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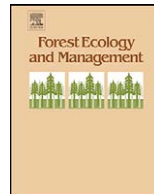
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Improving predictions of forest growth using the 3-PGS model with observations made by remote sensing

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ABSTRACT

Measurements made by remote sensing can characterize the leaf area density and nitrogen/chlorophyll content of forest canopies, as well as maximum photosynthetic capacity and above-ground structure and biomass. Combining these with climate data estimated from relationships based on temperature measurements and using an appropriate process-based model, it is possible to calculate, with useful accuracy, carbon sequestration and wood production by different forest types covering large land areas. To broaden its application and reduce the need for detailed information on stand characteristics, a satellite-driven version of the model 3-PG, was developed. The 3-PGS model incorporates the major first-order physiological processes that determine forest growth, and the biophysical factors that affect and govern those processes. It incorporates remotely sensed estimates of seasonal variation in canopy light interception ($fPAR$) and includes physiological variables (stomatal conductance and canopy quantum efficiency) that can be estimated by remote-sensing measurements of factors that influence those variables. 3-PGS therefore provides a useful framework within which to evaluate how data from the array of airborne and satellite-borne sensors now available might be used to initialize, drive, and test process-based growth models across regions with diverse soils and climates. We address the question: to what extent might additional remote-sensing techniques improve 3-PGS predictions?

Sensitivity analyses indicate that model accuracy would be most improved through better estimates of seasonal changes in canopy photosynthetic capacity (α) and canopy conductance (G_c). Canopy photosynthetic capacity depends on the amount of light absorbed by the canopy, estimated as a fraction of photosynthetically active radiation ($fPAR$), and on foliage nitrogen or chlorophyll content, which can be estimated using multi-spectral imagery. G_c depends on canopy leaf area index (L) and stomatal conductance of the foliage (g_s), which is affected by the vapor pressure deficit of the air and soil water content. The onset and effects of drought can be determined from changes in canopy reflectance and $fPAR$ identified from sequential measurements; the same measurements, coupled with calculations of evapotranspiration using climatic data and standard formulae, provide estimates of total available water in forest root zones. Periodic surveys with Light Detection and Ranging (LiDAR) and interferometric RADAR may serve to validate model predictions of above-ground growth (NPP_A), while progressive reduction in light-use efficiency ($NPP_A/APAR$) may identify forests with declining vigor that are likely to succumb to attack from insects and pathogens.

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1. Introduction

Although the spatial extent of land-use changes has been fairly well documented by satellite coverage over the last half-century, the significance of these changes on local and regional carbon and water balances is difficult to quantify. With improved understanding of how ecosystems work, process-based models have

been developed to evaluate changes in water use and carbon sequestration under present and future climatic conditions (Harper et al., 2005). The implications of a recent drought in France and across all of Europe (Ciais et al., 2005; Verbeeck et al., 2008), the effects of severe weather on primary production and soil pastures (Wang and Hall, 2004), and the optimum locations for pastures and plantations have all been identified with such models (Zug et al., 2006).

There is a range of process-based models that predict growth and water use by individual species as well as mixed species stands, reviewed by Landsberg (2003) and Nightingale et al.

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(2004). There are, however, concerns, about the dependence of model predictions on extrapolations, not only of climatic conditions and soil properties, but on short-term measurements acquired at a limited number of well-instrumented sites. Although it is easy to distinguish agricultural crops and tree plantations from native forests using standard remote-sensing classification schemes, it is difficult to obtain other properties of the vegetation necessary to predict growth accurately.

