

## REGIONAL-SCALE RELATIONSHIPS OF LEAF AREA INDEX TO SPECIFIC LEAF AREA AND LEAF NITROGEN CONTENT<sup>1</sup>

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**Abstract.** Specific leaf area (SLA) is an important link between vegetation water and carbon cycles because it describes the allocation of leaf biomass per unit of leaf area. Several studies in many vegetation types have shown that canopy SLA is closely related to canopy leaf nitrogen (N) content and photosynthetic capacity. SLA increases as light is attenuated by leaf area down through a plant canopy. It therefore follows that across an individual biome the spatial patterns in canopy-average SLA and leaf N content should be significantly correlated with the spatial patterns in leaf area index (LAI) and canopy transmittance. In this paper, we show that the LAI across the Oregon transect is closely related to canopy-average SLA ( $R^2 = 0.82$ ) and leaf N content on a mass basis ( $R^2 = 0.80$ ). Canopy-average leaf N per unit area is highly correlated to canopy transmittance ( $R^2 = 0.94$ ) across the transect. At any given site, canopy-average SLA and leaf N per unit area do not vary significantly, either seasonally or between different codominant species occupying the same site. The results of this study suggest that the spatial distribution of canopy-average SLA and leaf nitrogen content (and perhaps canopy photosynthetic capacity) can be predicted across biomes from satellite estimates of LAI.

**Key words:** *biome; canopy transmittance; carbon cycle; coniferous forest; ecosystem modelling; leaf area index; leaf biomass; leaf nitrogen; Oregon transect; OTTER project; photosynthetic capacity; spatial patterns; specific leaf area.*

### INTRODUCTION

Specific leaf area (SLA, also known as leaf mass per unit area, specific leaf mass, or leaf specific mass) is defined as the leaf area per unit of dry leaf biomass. SLA is an important link between plant carbon and water cycles because it describes the distribution of plant biomass relative to leaf area within a plant canopy. Canopy-average SLA is an important ecosystem variable in many large-scale ecosystem models (Jandacek et al. 1989, Running and Gower 1991).

Common garden experiments reveal that SLA is genetically encoded (Mooney et al. 1978), but significant plasticity in SLA occurs within and between individual plants of the same species. Comparing leaves from within a single plant canopy, Bjorkman and Holmgren (1963) found that sun leaves typically have lower SLA and higher photosynthetic capacity than shade leaves. The distribution of SLA within a plant canopy is closely related to canopy photosynthetic capacity (Gutschick and Wiegand 1988).

Several studies have shown that the photosynthetic capacity of plants is closely coupled to the resources (light, water, and nutrients) available for growth (Field 1991). The availability of these resources during leaf

expansion is an important determinant of SLA (Tucker and Emmingham 1977). Plant species grown in water-limited environments typically have reduced SLA in comparison to the same species grown in non-water-limited environments. The reduction in SLA is correlated with an increase in both the number of mesophyll cells (Nobel et al. 1975) and leaf nitrogen (N) (Gulmon and Chu 1981) per unit of external leaf area, leading to an overall increase in plant water-use efficiency (Field et al. 1983). Along elevational (and hence temperature and nutrient) gradients, Körner (1989) found that regardless of life-form, higher altitude plants always had a lower SLA and higher leaf N per unit area than the same species at lower elevations.

In forest canopies, the vertical heterogeneity in SLA is closely coupled to the light environment inside the canopy. Hollinger (1989) demonstrated that SLA increases and leaf N per unit area and  $A_{max}$  (light-saturated photosynthetic rate under non-limiting environmental conditions) decrease with depth (and hence light intensity) in an evergreen *Nothofagus* canopy. Ellsworth and Reich (1993) reported the same patterns between SLA, leaf N, and  $A_{max}$  for deciduous forest canopies. Jurik (1986) showed that SLA at any point within a deciduous forest canopy is closely correlated to the leaf area above that point. For *Eucalyptus* forests along bioclimatic gradients, Mooney et al. (1978) and Specht and Specht (1989) found that canopy-average SLA decreases with increasing aridity. Mooney et al.

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TABLE 1. Characteristics of the study sites across the Oregon transect; adapted from Runyon et al. (1994: Tables 1 and 3). PAR = photosynthetically active radiation; LAI = leaf area index.

