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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.

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 function 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 (extrinisic 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 sideslope 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