What are the properties needed to do this? Most models require good estimates of seasonal variation in canopy leaf density. Some have been simplified to ignore local variation in soil fertility and water storage capacity (Zhao et al., 2006) while others have extended the time step for analysis from daily to monthly intervals (Aber and Federer, 1992; Landsberg and Waring, 1997). Models may be species specific (Landsberg and Waring, 1997; Battaglia and Sands, 1997) or merge canopy properties (Nightingale et al., 2004). From sensitivity analyses, areas where drought may be a problem can be identified through observed reductions in canopy leaf density (Nightingale et al., 2007). Where water supply is unlikely to be limiting, a denser canopy might be indicative of more fertile soils (Waring et al., 2005). But canopy density is not always a good indicator of water supply or soil fertility. For example, fertilized plantations of eucalyptus in Brazil support half the canopy density of adjacent rainforests but are more than twice as productive, while using similar amounts of water (Almeida and Soares, 2003; Hutyra et al., 2007; Alton et al., 2007). The explanation for these observations is that the maximum photosynthetic capacity (α_{max}) and stomatal conductance ($g_{s,max}$) of eucalyptus plantations (Almeida et al., 2004; Stape et al., 2004a) are twice those of the native rainforest (Hutyra et al., 2007).

Soil properties may be inferred from maps developed from field surveys, but such maps do not identify areas where additions or losses of nutrients have occurred (Coops and Waring, 2001a,b; Ringrose and Neilsen, 2005). Interactions between climatic conditions and soil properties are important because they affect the proportion of growth allocated above and belowground. In addition, as trees grow in height, water transport is restricted, imposing additional limitations on gas exchange through leaf stomata (Brodrigg and Feild, 2000; Hubbard et al., 2001; Ambrose et al., 2009).

Coops et al. (1998) developed a general forest growth model, 3-PGS (Physiological Principles Predicting Growth with Satellites) that has been applied to predict the effects of climatic variation on forest productivity (Coops, 1999; Coops and Waring, 2001a; Coops et al., 2001). Smith et al. (2002) greatly improved predictions of above-ground growth in the White Mountains of New Hampshire by incorporating satellite-derived estimates of canopy nitrogen content in their model. The 3-PGS model incorporates most of the first-order physiological processes that determine forest growth, and the biophysical factors that affect and govern those processes. It therefore provides a very useful framework within which to evaluate how data from the array of airborne and satellite-borne sensors now available might be used to initialize, drive, and test process-based growth models across regions with diverse soils and climates.

In this paper, we first describe the data requirements and operation of 3-PGS, and then review the information that can be obtained from a variety of sensors. We outline how this information might logically be used to: 1) delineate forests with similar structural properties, 2) assess nutrient limitations on canopy photosynthetic capacity, and 3) evaluate interactions with tree height and soil properties that affect above-ground net primary production.

It is our view that the use of models such as 3-PGS, in association with the appropriate measurements made by remote sensing will lead, in the near future, to considerable improvements

in our ability to estimate carbon sequestration and wood production by forests.

2. Description of 3-PGS model

The 3-PGS model calculates the carbon and water balances of forest stands or forested regions at monthly and annual time steps using data describing the climate, soils, and selected biological variables (Fig. 1).

2.1. Climatic data

The climatic data required for the 3-PGS model include monthly mean solar radiation (S_{rad}), photosynthetically active radiation (PAR), temperature (T_a), daytime humidity deficits (VPD), precipitation (P), and the frequency of frost (F_f). Given information on latitude, elevation, and date, it is possible to estimate values for all these variables, except precipitation, from monthly mean minimum and maximum temperatures (Coops et al., 2000; Waring and McDowell, 2002).

2.2. Soil properties

Only two soil properties are required to initialize 3-PGS, but both are difficult to obtain. One is an index of soil fertility (FR), which takes values between 0 (very low fertility) and 1 (nutrition non-limiting), while the other is a measure of the maximum amount of water available in tree root zones (θ_{max}). FR is conventionally determined by bioassays in the laboratory (Waring and Youngberg, 1972) or in the field by comparing growth of fertilized with unfertilized trees (Stape et al., 2006). It can also be estimated on the basis of conventional soil chemical analyses, although the correlation between tree performance and the results obtained from these is frequently poor. Root zone water storage capacity can be assessed in the laboratory from soil samples collected to the depth of rooting (Soares and Almeida, 2001) or by calculating the amount of water extracted during a drought until the vegetation shows complete stomatal closure (Running, 1994; Oren et al., 1998).