Site	Code*	Species	Elevation (m)	1990 annual precip. (mm)	1990 mean annual air temp. (°C)	Total annual incident PAR (MJ/cm <sup>2</sup> )	Max. LAI	
							Mean	SE
Cascade Head (alder)	1A	<i>Alnus rubra</i>	200	2510	10.1	1887	4.3	0.35
Cascade Head (old-growth)	1	<i>Tsuga heterophylla</i>	240	2510	10.1	1887	6.4	0.79
Waring's Woods	2	<i>Pseudotsuga menziesii</i>	170	980	11.2	2146	5.3	0.97
Scio†	3C, 3F	<i>Tsuga heterophylla</i>	800 (640)	1180	10.6	2113	8.6	0.95
Santiam Pass	4	<i>Tsuga mertensiana</i> <i>Picea engelmannii</i> <i>Abies lasiocarpa</i>	1460	1810	6.0	2087	2.8	0.48
Metolius	5C, 5F	<i>Pinus ponderosa</i>	1030	540	7.4	2385	2.0	0.17
Juniper	6	<i>Juniperus occidentalis</i>	930	220‡	9.1	2385	0.4	0.05

\* "C" denotes control plot, "F" denotes fertilized plot in Fig. 1a–c.

† Fertilized plot data in parentheses when different from control.

‡ Juniper site climate data from 20-yr National Oceanic and Atmospheric Administration (NOAA) averages for Redmond, Oregon.

(1978) suggest that the reduction in canopy-average SLA with increasing aridity acts to increase leaf N and Amax per unit of leaf area.

Global-scale ecosystem models designed to simulate carbon cycle dynamics across whole biomes are typically not sensitive to biome-wide variations in canopy photosynthetic capacity. Yet variations in photosynthetic capacity significantly influence the overall ability of individual biomes to sequester carbon. If canopy-average SLA, leaf N, and Amax are closely related to leaf area index (LAI), then information on the spatial patterns in LAI should be useful in describing the variations in photosynthetic capacity across a particular biome.

In this paper we report on the regional-scale relationship between LAI and canopy-average SLA and leaf N for six sites across a bioclimatic gradient in western Oregon. We show that canopy-average SLA and leaf N per unit area are closely related to site LAI in conifer forests. We also demonstrate that the use of these relationships for parameterizing large-scale carbon cycle models can significantly improve biome-wide estimates of carbon uptake.

## METHODS

### Study sites

Six sites incorporating almost the complete range in annual aboveground net primary production (ANPP) of western U.S. conifer forests (Gholz 1982) were sampled for LAI (leaf area index), SLA (specific leaf area), and leaf N (Table 1), as well as other canopy chemicals (Matson et al. 1994 [this issue]). The sites are located on a west–east bioclimatic gradient in western Oregon.

Winter storms from the Pacific Ocean provide most of the precipitation across the transect. Precipitation patterns are also heavily influenced by two north–south-trending mountain ranges, the Coast Range and the Cascade Range, leading to a reduction in precipitation, LAI, and ANPP from west to east (Gholz 1982).

Three additional stands were measured at three of the six sites because of their enhanced nitrogen status, for a total of nine plots at six sites across the transect. Nitrogen-fertilized stands at Scio and Metolius, as well as a stand of the nitrogen-fixing species alder (*Alnus rubra*) at Cascade Head, were included. A more complete description of the transect and study sites is provided by Runyon et al. (1994 [this issue]).

### LAI measurements

LAI for each site was measured using three independent methods: (1) allometric equations for the ratio of sapwood area to leaf area, (2) the LI-COR LAI-2000 (Gower and Norman 1991), and (3) the Sunfleck Ceptometer (Pierce and Running 1988). Measurements of sapwood radius at breast height were used to estimate leaf area of individual trees, which was summed and divided by the plot area to determine plot LAI (Runyon et al. 1994). The LAI-2000 relies on simultaneous measurements of blue light attenuation through the canopy at five zenith angles to estimate LAI. The Sunfleck Ceptometer measures canopy transmittance at solar noon and uses a Beer's Law transformation to estimate LAI. Each of these three measurements was averaged to obtain an estimate of the LAI for each site (Table 1). Runyon et al. (1994 [this issue]) provide a more complete description of the LAI measurements.

The accuracy of ceptometer measurements is ques-

tionable at high LAIs (Pierce and Running 1988), so this measurement was excluded when calculating the average LAI for Scio. The LAI at the Santiam Pass site was less than maximum due to an infestation of the western spruce budworm, which defoliated the current year's needles (Runyon et al. 1994). Therefore the canopy at Santiam Pass was comprised primarily of needles > 1 yr old that had developed under potential LAIs prior to infestation. Because the LAI-SLA-leaf N relationship of individual needles was formed under conditions of maximum LAI (Tucker and Emmingham 1977), we assumed the LAI of the Santiam Pass site to be at its potential (2.8), as suggested by Runyon et al. (1994). The large trees at Metolius were logged in 1989 after the study began (Runyon et al. 1994), reducing the one-sided LAI from a maximum of 3 (Gholz 1982) to 0.9 on the remaining smaller trees. Needles > 1 yr old developed under the maximum LAI, while current-year needles developed under an LAI of 0.9. To best approximate the canopy conditions during needle development, we assumed an average LAI of 2.0 at Metolius.

