

INTERPRETING WOODY PLANT RICHNESS FROM SEASONAL RATIOS OF PHOTOSYNTHESIS

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Abstract. In forested portions of Oregon, species richness of woody plants on plots 400–500 m² ranged from 1 to >20. We investigated what might account for this variation using a satellite-driven process model that predicts gross photosynthesis and establishes, on a monthly time step, the most constraining environmental variable. Independent satellite and ground-based data confirmed that the highest species richness occurs on sites of intermediate productivity, where 60–70% of the light is intercepted by vegetation. We demonstrated that most photosynthesis takes place during the spring and summer months for both evergreen and deciduous species. We estimated that the spring to summer ratio of gross photosynthesis (ΔP_G) varies from <1 to >5 across the state. Both the most productive coastal rainforests and least productive arid woodlands exhibited the lowest values of ΔP_G near 1, and had lowest species richness. Plots with highest species richness were located in areas with mild, moist, spring weather conditions, followed by a summer drought, with ΔP_G averaging above 3. Satellite-derived estimates of gross photosynthesis are available for more extensive analysis.

Key words: biodiversity; environmental analyses; Oregon (USA) forests; photosynthesis; process modeling; site index, species richness.

INTRODUCTION

Growing concerns about the loss of biological diversity associated with degradation in and replacement of indigenous forests has spurred interest in developing models that predict local and regional variation in species diversity in a more functional manner (Currie and Paquin 1987, Kareiva 1993, O'Brien 1998). A link between species diversity and aboveground net primary production (NPP) within a region is suggested by observations that the greatest biodiversity often, but not exclusively, occurs at intermediate levels of NPP (Waide et al. 1999). It has been hypothesized that the number of species is restricted on favorable environments because dense canopies created by a few species limit understory diversity to all but the most shade-adapted taxa. On harsh environments, light is not limiting, but conditions are otherwise so extreme that few species are able to establish and grow (Rosenzweig and Abramsky 1993, Huston 1994).

Evolutionary history plays an obvious role in defining the species' pool size, but within a region, local differences in the environment, including those associated with the spatial distribution of the canopy (Moffett 2001), probably account for much of the variation in species richness. Within this context, we believe that ecosystem process models may have a role to play in interpreting and eventually predicting variation in spe-

cies richness. Such models explicitly weigh how seasonal variation in temperature, atmospheric vapor pressure deficits, soil drought, and fertility affect photosynthesis, growth, competition, and ultimately, survival (see reviews by Shugart 1984, Waring and Running 1998). Previous research in southwestern Oregon demonstrated that process models accurately predict growth and seasonal water limitations (i.e., account for more than 75% of the observed variation) if sufficient information on soils is available (Coops and Waring 2001a). In this report, soils data were inadequate, but we demonstrate that modeling just the seasonal variation in photosynthesis spatially across forested regions in Oregon provides a general pattern comparable to that observed in woody plant species richness.

Our specific objectives are (1) to test the hypothesis that the highest number of woody plant species occurs on sites of intermediate productivity in Oregon, and (2) to provide an ecological explanation for such a pattern using a physiologically based process model.

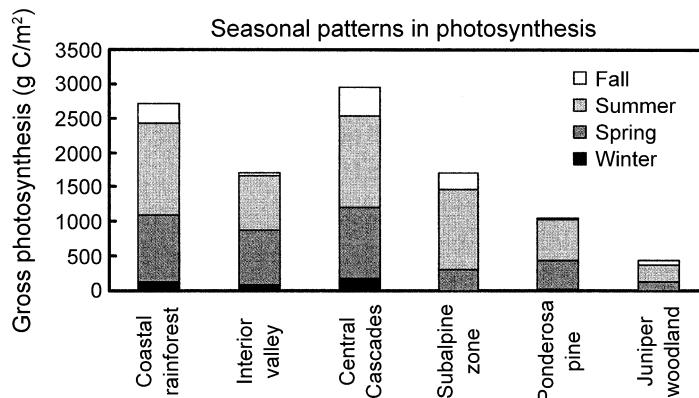
METHODS

A reanalysis of data acquired earlier across a broad range of Oregon forests growing in distinctly different environments demonstrates that evergreen as well as deciduous forests carry on most of their photosynthesis during the spring and summer months (Fig. 1). In our quest to describe more functionally the environmental distribution of all woody plant species, which includes deciduous shrubs and trees as well as evergreens, we chose to compare differences in the spring to summer