2.3. Biological features

The vegetation features required to initialize the 3-PGS model include the physiological properties (α_{max} and $g_{s,max}$), and the optical property ($fPAR$) - the fraction of light intercepted by the canopy. Maximum stomatal conductance ($g_{s,max}$) provides a reference value. This is modified (constrained) by atmospheric humidity (vapor pressure deficit) to give actual stomatal conductance, g_s . Fig. 1 shows that the value of α_{max} is influenced by soil fertility as well as by g_s . Through Beer's Law, $fPAR$ increases exponentially with canopy leaf area index (L , see Section 3.3). Canopy conductance (G_c) is determined by L and g_s ; the stomatal conductance of all the leaves in the canopy is in parallel, so sums algebraically to give G_c . If the canopy is approximated by n layers of foliage, each with a leaf area l_i per unit ground area and an average stomatal conductance g_{si} , G_c can be estimated by $G_c = \sum_{i=1}^n g_{si} l_i$. Bulk aerodynamic conductance has little influence on G_c if $L \geq 3$ (see Kelliher et al., 1995). The height of the vegetation is also important as it influences how effectively canopies are coupled to the atmosphere (Jarvis and McNaughton, 1986; Monteith and Unsworth, 2008) and, because of limitations associated with the hydraulic architecture of tall vegetation imposes constraints on G_c required for the calculation of evapotranspiration (Hubbard et al., 2001; Novick et al., 2009).

In 3-PGS, the monthly maximum potential gross primary production (GPP) is equal to the product of the light absorbed by