#### *SLA and leaf N measurements*

Canopy-average SLA and leaf N were measured for the dominant overstory species at each site on four different dates: May 1990, August 1990 (Cascade Head alder site excluded), October 1990, and June 1991. Leaf N was also measured during March 1990, except at the Cascade Head alder site, which was leafless at the time of measurement. At each date and site one randomly chosen branch was removed with a shotgun from the mid-canopy position of each of five different trees that occupied a co-dominant position in the overstory (R. H. Waring, *personal communication*). All foliage was removed from the branch and transported on ice to the Forestry Sciences Laboratory at Oregon State University (OSU; Corvallis, Oregon). At OSU, representative leaves of all age classes were combined for determination of fresh leaf area (one-sided) with the LICOR leaf area meter. The leaves were dried at 70°C to a constant mass and their specific leaf area (in square centimetres per gram) was determined (Runyon et al. 1994).

Foliage samples were transported to National Aeronautics and Space Administration (NASA)-Ames Research Center (ARC) on dry ice at -60°C. At ARC all age classes on a branch were combined, freeze-dried, and ground for measurement of foliar chemical content. Total leaf N concentration (in milligrams per gram) was measured colorimetrically with a continuous flow analyzer after block digestion using a sulfuric acid-mercuric oxide catalyst (Matson et al. 1994 [this issue]). Total leaf N concentration per unit area (in milligrams per square centimetre) is the product of specific leaf mass (1/SLA) and leaf N per unit mass. Leaf N per unit area (in milligrams per square centimetre) was

calculated using measurements of specific leaf area and leaf N per unit mass (in milligrams per gram) from the same sample branch. Averages of SLA and leaf N were calculated for each branch, and these averages were pooled to estimate canopy-average SLA and leaf N at each site on each date.

Because of the number of individual plots and measurements involved in any regional-scale ecological study, we assumed that a mid-canopy measurement could represent canopy-average SLA and leaf N. For forest canopies this would appear to be a good approximation, as suggested by the data of Hollinger (1989) and Ellsworth and Reich (1993), particularly for leaf N. To assess the accuracy of our sampling strategy in representing a true canopy-average SLA for conifer forests, we used the data of B. Yoder and R. H. Waring (*unpublished data*) and found that at the Scio site mid-canopy estimates were within 10% of true canopy-average SLA, even though SLA varied more than 100% throughout the canopy. Finally, we evaluated the utility of a predictive model of a canopy-average SLA within the framework of an ecosystem model.

Variations in canopy-average SLA and leaf N across dates for each site and across sites for each date were statistically evaluated using a one-factor analysis of variance. A post-hoc Scheffé test was used to determine significant ( $P = .05$ ) differences when temporally and spatially comparing site means of SLA, leaf N per unit mass, and leaf N per unit area. The Cascade Head alder site was excluded from all regression analyses between LAI and canopy-average SLA and leaf N. Fundamental differences in canopy light interception and nutrient cycling in the broadleaved, deciduous nitrogen-fixer *Alnus rubra* led to quite different relationships between LAI and canopy-average SLA and leaf N at the alder site in comparison to the other sites.

## RESULTS AND DISCUSSION

### *Seasonal variation in SLA and leaf N*

Significant seasonal variation in canopy-average SLA (specific leaf area) did exist across dates for each site, except for the Waring's Woods site (Fig. 1a). For a majority of the sites, the spring and summer measurements (May, August, and June) of SLA were not significantly different, while the autumn measurements (October) of SLA were significantly different from the other dates. Only at the Scio Control and Fertilized sites were there significant differences between the May 1990 and June 1991 measurements of SLA. Canopy-average SLA tended to be lowest in the spring, and increase through the summer to a peak value in October, except for the Scio Control site which showed the reverse trend. Canopy-average SLA at the Cascade Head alder site was highest in May 1990 and lowest in October 1990.