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FIG. 1. Although gross photosynthesis varies by more than five-fold in forested ecosystems distributed across a steep environmental gradient in Oregon (east–west transect at latitude 44° N, longitude 121–124° W), most of the activity is concentrated in the spring and summer months (derived from information provided in Runyon et al. [1994] and monthly climatic data on file at the Oak Ridge National Laboratory).⁵



ratio of gross photosynthesis using a physiologically based process model, 3-PGS (Coops et al. 1998).

Modeling photosynthesis

The 3-PGS (Physiological Principles Predicting Growth from Satellites) model from Coops et al. (1998) is a simplified version of the original implementation of the 3-PG model (Landsberg and Waring 1997, with modifications documented by Sands 2000). The 3-PGS model uses many of the principles that underlie earlier models such as FOREST-BGC (Running and Coughlan 1988), BIOMASS (McMurtrie et al. 1990), and PnET (Aber and Federer 1992). Like these, it first estimates the visible light (400–700 nm), designated as photosynthetically active radiation (ϕ_p), which is assumed to be 50% of incoming shortwave radiation (ϕ_s). The fraction of absorbed photosynthetically active radiation (ϕ_{pa}) is determined from a linear conversion of 1 km resolution, Normalized Difference Vegetation Index (NDVI) imagery for 1995, based on calibration with ground-based measurements across a transect in western Oregon (Goward et al. 1994, Coops and Waring 2001a).

$$\phi_{pa} = 1.27(\text{NDVI}) - 0.03. \quad (1)$$

The actual amount of ϕ_{pa} utilized (ϕ_{pau}) is obtained by reducing the value of ϕ_{pa} by amounts determined by modifiers (i.e., dimensionless factors with values varying between zero and unity). The modifiers reflect constraints imposed on the utilization of absorbed radiation because of partial to complete leaf stomatal closure, associated with high atmospheric vapor pressure deficits, the effects of subfreezing temperatures, and drought. Drought effects are imposed by calculating a soil water balance, which is the difference between total monthly rainfall, plus available soil water stored from the previous month, and transpiration, calculated using the Penman-Monteith equation with canopy stomatal conductance (G_s) modified by the vapor pressure deficit of the air, the availability of soil water,

and the leaf area index (L) of the forest (Monteith 1965).

Gross photosynthesis (P_G) is calculated by multiplying ϕ_{pau} by a maximum canopy quantum efficiency coefficient (α) that is a function of soil fertility. Here we assume soil fertility constant and assigned α equal to 0.05 mol C/mol photon (2.74 g C/MJ ϕ_{pau}). To further simplify the analysis, the model was parameterized with uniform values of available soil water storage, (θ), set at 200 mm. We set θ at 200 mm to ensure that vegetation growing on drought-prone sites will experience late summer limitations on photosynthesis (Running 1994). Expressing photosynthesis as a seasonal ratio (ΔP_G) compensates for any variation in soil fertility and its effects on light-quantum efficiency.

In the study by Coops and Waring (2001a), where the exact location of plots was known, terrain-adjusted extrapolation of 30-yr monthly mean precipitation and temperatures extremes derived by Daly et al. (1994) were made to a resolution of 200×200 m (0.04 km²). In this study, however, the exact locations where species richness was recorded were not available on private land, forcing us to model at minimum resolution of 1 km². The mean temperature extremes were converted, based on meteorological principles (Running et al. 1987, Thornton et al. 1997), to provide the specific climatic data required to drive the model at monthly time steps: actual shortwave incident solar radiation (i.e., adjusted for clouds), daytime vapor pressure deficits, mean temperature, and frequency of frost (monthly summaries across Oregon are available online).⁶ Values for ΔP_G were generated and mapped at a spatial resolution of 1 km² across the state.

