class and spatial proximity of sites examined. This is evidenced by the wide range of spatial coherence found within sites (BBP) and among sites (NPP_B), the variability of climatic factors associated with NPP_B at different sites across the landscape, and specific years of high spatial coherence across all sites. The wide range in the degree of spatial coherence between sites across the landscape found in our study differs to some extent with the range of spatial coherence of NPP ($r = 0.46$ – 0.83) found by Graumlich et al. (1989) in forests in the Cascades of Washington. Several possible causes exist for these differences. Our study had a larger number of sites spanning a wider range of ages, elevations, and moisture regimes, which may have led to lower spatial coherence. The comparisons in our study were also made over a much shorter time period (10–30 yrs versus 200 yrs in Graumlich et al. (1989). Longer study periods likely result in wider range of climatic conditions. Therefore, it is possible that if our study period was extended spatial coherence between our sites may increase.

Examination of IAV and spatial coherence of tree BBP within sites and NPP_B among sites across the landscape resulted in the emergence of similar behaviors across spatial scales. Individual trees with BBP less than the site average were more spatially coherent than those higher. As mean BBP increased spatial coherence between trees decreased and IAV increased. The wide range of spatial coherence between individual trees decreases IAV within a site, resulting in modulation of site NPP_B. Our analysis suggests