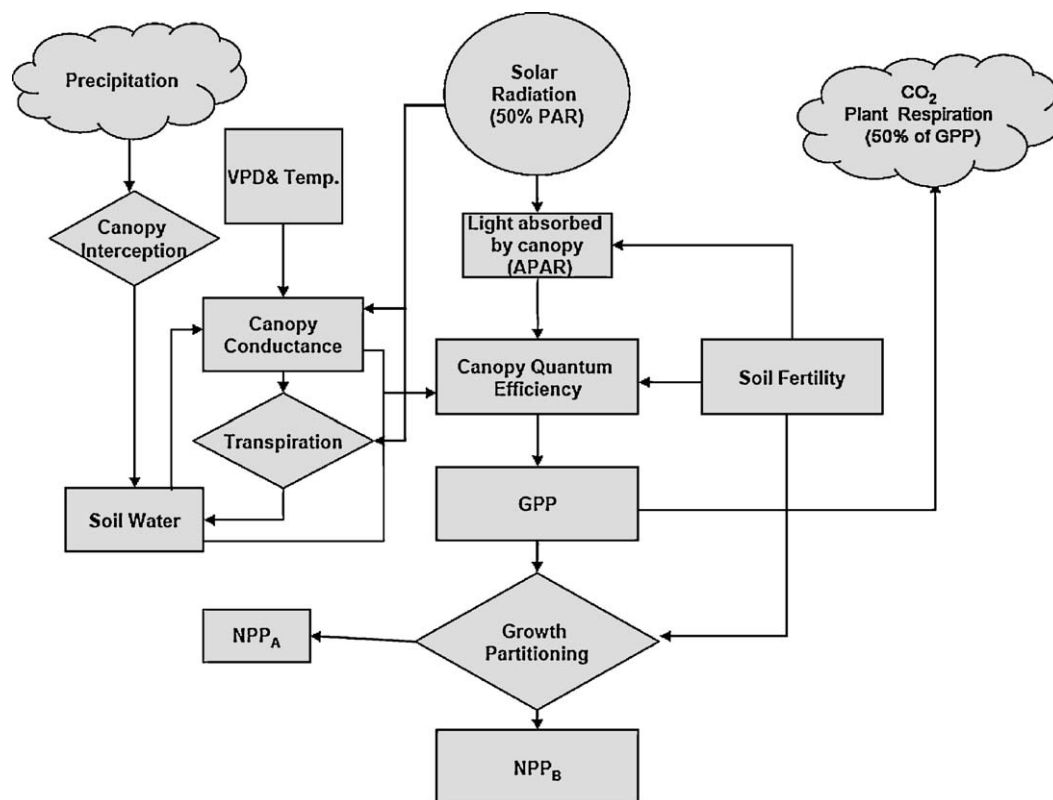


Fig. 1. Schematic diagram of the 3-PGS model. Gross (GPP) and net primary production (NPP) are ultimately functions of the amount of light absorbed by the canopy ($APAR$) and the canopy quantum efficiency (α). Additional restrictions are imposed on photosynthesis through reduction in stomatal conductance (g_s ; see text) if air temperatures, atmospheric humidity deficits (VPD) or the available soil water supply (θ) are suboptimal. GPP is partitioned equally into NPP and autotrophic respiration. NPP is further partitioned into belowground (NPP_B) and above-ground (NPP_A) components depending on soil fertility and available water (modified from Coops et al., 1998).

the canopy ($APAR$) and the canopy quantum efficiency (α_{max}). Actual GPP is calculated each month by reducing α_{max} by modifiers determined by frost, humidity deficits and/or, drought, and temperatures that depart from optimum for a particular type of vegetation. Frost effects are accounted for in the model by multiplying the solar radiation absorbed by leaves in any month of length d days, by $(1 - d_f/d)$, where d_f is the number of days in the month in which air temperature falls below freezing. Reductions caused by drought or vapor pressure deficits are those imposed by the more limiting variable, scaled in relative units between 0 (completely limiting) and 1 (optimum) (Coops et al., 1998).

2.4. Autotrophic respiration and net primary production

Autotrophic (plant) respiration is calculated in 3-PGS on an annual basis as a fixed fraction ($\sim 50\%$) of GPP , based on calculations of stand carbon balances developed by Ryan (1991) and reported in papers by Waring et al. (1998) and Gifford (2003). This simplification is robust, but may differ between life forms and biomes (Ryan et al., 1997).

Net primary production (NPP) in 3-PGS is partitioned into above- (NPP_A) and belowground (NPP_B) components. The NPP_B fraction, which includes photosynthate allocated to roots, mycorrhizae and exudates, varies from $\sim 20\%$ to 60% of NPP , depending on the extent to which soil fertility (FR) and water (θ) are suboptimal (Waring et al., 1998; Ceulemans et al., 1999). Generally, if environmental conditions permit GPP to exceed $2500 \text{ g C m}^{-2} \text{ yr}^{-1}$, the ratio of NPP_B/NPP_A can be expected to approach a minimum (Litton et al., 2007).¹ Even if GPP is as low as $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$, as it is for boreal

forests of *Populus tremuloides* growing on moderately fertile soils, the fraction of NPP partitioned to NPP_B may be minimum (Ryan et al., 1997). On the other hand, drought, infertile soils or water-logged substrates result in proportionally more photosynthate being allocated belowground (Chen et al., 2003; Litton et al., 2007).

2.5. Light-use efficiency (LUE)

3-PGS calculates above-ground light-use efficiency as the ratio of $NPP_A/APAR$, which varies from $\sim 0.7 \text{ g C MJ}^{-1} APAR$ under optimal growing conditions for young forests to $< 0.1 \text{ g C MJ}^{-1} APAR$ for older forests approaching maximum height or subjected to severe drought (Runyon et al., 1994a,b). The LUE is related to annual wood-growth efficiency (stemwood production/ L), which is widely applied to assess tree resistance to attack from insects and pathogens (Waring, 1987).