Species richness

The richness in woody plant species was recorded on more than 10 000 plots as part of regional inventory and ecology programs (Ohmann and Spies 1998). We used a subset of these data ($n = 1966$) that provided good coverage of most forested areas in the state, min-

⁵ URL: (<http://www-eosdis.ornl.gov/OTTER> project)

⁶ URL: (<http://www.fsl.orst.edu/bevr>)

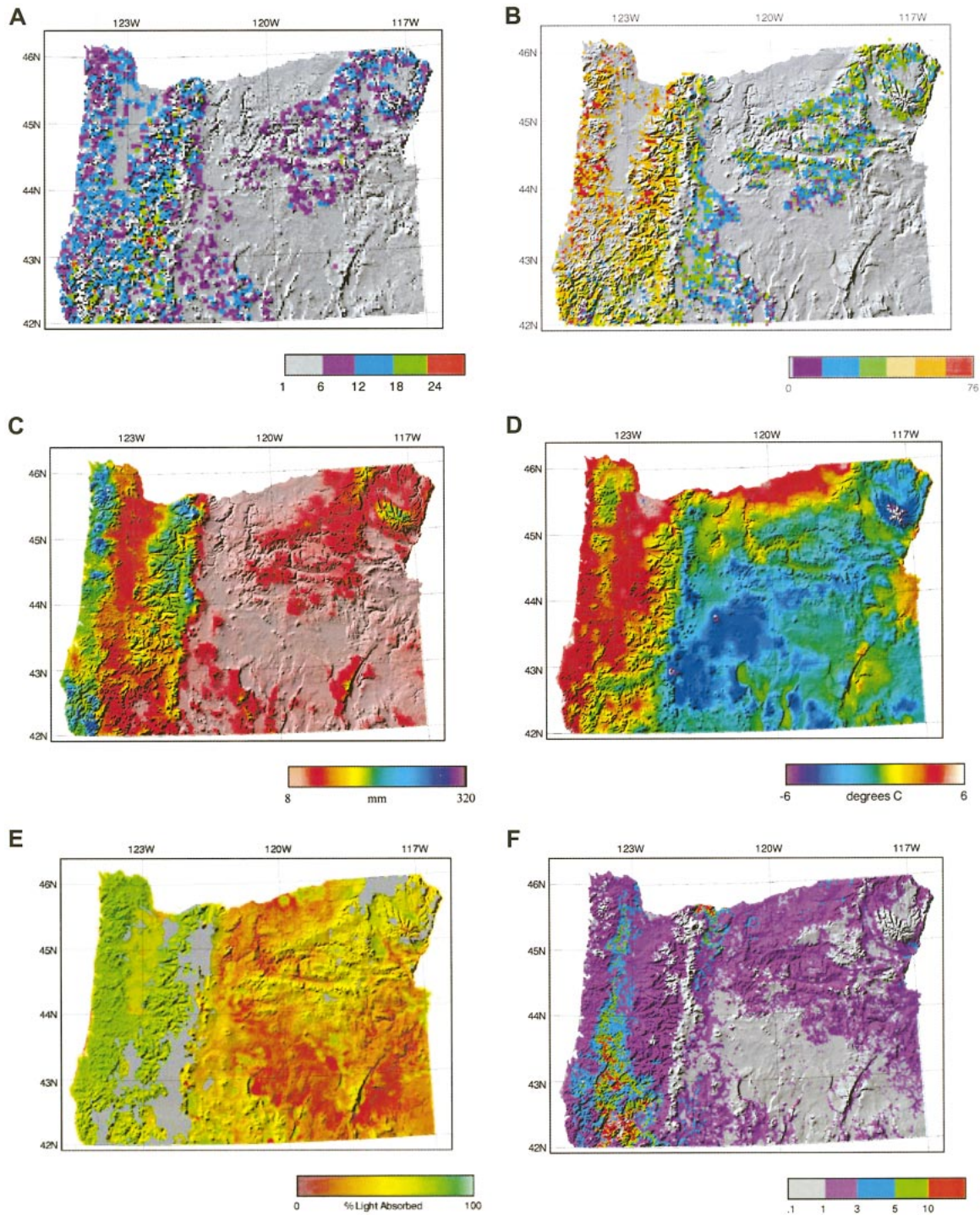


FIG. 2. (A) Richness of woody plant species on field plots in forested areas of Oregon is generally highest in southwestern Oregon and lowest in central Oregon, with intermediate to low values in the most productive zone along the Pacific Coast ($n = 1966$). (B) Site index, recorded at 5376 plots located in forested areas of Oregon, represents tree height (m) attained in 100 yr (each of the six divisions equals intervals of 12 m). Maximum mean annual wood increment over this range in site indices varies from 1 to 20 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Forests in northwestern Oregon, and particularly those growing in the coastal mountains, are among the most productive, whereas those in the eastern part of the state are the least productive. Southwestern Oregon is highly variable, but generally intermediate in productivity (Coops and Waring 2001*b*). (C) Mean April precipitation; western Oregon is generally well supplied with moisture during the spring, whereas central and eastern portions of the state receive minimum precipitation, except in areas with high mountains (data for additional months are available online. See footnote 6). (D) Mean minimum April temperatures; photosynthesis in western Oregon is not limited by frost, whereas in

imized variation in plot size, and provided a random selection of 100 points for all but three richness classes (1 = 33, 20 = 78, 21 = 55). Plots with >21 species recorded were excluded because <10 samples were available. A range of age classes, forest cover, and disturbance histories is incorporated in the data set. Most plots in federal ownership were in forests >80 yr old, whereas those on private land were in younger stands, often recently disturbed by logging activities. The survey plot sizes varied somewhat but were generally between 400 and 500 m². Within this range, woody species richness was not correlated with plot size. The subsample of plots used in our analysis included 74% of the total number of species recorded on the survey with $n = 10\,000$ (i.e., 214 out of a total of 289 species).