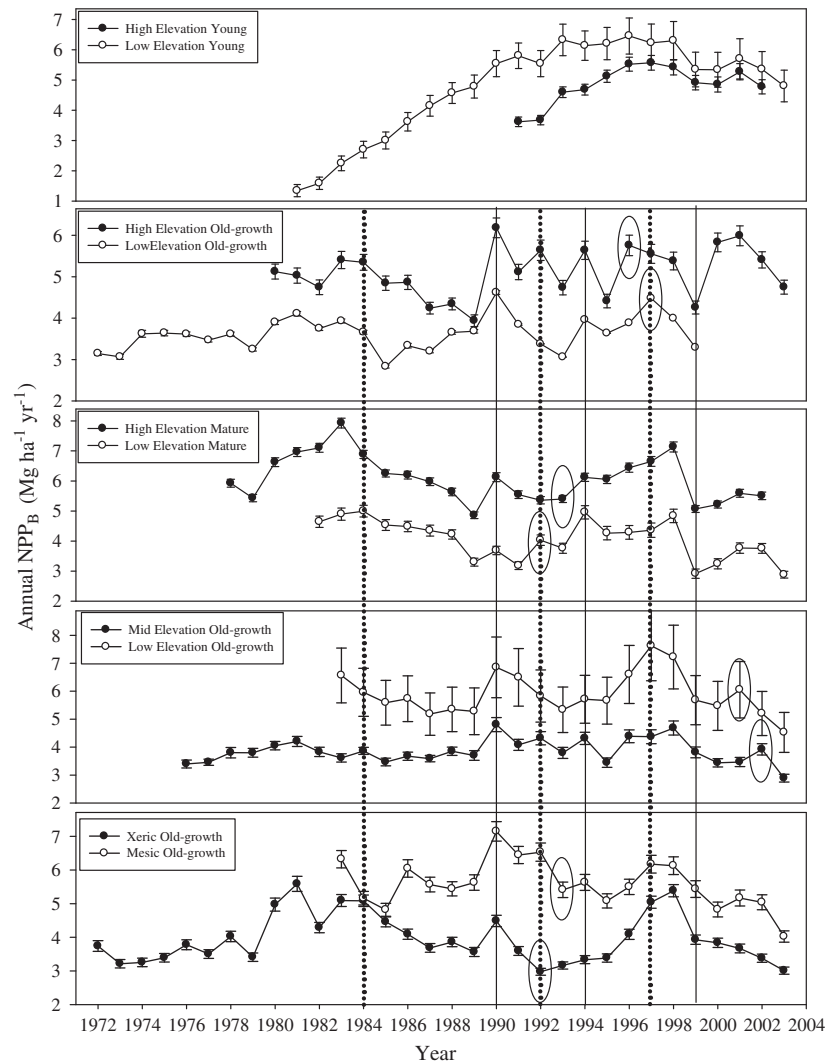


Fig. 5. Annual NPP_B ($\text{Mg ha}^{-1} \text{yr}^{-1}$) over time for eight sites of varying age, elevation, and moisture regime. Panels represent comparisons within age classes. Error bars are the SD of 10,000 Monte Carlo simulations. Vertical solid lines indicate high degree of spatial coherence in that year for all sites. Dotted lines indicate decreased spatial coherence in that year. Circles indicate possible lags in response of NPP_B between sites in that comparison.

that the degree to which NPP_B and IAV is modulated in a given site depends on the ratio of slow growing to fast growing trees.

Similar to behaviors found at the tree to site scale, the pattern of spatial coherence of NPP_B between sites has direct implications for estimates of landscape level annual NPP_B . Over time our estimate of “landscape” level NPP_B (we acknowledge that the 11 site average only approximated a landscape level value and was not exact) was modulated in most years due to lack of spatial coherence among sites, but in some years response between sites was spatially coherent and caused larger fluctuations (amplification) in average NPP_B (Fig. 6). As a result of the low level of spatial coherence among sites throughout the study period, IAV of NPP_B at the landscape scale is likely dampened. This result is comparable to findings from simulation studies (Smithwick et al., 2007) in which increased heterogeneity of site histories across a landscape dampened year to year variability in changes in landscape carbon balance.

Annual changes in the overall ecosystem carbon balance across the landscape will in part reflect the spatial coherence of NPP_B and thus the heterogeneity of response to climate variations, or lack thereof, within sites and across the landscape. The values of spatial coherence of NPP_B across our sites are likely much lower than can be predicted by current BGC models. The complex patterns and

“emergent” behaviors (Smithwick et al., 2003) of spatial coherence between sites we observed may not be possible to predict by simple scaling up of physiological–climatic relationships of individual trees. The two young sites in this study (spatially distant and apparently responding to different climatic drivers) exhibited a high degree of spatial coherence, suggesting that during early stages of succession stand dynamics (i.e., increases in leaf area) and physiology may be in synchrony regardless of spatial location. In landscapes dominated by young stands, it is likely current BGC models would perform well in predicting spatial synchrony. However, in landscapes of mixed age classes where NPP_B is not being driven by increasing leaf area, these models may not capture the variation in spatial synchrony we observed. Several strategies might be used to incorporate these aspects of spatial synchrony into BGC models. An empirical approach might be to degrade synchrony statistically to match observed values. However, this would depend on measuring the degree of synchrony in specific landscapes and would be hard to generalize. Alternatively, a mechanistic approach might be used. Recently, BGC models have attempted to represent population, community, and disturbance processes more explicitly (e.g., Fisher et al., 2010). Our observation within sites that slower growing individuals are more synchronous than faster growing ones suggest that one strategy might be to stratify