2.6. Ecosystem respiration and net ecosystem exchange

Although 3-PGS does not calculate ecosystem respiration (R_e) or net ecosystem exchange (NEE , equal to $GPP - R_e$), a recent analysis of a total of 504 years of data from 125 separate sites where net CO_2 exchange has been continuously monitored indicates a linear relation between GPP and R_e (Baldocchi, 2008). For undisturbed vegetation about $77 \text{ g C m}^{-2} \text{ yr}^{-1}$ are released for every $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ of GPP ($r^2 = 0.89$). For sites disturbed by fire, wind throw, logging, or other causes, the relationship is steeper, on average about $94 \text{ g C m}^{-2} \text{ yr}^{-1}$ are released for every $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ of GPP (Baldocchi, 2008). By recognizing that an area has been recently disturbed to various degrees, (see next section) it should be possible to estimate annual variation in both R_e and NEE through linear correlations with GPP .

¹ In this paper the ratio includes autotrophic respiration along with NPP_B .

3. Remote sensing of ecosystem properties

This section contains a brief review of remote-sensing techniques available to initialize process-based growth model, to provide (or confirm accuracy of) climatic data to drive them, and to evaluate their success in predicting annual above-ground production and light-use efficiency. The sensors available acquire data over a wide spectral range from ultraviolet and visible (200–700 nm) to near and mid-infrared radiation (700–3000 nm), to thermal (3–10 μm) and microwave (up to 1 m).

3.1. Land cover/disturbance

Many landscape-level analyses depend on our ability to distinguish different types of vegetation from one another (Coops and White, 2003). Conventionally, differences in land cover have been assessed by looking for statistically significant differences in reflectance from a number of distinct spectral bands in the visible and shortwave spectral regions. Running et al. (1994) pointed out the advantages of including longer wave bands that measure thermal emissivity to provide an integrated measure of surface temperature (LST). As the density of vegetation cover increases, emissivity from the ground surface is reduced and LST measurements approach ambient air temperature (Goward et al., 1985; Nemani et al., 1996). Differences observed in the seasonal patterns of greenness and LST have enabled much improved land cover classifications at local, regional and continental scales (Borak et al., 2000; Lambin and Ehrlich, 1995; Nemani and Running, 1997; Roy et al., 2005). Mildrexler et al. (2007) built on these principles to recognize disturbances and recovery by following shifts in the ratio of canopy greenness to LST relative to long-term averages. Additional refinements may be required to distinguish between vegetation with similar greenness and LST properties that differ substantially in height. Sensors that can estimate biomass and NPP_A with some accuracy will be covered in Section 3.6.

3.2. Climatic drivers

Over the past three decades a range of approaches has been developed to predict incident S_{rad} and PAR from satellite-derived data (Eck and Dye, 1999; Pinker and Laszlo, 1992). Goward et al. (1994) and Dye and Shibasaki (1995) estimated monthly integrated incident solar radiation using ultraviolet reflectance from the Total Ozone Mapping Spectroradiometer (TOMS). Wang et al. (2000) combined finer scale Landsat imagery, a DEM, and an atmospheric transmission model (LOWTRAN) to estimate surface net solar radiation over an agricultural site in the US with an average error of less than 1%. More recently Liang et al. (2006) produced accurate daily estimates of incident solar radiation and PAR at a spatial resolution of 1 km² or less by combining information from a number of satellite sensors.

Surface estimates of vapor pressure deficits can also be retrieved at a similar resolution to PAR with good results up to VPD of 2.5 kPa using LST data acquired by MODIS, except where vegetation is very sparse (Nemani, 2008; Hashimoto et al., 2008). On overcast days when surface temperatures cannot be retrieved it is unlikely the VPD will be suboptimal. Frozen soils can be detected with RADAR to define conditions when stomata are closed and growth cannot occur (Kimball et al., 2005). On clear days LST can be estimated and compared with values extrapolated from a variety of sources.

Precipitation is the most difficult climatic variable to acquire remotely and consistently across large areas. As a result most process-based models utilize ground networks of precipitation extrapolated across space and time. However, progress is being

made using a combination of passive microwave sensors (Nesbitt et al., 2004) with a number of new satellite missions planned to resolve this data gap.