The overstory at the Santiam Pass site was occupied

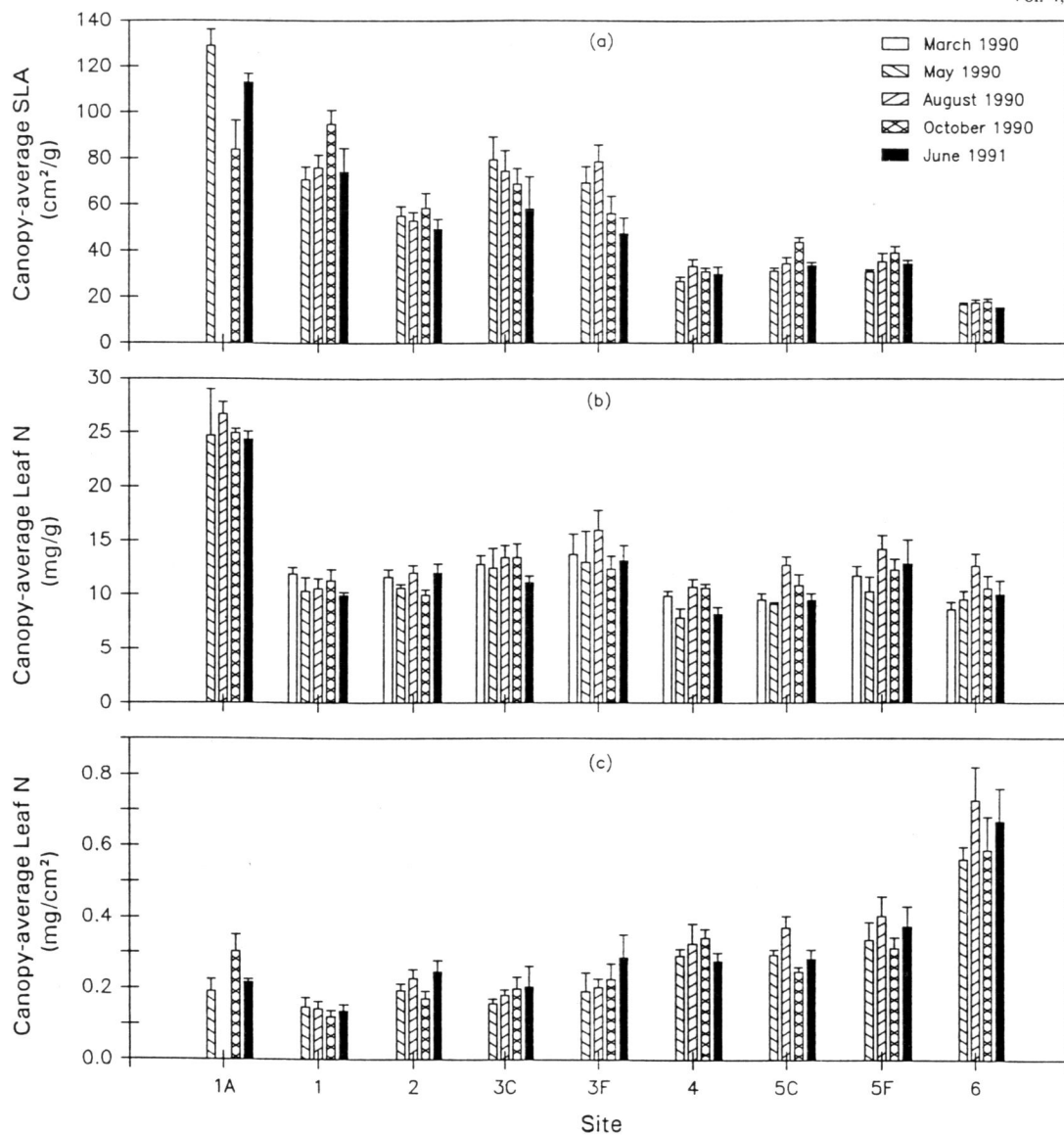


FIG. 1. Spatial and seasonal variability in canopy-average (a) specific leaf area (SLA), (b) leaf nitrogen per unit mass, and (c) leaf nitrogen per unit area for the sites across the Oregon transect. SLA and leaf N per unit area were not measured at any site in March 1990. SLA and leaf N per unit area were not measured at site 1A in August 1990. Error bars represent 1 SE. Site codes along the x axis: 1A = Cascade Head (alder); 1 = Cascade Head (old-growth); 2 = Waring's Woods (Corvallis); 3C = Scio, control plot; 3F = Scio, fertilized plot; 4 = Santiam Pass; 5C = Metolius, control; 5F = Metolius, fertilized; 6 = Juniper.

by three different species of conifers (Table 1). During August 1990 only *Picea engelmannii* was sampled for SLA and leaf N, while during October 1990 and June 1991 only *Abies lasiocarpa* and *Tsuga mertensiana*, respectively, were sampled. No significant differences were observed in measured canopy-average SLA among these three species or dates, suggesting that in natural vegetation at any given site, the primary determinant of canopy-average SLA is environmental conditions rather than species-specific characteristics (although the two are closely related).

Canopy-average leaf N per unit mass also varied seasonally for a majority of sites, although the variation in leaf N was less than the variation in SLA (Fig. 1b). In general, the autumn (August, October) measurements of leaf N were always the highest, while the spring (March, May, June) measurements were always the lowest. However, there were no significant seasonal differences in leaf N concentrations for the Cascade Head alder and old-growth sites, or the Scio Control and Fertilized sites. For the other sites, only a minority of dates were significantly different and these differ-



ences were usually between spring and autumn measurements of leaf N.