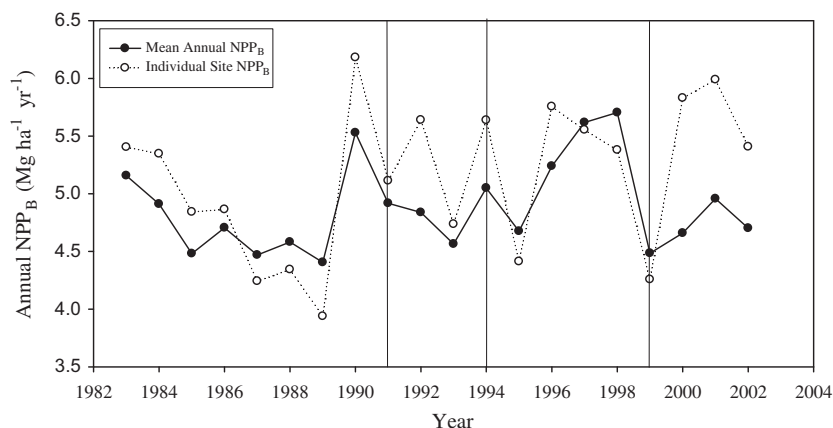


Fig. 6. Mean annual NPP_B across all sites compared with annual NPP_B of an individual site. Solid vertical lines indicate amplification of landscape response due to increased spatial coherence between sites in those years. Peak NPP_B in 1998 is from successive increase of NPP_B across most sites in 1996, 1997, and 1998. In remaining years, landscape NPP_B was modulated.

individuals (or classes of individuals) within BGC models according to growth rate. This may result in more realistic spatial coherence between sites, but needs to be explored using a large number of sites within landscapes as well as in other types of landscapes.

The high degree of spatial coherence between young sites versus the variability of spatial coherence that older forests we observed could have implications on how landscapes respond to future climate particularly if IAV in climate increases. In landscapes dominated by young forests our results suggest the potential for high IAV in NPP that would reflect increasing year to year variation in climate. Conversely, in landscapes dominated by older forests our results suggest that year to year climatic variation might be modulated resulting in lower than anticipated IAV. If landscape scale age structure overrides other drivers (i.e., climate) affecting NPP and spatial coherence then this has implications for management of heterogeneity across landscapes, and to a certain degree the perceived stability of ecological systems. It also has implications for monitoring responses to climate change (Larsen et al., 2001). In landscapes with high spatial synchrony, it should be possible to monitor few sites and understand responses of landscapes. However, in landscapes with low and variable spatial synchrony it will necessary to monitor many sites to understand landscape responses.

A deeper understanding of the specific mechanisms that control spatial coherence of NPP_B rather than the broader generalizations discussed here, would be the next research step to aid modeling and scaling of ecosystem NPP_B at landscape scales. It is imperative to have field measurements to help evaluate the performance of process models (Jenkins et al., 2001) and improve predictions of ecosystem processes such as NPP_B . This study was an attempt to begin to attain those measurements in the Pacific Northwest at an annual time step to compare with models of forest productivity for the region (e.g. Biome BGC, 3PG, etc.). Future studies directly comparing field measurements and biogeochemical models may be necessary to fully understand the uncertainties associated with scaling results using physiologically based parameters. Explicit incorporation of spatial coherence may improve our ability to scale NPP both spatially and temporally.

5. Conclusions

The results from this study suggest that spatial coherence of annual NPP_B between sites is much more variable than generally assumed. The variability in spatial coherence leads to both complex behaviors over time and a likely modulation of IAV of NPP_B

at the landscape scale. Significant correlations with climatic variables, combined with the high spatial coherence of NPP_B between some sites and among all sites in some years, indicates spatial coherence between trees (BBP) and between sites (NPP_B) was in part a function of climate. However, the climatic factors associated with IAV varied from site to site across the landscape. Local intrinsic factors (i.e., stand dynamics), spatial proximity, and stand age were also notable factors driving patterns of spatial coherence. Therefore, heterogeneity of the landscape with respect to land use (i.e., varying age classes) modulated the response of mean annual NPP_B . This has implications for management and monitoring of forests into the future under changing disturbance regimes and climate.

The climate–physiological interactions driving current biogeochemical models may not in fact be realistically constant as evidenced by the inconsistent relationships between NPP_B and climate across the landscape. The addition of intrinsic drivers to current physiologically based models should result in much lower modeled values of spatial coherence of NPP_B across the landscape. As a consequence, the year to year variability of productivity at the landscape scale would be more modulated than predicted by these models. As responses of ecosystem processes to future global change are forecasted, accounting for changes in spatial coherence when considering ecosystem management should result in more realistic and accurate representations of past, present, and future ecosystem productivity.

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