Site productivity

The most widely accepted measure of forest growth capacity in the United States is the maximum height attained by trees at a given age, called the site index (SI). To provide an overview of how the productive capacity of forests varies in comparison to species richness, we extracted height and age data from 5376 forest inventory plots. This sample included some, but not all of the same plots used for estimation of woody plant richness, as well as many additional plots. The values, acquired for a number of different tree species, were normalized for the height reached at 100 yr by the two most widely distributed conifers in the study area, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (McArdle 1961) and ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) (Meyer 1938). For native forests, the productivity values recorded in Oregon encompass the full range available in North America (i.e., from 1 to 30 Mg·ha⁻¹·yr⁻¹) (Jarvis and Leverenz 1983).

Comparison of seasonal photosynthetic ratio with species richness

Values for ΔP_G were assigned to each square kilometer where forest vegetation was present. About 10% of the sampled plots shared the same square kilometer with one or more other plot. When this occurred, the richness values were averaged. We had originally planned to correlate ΔP_G values with species richness, but we found by using 30 m Landsat TM imagery that too much variation existed within a square kilometer, both in vegetative cover and in microclimate associated

with topography. Alternative sampling designs will be considered in the discussion section.

RESULTS

The highest woody species richness in Oregon is concentrated in the southwestern portion of the state (Fig. 2A; see Plate 1). Southwestern Oregon is highly variable in recorded site indices, ranging from a low of 5 m to a high of 55 m at 100 yr (Coops and Waring 2001b), but is generally intermediate between the more productive Coast and western Cascade Ranges and the less productive region of eastern Oregon (Fig. 2B).