When expressed on an area basis, leaf N was less variable between dates than either SLA or leaf N per unit mass (Fig. 1c). Only the Waring's Woods, Metolius Control, and Cascade Head alder sites showed any significant differences between dates, and these differences involved only one date being significantly different from the three remaining dates. There were no significant seasonal or species differences in leaf N (mass or area basis) at the Santiam Pass site.

#### *Spatial variation in SLA and leaf N*

The variation in canopy-average SLA was much higher across the Oregon transect than it was at any one place within the transect. On average, SLA varied > 130% from site to site across the transect, excluding the highest SLAs at the Cascade Head alder site. At any particular site, canopy-average SLA varied only 27% seasonally. There were no significant differences in canopy-average SLA between the Fertilized and Control plots at Scio or Metolius on any measurement date.

Canopy-average SLA decreased from west to east along the transect, closely corresponding to patterns of precipitation, leaf area index (LAI), and light availability (Table 1). LAI and canopy-average SLA were positively and significantly correlated ( $P < .05$ ) across the Oregon transect for all five measurement dates (Table 2; Fig. 2). Table 1 indicates that there is some variation among the three techniques used to estimate LAI at each site. To assess the impact that this variation has on estimates of canopy-average SLA, we assumed an average LAI of  $4.3 \text{ m}^2/\text{m}^2$ , with an average standard error of 0.54 (Table 1). Variations in LAI of this magnitude (14%) would cause variations in estimates of canopy-average SLA of 7%, using the relationship in Fig. 2.

In comparison to the other sites, canopy-average leaf N per unit mass was almost twofold higher at the Cascade Head alder site, which was dominated by the nitrogen-fixing species *Alnus rubra* (Fig. 1b). For the conifer forest sites, the Fertilized sites at Scio and Metolius consistently had the highest leaf N concentrations, while the coldest site at Santiam Pass had the lowest leaf N concentrations. Sites with high LAI typically had higher leaf N concentrations than sites with low LAI.

Leaf N per unit mass varied almost as much seasonally (24%) as it did across the transect (36%, excluding the Cascade Head alder site). For the conifer forest sites, leaf N per unit mass was significantly correlated ( $P < .05$ ) with LAI during March and May 1990 (Table 2; Fig. 3). We hypothesize that there are two primary reasons why leaf N per unit mass is best correlated to LAI in early spring. First, significant mobilization of nitrogen (both in uptake and within the

TABLE 2. Coefficients and statistics for linear regressions of leaf area index (LAI) vs. canopy-average specific leaf area (SLA), LAI vs. leaf nitrogen per unit mass, and canopy transmittance vs. leaf N per unit area across sites by date. The regression equations have the form  $y = ax + b$ . SEE = standard error of the estimate. The Cascade Head alder site was excluded from all regression analyses (see *Methods: SLA and leaf N measurements*).

Date	a	b	R <sup>2</sup>	SEE
LAI ( $\text{m}^2/\text{m}^2$ ) vs. Canopy-average SLA ( $\text{cm}^2/\text{g}$ )				
May 1990	7.34	14.47	0.94*	6.28
August 1990	7.22	17.75	0.94*	6.02
October 1990	5.72	25.56	0.57*	16.93
June 1991	4.67	11.93	0.64*	11.93
Average	6.24	19.86	0.82*	9.89
LAI ( $\text{m}^2/\text{m}^2$ ) vs. Canopy-average leaf N (mg/g)				
March 1990	0.49	9.03	0.80*	0.84
May 1990	0.43	8.45	0.66*	1.05
August 1990	0.16	12.04	0.09	1.84
October 1990	0.21	10.45	0.33	1.03
June 1991	0.23	9.83	0.17	1.71
Average	0.31	9.96	0.48	1.10
Canopy transmittance vs. Canopy-average leaf N (mg/cm <sup>2</sup> )				
May 1990	0.49	0.15	0.97*	0.04
August 1990	0.67	0.16	0.98*	0.03
October 1990	0.48	0.16	0.85*	0.06
June 1991	0.53	0.18	0.85*	0.07
Average	0.54	0.16	0.94*	0.04

\*  $P = .05$ .

tree) may occur at this time in preparation for new leaf construction. Second, during the three remaining field campaigns presumably seasonal changes in leaf mass caused by site-to-site variations in leaf and canopy processes caused leaf N to vary seasonally while LAI was assumed to be constant (Matson et al. 1994 [this issue], Spanner et al. 1994 [this issue]). However, total canopy nitrogen (in kilograms per hectare) was correlated to leaf biomass (and LAI) on all dates across the transect (Matson et al. 1994).