3.3. Leaf area index and fPAR

In addition to information on land cover, remote-sensing data can provide frequent estimates of biologically important variables such as leaf area index (L) and fPAR. Mapping L from satellite-derived reflectance in the near-infrared and red wavelengths has a long history through correlations with simple vegetation indices such as the Normalised Difference Vegetation Index (NDVI) (Tucker, 1979; Chen and Cihlar, 1996). At low values of L , reflectance from the ground surface corrupts the signal (van Leeuwen and Huete, 1996) and at high values the spectral indices saturate (Fassnacht et al., 1997; Turner et al., 1999).

Huete et al. (2002) created an Enhanced Vegetation Index (EVI) that is less sensitive to background soil and saturates at higher L values than NDVI by adding blue wavelengths to the calculation (Waring et al., 2008). Because of the saturation at L values >4 , it is reasonable to apply a nearly linear relationship between NDVI or EVI and fPAR.

3.4. Canopy nitrogen and chlorophyll content

Over a fairly wide range, canopy nitrogen content is positively related to NPP_A because nitrogen stimulates stem and leaf growth as well as photosynthesis (Reich et al., 1998). Martin and Aber (1997) demonstrated that NASA's Airborne Visible/Infrared Imaging Spectroradiometer (AVIRIS), with 10–20 nm spectral resolution, could predict canopy nitrogen content of deciduous hardwood canopies at Harvard Forest in Massachusetts. These relationships permitted continuous mapping of canopy nitrogen content required to predict NPP with a process-based model, PnET (Aber and Federer, 1992). Predictions of foliar N in northeastern mixed hardwood and coniferous forests have been scaled up using satellite hyperspectral HYPERION imagery with precision within 0.25% N of leaf dry mass, compared with the AVIRIS airborne measurements of 0.19% (Smith et al., 2003).

Ollinger et al. (2008) reported success in correlating total short-wave reflectance (albedo) with canopy nitrogen content (N) using the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on NASA's Terra and Aqua satellites ($r^2 = 0.88$). The relation between albedo and canopy photosynthetic capacity was less precise ($r^2 = 0.73$), which is to be expected because not all forms of nitrogen in leaves are involved in the photosynthetic process (Wilson et al., 2000; Cheng et al., 2003).

The amount of light absorbed by chlorophyll pigments is a better estimate of photosynthetic capacity than N content. A wide range of studies indicates that the most sensitive part of the visible spectrum is reflectance measurements made around 550 nm (Thomas and Gausman, 1977; Carter and Knapp, 2001) and between 690 and 740 nm (Curran et al., 1990; Horler et al., 1983; Rock et al., 1988; Ustin et al., 1998; Curran et al., 1990; Blackburn, 1999).

As hyperspectral imagery is becoming more readily available, larger areas can be surveyed (Sampson et al., 2003; Coops et al., 2004). With the launch of a space-borne platform carrying Envisat's Medium Resolution Imaging Spectrometer (MERIS) a Terrestrial Chlorophyll Index is now available to initialize α_{max} in 3-PGS and related process-based models, although the amount of light absorbed by chlorophyll in the upper canopy may be a better measure that can be derived with sophisticated models of radiation-transfer through canopies (Jenkins et al., 2007; Zhang et al., 2005, 2009; Houborg et al., in press).

Table 1

Environmental and ecosystem properties that can be remotely sensed and used to drive, parameterize, and assess 3-PGS and other process-based models.