Mean annual precipitation varies from <300 mm to >3000 mm across Oregon, but <10% falls during the summer months. The growing season begins in March at lower elevations west of the Cascades. April patterns of precipitation and minimum temperatures, presented in Fig. 2C and D, indicate major differences in midspring climate across the state. In the western third, precipitation is sufficient and temperatures generally above freezing, whereas the eastern two thirds of the state has limited precipitation at most elevations and subfreezing temperatures throughout most of the spring. Summer is a period of statewide drought, except in the northwest corner and a fog-drip zone that extends inland from the Pacific Ocean ~20 km. In most of the Coast Range Mountains, soil drought is minimal. Outside this area, summer drought can be extreme, particularly toward the south and east (Franklin and Dyrness 1973).

The maximum fraction of light absorbed (ϕ_{pa}) by vegetation in midsummer (Fig. 2E), derived from the satellite measurements of near infrared and red reflectance from which Normalized Difference Vegetation Index (NDVI) is calculated, indicates that the most productive areas support dense vegetation that absorbs >95% of incoming sunlight. Where species richness is greatest, the vegetation on average absorbs between 60% and 70% of the light. East of the Cascade Mountains the vegetation is generally sparse and ϕ_{pa} values are much lower, except in the relatively mesic northeast mountains (Franklin and Dyrness 1973).

The modeled spring:summer ratio of gross photosynthesis (ΔP_G) is presented in Fig. 2F. Both the most productive coastal forests and the least productive arid woodlands exhibit ΔP_G values near 1, whereas in southwestern Oregon ΔP_G values range up to 5 on forested lands, and to 15 on non-forested pastures and farmland.

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central and eastern Oregon, frost is a major constraint during the spring. (E) The satellite-derived Normalized Difference Vegetation Index (NDVI) obtained in midsummer indicates that the most productive forest zone in the Coast Range has the most dense cover with >95% of the visible solar radiation absorbed by vegetation, whereas the zone east of the Cascade Mountains contains the most open vegetation. Intermediate cover, absorbing between 60% and 70% of solar radiation, overlaid with a gray mask, is predominant in southwestern and a small portion of northeastern Oregon. (F) The ratio of spring (March–May) to summer (June–August) photosynthesis generated by the process model (3-PGS) shows that both the most and least productive areas across the state have ratios ≤ 1 . In southwestern Oregon, where woody plant diversity is highest, the seasonal photosynthetic ratio, ΔP_G , is generally above 3.



PLATE 1. In the Miller Lake drainage in southwestern Oregon (Latitude 42°03' N, Longitude 123°13' W), tree species richness peaks with more than a dozen conifers including *Picea breweriana* S. Wats. (upper left), *Cupressus bakerii* Jeps. (upper right), *Pinus attenuata* Lem. (lower left) and a number of endemic shrubs, such as *Quercus sadleriana* R.Br. (detail, lower right). Other conifers present in the drainage include: *Abies concolor* (Gord. & Glend.) Lindl., *Abies magnifica* Murr. v. *shastensis* Lemm., *Chamaecyparis lawsoniana* Parl., *Juniperus sibirica* Burgsd. *Pinus lambertiana* Dougl., *Pinus monticola* Dougl. ex D. Don, *Pinus ponderosa* Dougl., *Pseudotsuga menziesii* (Mirb.) Franco, *Taxus brevifolia* Nutt., and *Tusuga mertensiana* (Bong.) Sarg. Photographs by R. H. Waring.

DISCUSSION

Within Oregon, the hypothesis that the highest species richness in woody plants should be found on sites of intermediate productivity appears to hold. In fact, it applies to all vascular plant species (Whittaker 1960, Waring 1969). But the boundaries of the analyses are arbitrary, and just happened to encompass the full range in forest productivity in North America. A different conclusion would result, for example, if we limited the analyses to only small parts of the state. In the Coast Range, where site index (SI) is >50 m at 100 yr, a dense canopy composed of a few species of trees or shrubs quickly develops following a major disturbance, allowing $<5\%$ of available light to penetrate through the canopy (Law and Waring 1994, Runyon et al. 1994; Fig. 2E). Understory light increases with age but remains low. On sites of low productivity (SI <30 m at 100 yr) typical of much of central and eastern Oregon, light is not limiting, but frequent frost in the spring and drought throughout the summer exclude less stress-tolerant taxa.