The variations in canopy-average leaf N per unit area were inversely related to the variations in SLA across the transect (Fig. 1c). Leaf N per unit area varied 125% across the transect, but varied only an average of 30% seasonally at any given site. The Juniper site had consistently higher leaf N per unit area and was significantly different ( $P = .05$ ) from all other sites. Leaf N per unit area was not significantly different between the sites at Metolius (Control and Fertilized) and Santiam Pass. Leaf N per unit area of these sites was significantly lower than Juniper but significantly higher than the other sites further to the west. Neither were there significant differences in leaf N per unit area between the Control and Fertilized sites at Scio. The highest LAI sites (Cascade Head old-growth and Scio Control) consistently had the lowest leaf N per unit area.

Canopy-average leaf N per unit area was significantly correlated ( $P = .05$ ) with canopy transmittance for all

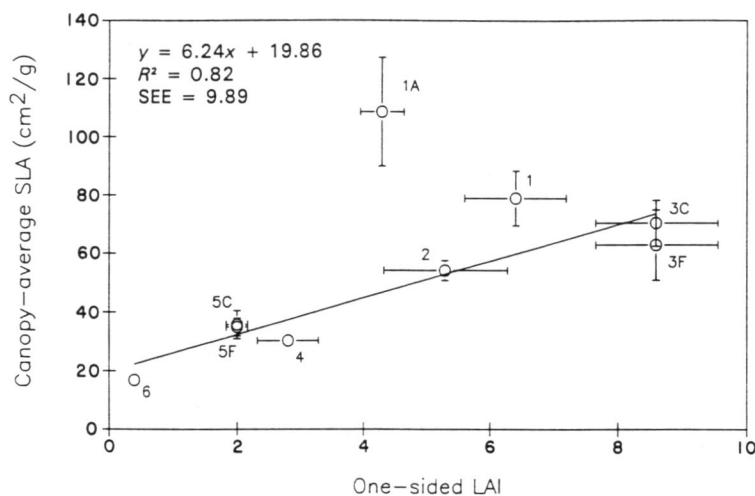


FIG. 2. The relationship between one-sided LAI ( $\text{m}^2/\text{m}^2$ ) and canopy-average specific leaf area (SLA) for the sites across the Oregon transect. For each site, canopy-average SLA is the mean value of measurements collected on each of four dates, except site 1A in which measurements of SLA were made on only three dates. Error bars represent  $\pm 1$  SE; SEE = standard error of the estimate. See Fig. 1 for a description of the site codes.

measurement dates (Table 2; Fig. 4). Canopy transmittance was calculated using the Beer-Lambert Law (see Runyon et al. 1994) which relates canopy transmittance ( $Q_i/Q_0$ ) to LAI and a canopy light extinction coefficient ( $k$ ) such that:

$$Q_i/Q_0 = e^{(LAI - k)}$$

$k$  is assumed to equal 0.5, a good approximation for conifer forests (Pierce and Running 1988).  $k$  for the Cascade Head alder site is closer to 0.6 (Runyon et al. 1994), which would reduce canopy transmittance at the Cascade Head alder site in Fig. 4 from 0.12 to 0.08.

On an area basis the canopy-average leaf N of the Cascade Head alder site was similar in magnitude to the other sites (Figs. 1c and 4) and was not an outlier in comparison to leaf N on a mass basis (Fig. 1b), or canopy-average SLA (Fig. 2).

Given the vertical (Hollinger 1989, Ellsworth and Reich 1993) and horizontal (Mooney et al. 1978) patterns of SLA and leaf N in other types of forest canopies, it is not surprising to see such strong relationships between canopy-average leaf N (per unit mass) and canopy transmittance. These studies show that variations in leaf N per unit area are important in scaling

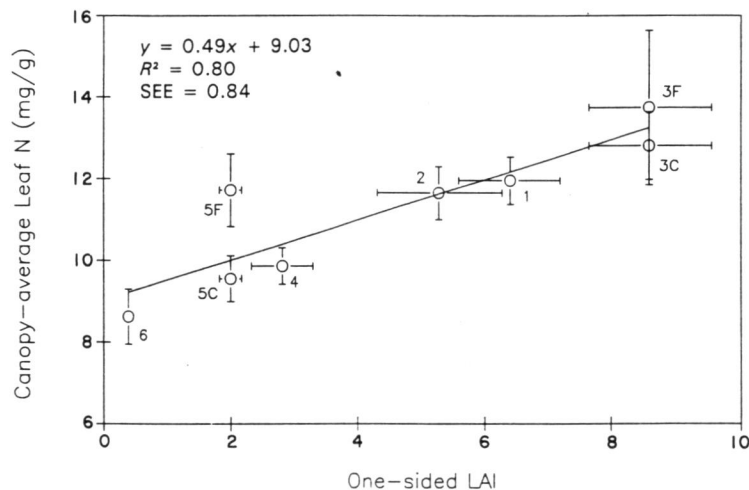


FIG. 3. The relationship between one-sided LAI ( $\text{m}^2/\text{m}^2$ ) and March 1990 canopy-average leaf nitrogen per unit mass for the conifer forest sites across the Oregon transect. Data show means  $\pm 1$  SE. The Cascade Head alder site was leafless during March 1990. SEE = standard error of the estimate. See Fig. 1 for a description of the site codes.