Variables	Value	Sensors
Land Cover/Disturbance	Initialization of model and confirm disturbance under stable climatic conditions	Multi-spectral optical data, and thermal IR to estimate LST
Climatic variables	Drive process-based models	Nearly full range of spectrum from μV to microwave
Seasonal variation in Leaf Area Index and $f\text{PAR}$	Distinguish vegetation types, set limits on light absorbed by leaves, and aid in calculation of LUE ($NPP_A/APAR$)	Visible, near and mid-infrared
Canopy N content and chlorophyll light-absorbance	Index to nutrient cycling and max photosynthetic capacity	Short-wave reflectivity and hyperspectral visible wavelengths
Photosynthetic efficiency	Confirm model estimates of α and G_s	Hyperspectral visible to calculate PRI
Above-ground height, biomass and structure	Model Initialization, Model validation of NPP_A and LUE	LIDAR and interferometric RADAR

3.5. Quantum efficiency

Hyperspectral remote sensing has significantly improved prediction of seasonal variation in α by monitoring changes in xanthophyll pigments that cycle from one form to another to prevent oxidative damage to the light-absorbing electron transfer process (Demmig-Adams and Adams, 2000). Gamon et al. (1990, 1992) demonstrated a shift in the absorption of different xanthophyll pigments at 531 nm compared to that at 570 nm, when plants were under stress, which led to the formulation of a photochemical reflectance index (PRI). Since then, a number of studies have confirmed a logarithmic relationship between α and PRI at the leaf level, with more recent work demonstrating that this signal is detectable at multi-canopy scales under a fairly wide range of view angles and illumination (Barton and North, 2001; Hilker et al., 2007; Hall et al., 2008). Research is underway to extend the application of PRI with lower spectral and spatial resolution MODIS satellite data (Drolet et al., 2008).

3.6. Biomass and above-ground growth

Although it is possible to group forests into broad age classes using passive optical sensors (Cohen and Spies, 1992), active sensors that send a pulsed signal and measure its return are required to obtain reasonable estimates of standing biomass (Lefsky et al., 2002). LiDAR and RADAR are both active sensors. In the case of LiDAR, near-infrared radiation is emitted at high pulse frequencies and the time elapsed recorded for a return signal (Goodwin et al., 2006; Wulder et al., 2008). Depending on the nature of the surface, a different portion and speed of the returned signal is recorded. Discrete return LiDAR systems have the capacity to record a limited number of signals, while full waveform systems have the capacity to record all reflected signals.

LiDAR surveys have proved a valuable tool to meet a range forest inventory needs (Nelson et al., 2003, 2008). Næsset and Økland (2002), using small foot print systems, report height measurements of maximum and mean canopy height with less than 0.5 m error. Stand volumes (Nilsson, 1996), biomass (Popescu et al., 2003, 2004; Hyde et al., 2007), and crown closure (Holmgren et al., 2003), are also well characterized with a range of LiDAR data (Means et al., 1999; Lim et al., 2003; Thomas et al., 2006).

Repeat LiDAR coverage should provide a means of documenting change in canopy height and biomass increment over time (Næsset and Nelson, 2007), assuming that the comparison is made at intervals sufficient to exceed errors in measurement (Wulder et al., 2008). Given the relatively new advances in the technology, repeat coverage with LiDAR is as yet rarely available.

Treuhaft et al. (2004) suggested combining microwave radar interferometry with LiDAR and other optical sensors to improve estimates of standing biomass across large areas. Recent studies in the tropics that combine radar backscatter measurements with interferometry look promising in estimating above-ground biomass between 5 and 350 Mg ha⁻¹ (Neeff et al., 2005; Hajinsek et al., 2009). Again, to achieve estimates of growth increment, rather than

standing biomass, two datasets covering a suitable time period will be required with comparable methods and sensors.

The main contributions of LiDAR and RADAR to models such as 3-PGS are to initialize and to validate. To initialize the model, tree height is of key interest because of its link to $g_{s,max}$ and hence to G_c . If there has been a disturbance, suggested by a shift in the ratio of greenness to LST, tree height might be expected to be reduced. If soil fertility has been mapped incorrectly, or recently changed, this will alter the partitioning of NPP by the model, as would a drought. Thus the accuracy to which 3-PGS or any other process-based model predicts height growth and NPP_A can only be assessed locally and regionally through the kinds of data acquired with LiDAR and RADAR sensors.

We end this section by listing in Table 1 remote-sensing variables that drive, parameterize or confirm estimates derived from process-based ecosystem models such as 3-PGS.