The degree of disturbance varied among the 1966 plots sampled for species richness. Private lands, sit-

uated mainly at lower elevations in northwestern Oregon, have been managed more intensively than federal lands and hold the preponderance of young, dense forests. In addition to disturbances associated with management, periodically fire, wind, insects, and disease create openings in forests throughout the state. Some disturbance may be necessary to maintain high species richness on the most productive sites. On sites of intermediate productivity, such as those found in southwestern Oregon, extreme levels of disturbance in the 1850s from hydraulic mining, fire, and logging (cited in Whittaker 1960) did not limit diversity, for today we find the highest species richness there (Fig. 2A). In Oregon, climate gradients appear to have a stronger association with general woody plant composition and diversity patterns than does disturbance or stand age (Ohmann and Spies 1998). Thus differences in disturbance should not negate our general findings.

Mean species richness at this scale is not strongly related to local variation in relief, as mountainous topography is common throughout the state. Likewise, local variation in soil fertility attributed to outcrops of serpentine and ultramafic igneous rocks, typical in the

Siskiyou Mountains, does not appear to be a dominant factor because high species richness is also recorded in the neighboring Cascade Mountains where the parent material is less variable (Fig. 2A). The properties common to both these areas are climatic rather than edaphic (Franklin and Dyrness 1973).

With good site-level data, process models can accurately estimate transpiration (Dye 2001), above- and belowground growth (Law et al. 2000), and set limits on net ecosystem carbon exchange (Waring and McDowell 2002). To provide similar accuracy across heterogeneous landscapes, however, may require remote assessment of canopy nutrition (Martin and Aber 1997, Coops and Waring 2001b) and vertical canopy distribution (Means et al. 1999, Lefsky et al. 2002). Even the best soil maps do not account for changes in soil fertility associated with atmospheric deposition or the presence of nitrogen-fixing shrubs and trees (Schlesinger 1997). By expressing spring and summer rates of photosynthesis as a ratio, we compensated for inadequate knowledge of soil fertility (set at a constant 0.7 for all sites), and chose a property that all species shared in common. In contrast, the partitioning of growth above and below ground differs considerably among the 214 species sampled in the survey, and would differ even more for annuals and other non-woody species. We would of course prefer to have absolute estimates of gross photosynthesis, but that too requires better knowledge of soil properties than are generally available. In a summer drought-prone region such as Oregon, the ratio of spring to summer photosynthesis is, we feel, an index that functionally integrates variation in radiation, temperature, and vapor pressure deficit.

Environmental analysis with the process model indicated that for all woody vegetation the most important seasons for photosynthesis are concentrated within six months: spring (March–May) and summer (June–August). The seasonal photosynthetic index (ΔP_G) proved useful in predicting general patterns in species richness across the state (Fig. 2F). For any one square kilometer, however, the predictive power of the model was poor ($r^2 = 0.11$, $P < 0.001$). This indicates that to predict species richness accurately at a finer scale will require information on local climate, soils, disturbance history, and a three-dimensional description of the canopy. With such information, gross photosynthesis and forest productivity could be predicted with acceptable accuracy (Landsberg et al. 2002).

At larger spatial scales, we advocate expanding the type of analysis presented in this paper to other ecological regions, recognizing that the pool size of species available may change. In expanding the approach it will be important to define changes in the beginning and end of the growing season using satellite-derived data. For the contiguous United States, climatic data and satellite-derived estimates of Normalized Difference Vegetation Index (NDVI) are available and being

used to estimate P_G at 8-d intervals (NASA/MODIS product, see Running et al. 1994; data available online).⁷ In other regions, different seasonal analyses of photosynthetic patterns than those introduced in this paper may be appropriate. With improved accuracy in geographic registration of information on soils, climate, and surveys of species richness, it should be possible to expand the use of process models to predict forest productivity and the degree of canopy closure, variables that can be independently assessed from aircraft if not yet from space (Means et al. 1999, Lefsky et al. 2002).

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⁷ URL: (<http://www.forestry.umd.edu/ntsg>)

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