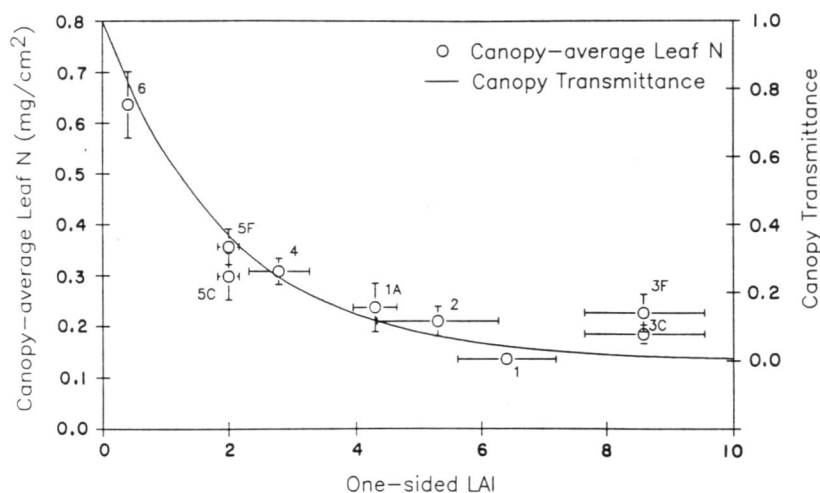


FIG. 4. One-sided LAI plotted against canopy-average leaf N per unit area and canopy transmittance for the sites along the Oregon transect. For each site, canopy-average leaf N is the mean value of measurements collected on each of four dates, except site 1A in which measurements of leaf N per unit area were made on only three dates. Error bars represent  $\pm 1$  SE. See Fig. 1 for a description of the site codes.

the photosynthetic capacity of forest canopies to availability of light inside the canopy. Across the Oregon transect Matson et al. (1994 [this issue]) found that total canopy N content averaged across all dates is well correlated to annual ANPP. Assuming that leaf N influences photosynthetic capacity (Field and Mooney 1986, Evans 1989), then photosynthetic capacity per unit leaf area across the Oregon transect should vary in proportion to our measurements of leaf N per unit area. Future studies will investigate the relationship between leaf N and  $A_{max}$  (light-saturated photosynthetic rate under non-limiting environmental conditions) across the Oregon transect.

#### *Consequences for ecosystem modelling*

The results of this study have important implications for modelling vegetation carbon and water cycles at regional and continental scales. First, some ecosystem parameters such as canopy-average SLA and leaf N per unit area vary significantly from site to site within a biome. Large-scale ecosystem models must be made sensitive to this variation in order to accurately estimate spatial and temporal carbon cycle dynamics.

Canopy-average SLA is important in many ecosystem models because it describes the relationship between canopy leaf area and biomass. As an example, we used FOREST-BGC (Running and Gower 1991) to simulate the annual aboveground net primary production (ANPP) for the Control sites at Scio (LAI = 8.6) and Metolius (LAI = 2.0), holding LAI constant and varying canopy-average SLA (and consequently leaf biomass) between simulations. In the first pair of simulations we varied SLA according to the line in Fig. 2 (74 and 31  $\text{cm}^2/\text{g}$ , respectively), while in the second

pair of simulations we held SLA constant at 50  $\text{cm}^2/\text{g}$ . Simulations of ANPP at the Scio Control site were within 6% of measured ANPP using a variable SLA vs. within 30% using a constant SLA. At the Metolius Control site, simulated ANPP was within 17% of measured ANPP using a variable SLA vs. 62% using a constant SLA.

Differences in estimated annual ANPP between the constant and variable canopy-average SLA models are due primarily to differences in leaf respiration. At the high LAI Scio Control site, the constant-SLA model underestimates canopy-average SLA, leading to an overestimation of leaf biomass and respiration and hence an underestimation of annual ANPP. The reverse is true for the low LAI Metolius Control site. The constant-SLA model overestimates canopy-average SLA, leading to an underestimation of canopy biomass and leaf respiration and an overestimation of site ANPP. Incorporating the spatial variability of canopy-average SLA within a biome into a modelling framework can significantly improve estimates of ANPP across a biome.