4. Discussion

Not all of the designated remotely sensed variables presented in Table 1 require measurement often or widely. In our view, measurement of mean canopy height ($H \pm SD$) and maximum photosynthetic capacity (α_{max}) deserve special emphasis. Maximum tree height is a direct measure of a site's productivity. Maximum photosynthetic capacity is a reflection of soil nutrient availability (FR). From a survey of published papers, Novick et al. (2009) showed that maximum canopy conductance ($G_{c,max}$) decreased exponentially as canopy height increased from 5 to 35 m. $G_{c,max}$ is probably more closely related to relative height than to absolute height because the total resistance to water flow through tree stems is similar once height growth ceases on poor or good sites (Ambrose et al., 2000; Hubbard et al., 2001). If this is so, monitoring relative changes in mean canopy height over a period of years may be sufficient to estimate $G_{c,max}$. This would be convenient because in areas where vegetation cover is dense, it is difficult to determine height accurately with either interferometric RADAR or LiDAR (Treuhaft et al., in press).

Maximum canopy photosynthetic capacity is directly correlated with chlorophyll concentration in the leaves that absorb most of the PAR (Waring et al., 1995). Zhang et al. (2009) report a linear relation between the amount of light absorbed by chlorophyll in a *Populus tremuloides* stand and GPP measured at an eddy-flux tower site in Canada ($r^2 = 0.7$). Because $f\text{PAR}_{chlorophyll}$ can be derived from measurements acquired globally with NASA's Moderate Resolution Spectrometer (MODIS), it may provide an acceptable alternative to mapping variation in soil fertility with ground-based field surveys.

A growing network of eddy-flux sites continues to offer places to compare modeled estimates of GPP, transpiration, evaporation, and above-ground growth with those derived with high resolution (spatial and spectral) remote-sensing instruments (Baldocchi, 2008). The quality of meteorological data at eddy-flux sites is excellent, and investigators at many sites are making an effort to quantify NPP_B as well as NPP_A (Luyssaert et al., in press). In addition, light penetration through the canopy is usually measured periodically throughout the year. Although eddy-flux sites were

selected to represent large areas of relatively uniform vegetation, disturbances will occur which will make it more difficult to interpret fluxes measured at a central tower. Remote sensing combined with modeling can help partition the landscape into similar functional units.

To predict future responses of vegetation under a changing climate with higher atmospheric CO₂ levels is a challenge because there are likely to be interactions between increases in CO₂, nutrient and water availability (Ceulemans et al., 1999; Beerling et al., 2002). On the other hand, if nutrients are provided, NPP_A may increase rapidly, but cause trees to be more susceptible to drought as a result of an imbalance between leaf and root production (Linder et al., 1987; Nilson, 1995).

Extensive plantations of genetically uniform trees in the tropics and subtropics offer ideal places to test for interactions among limiting factors as the harvest rotations are short and the growth potential highly variable (Mummery and Battaglia, 2001; Sánchez-Rodríguez et al., 2002; Stape et al., 2004b; Rodríguez et al., in press). Where experiments are established, they should be laid out in blocks of sufficient size and number to enable remotely sensed estimates of forest structure and physiology to be obtained over extended periods.

5. Summary

Local and regional variation in soil properties make it difficult to predict growth and water use by vegetation, even where climatic conditions are similar. Although seasonal variations in *L* and *fPAR* are important variables to measure, they are insufficient as a basis for such predictions. We propose that landscapes be stratified into more functional units with the additional measurement of canopy height, and therefore by inference α_{\max} , and G_{\max} . We review advances in remote-sensing technology, which if employed, offer promise of increasing accuracy in modeling and measuring NPP_A. Although LiDAR and RADAR sensors may be able to track annual changes in biomass over large areas in the future, that capacity is not yet available. Even when available, we see advantages in using process-based models, such as 3-PGS, in concert with remotely sensed measurements of biomass to provide explanation for seasonal and interannual variation in growth and water use.

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