#### CONCLUSIONS

Using site LAI (leaf area index) to estimate canopy-average SLA (specific leaf area) and leaf N may provide inappropriate estimates of SLA in canopies that have recently been disturbed. Such is the case at the Santiam Pass and Metolius sites. Using actual LAI to estimate canopy-average SLA of the Santiam Pass site would underestimate canopy-average SLA in the year following defoliation because the canopy would not yet have adapted to the modified light environment. A similar problem would occur at the Metolius site in which

current year needles developed under a different light regime than did needles >1 yr old, due to removal of overstory trees. Full canopy replacement (which takes 2–4 yr in most conifer forests) is required before site LAI can be used to accurately estimate canopy-average SLA and leaf N.

In this study, variations in canopy-average leaf N per unit mass (9–13 mg/g, 36%) among the conifer forest sites across the Oregon transect were insignificant in comparison to variations in LAI (0.4–8.6 m<sup>2</sup>/m<sup>2</sup>, 190%), canopy-average SLA (16–79 cm<sup>2</sup>/g, 130%), and leaf N per unit area (0.15–0.65 mg/cm<sup>2</sup>, 125%). Mooney et al. (1978) reported similar patterns of SLA and leaf N for evergreen *Eucalyptus* forests in Australia. They found that: (a) midsummer measurements of leaf N per unit mass did not follow any particular pattern across a bioclimatic gradient, (b) the range in leaf N per unit mass was rather low (11–17 mg/g) and did not vary in any predictable fashion, and (c) canopy-average SLA and leaf N per unit area were closely related to climate (the ratio of precipitation to potential evaporation), and presumably to LAI and canopy transmittance. Mooney et al. (1978) also found that leaf N per unit area was highly correlated to A<sub>max</sub> (light-saturated photosynthetic rate under non-limiting environmental conditions) across their bioclimatic gradient. Field and Mooney (1986) and Evans (1989) have shown that increases in leaf N on a mass or area basis generally lead to increases in A<sub>max</sub>.

Our results agree with the results of the previously mentioned studies that focus on the effects of resource availability on LAI, SLA, and leaf N. The driest site (Juniper) had only sufficient water to support the lowest LAIs. At Juniper, water primarily limits photosynthesis (Runyon et al. 1994) so that leaf biomass is allocated towards efficient water use. Canopy-average SLA was lowest at Juniper, which has the effect of increasing the amount and area of internal mesophyll cells ( $A_{mes}$ ; Nobel et al. 1975) and leaf N per unit of external leaf area. Increases in both  $A_{mes}$  and leaf N per unit of external leaf area act to increase A<sub>max</sub> per unit of external leaf area (Gulmon and Chu 1981, Mooney et al. 1978).

The reverse was true for the cool, moist sites at Scio and Cascade Head, which supported some of the highest LAIs along the transect. In this case, light availability limits canopy photosynthesis (Runyon et al. 1994 [this issue]) so that leaf biomass is allocated to increase light and CO<sub>2</sub> uptake. At these two sites, canopy-average SLA was high, which had the net effect of increasing the leaf area per unit leaf biomass invested in canopy construction, leading to a canopy that is more efficient at light harvesting. Increases in canopy-average SLA lower leaf N and A<sub>max</sub> per unit area to levels that are suitable to the average light environment inside the canopy (Hollinger 1989).

For conifer forests, and perhaps for other biomes such as *Eucalyptus* forest (Mooney et al. 1978), chap-

paral (Field et al. 1983), deciduous hardwoods (Jurik 1986, Ellsworth and Reich 1993), tundra/alpine (Korner 1989), and grasslands (Schimel et al. 1991, Olff 1992), it may now become possible to predict the spatial patterns of canopy-average SLA and leaf N if we know the spatial patterns in LAI across a biome. Transects across bioclimatic gradients provide the best mechanism for studying the relationships between vegetation structure and function. However, multiple transects need to be established within a biome to ensure that the relationships between structure and function do not vary latitudinally, as suggested by Specht and Specht (1989).

Canopy-average SLA and leaf N are important ecosystem variables that can provide information on the spatial variation of photosynthetic capacity (Field and Mooney 1986, Gutschick and Wiegand 1988, Evans 1989). Given that satellite data provide a tool for estimating the spatial patterns of LAI across various biomes (Pierce et al. 1992, Spanner et al. 1994 [this issue]), then satellite estimates of LAI should allow quantification of the regional-scale patterns in canopy-average SLA, leaf N, and A<sub>max</sub>. Information on biome-wide variations in photosynthetic capacity can then be used to parameterize large-scale ecosystem models, improving estimates of carbon cycle dynamics across individual biomes.

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