GPP IN LOBLOLLY PINE: A MONTHLY COMPARISON OF EMPIRICAL AND PROCESS MODELS

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Abstract— Monthly and yearly gross primary productivity (GPP) estimates derived from an empirical and two process based models (3PG and BIOMASS) were compared. Spatial and temporal variation in foliar gas photosynthesis was examined and used to develop GPP prediction models for fertilized nine-year-old loblolly pine (*Pinus taeda*) stands located in the North Carolina Sandhills. Foliar gas exchange in both the upper and lower thirds of crowns was monitored monthly for a year. Based on these data, empirical models were developed for the growing and non-growing seasons and upper and lower crown levels. Common empirical models include the variables photosynthetically active radiation (PAR), Ln(PAR), and VPD. Statistical differences in model estimates for crown positions and for both the growing and non-growing seasons indicated that the use of separate empirical models was appropriate for GPP estimations, yet simulated light-response curves yield similar rates. Monthly GPP estimates derived from empirical models were compared with process model predictions. Average monthly environmental data were applied to models to estimate GPP. Both process models predicted a greater relative GPP during the growing season (80 percent) compared with the empirical model (65 percent), while the opposite trend was apparent for the non-growing season. Monthly GPP variability was greater in the 3PG and BIOMASS predictions, appearing to reflect monthly temperatures and stand growth, while the empirical analysis predicted a relatively high contribution to yearly GPP during the non-growing season. Predicted GPPs for the entire year were 192.8, 142.8, and 192.4 mol C/m^2 for the empirical, BIOMASS, and 3PG models, respectively.

INTRODUCTION

Gross primary productivity (GPP) is a measure of the potential carbon gain by a stand prior to respiratory losses. GPP can not be measured directly and therefore must be estimated using models developed to predict the total carbon yield or biomass accumulation prior to respiration. Process models have become increasingly important and useful in assessing stand productivity since they integrate several biological functions that directly define the growth potential of a tree and ultimately the stand (Johnson and others 2001).

3PG and BIOMASS are photosynthesis-stomatal conductance process models, which integrate physiological plant responses, ecological processes, and physical relationships within the stand to predict stand growth. Both have been calibrated for loblolly pine. 3PG and BIOMASS primarily utilize quantum efficiency and maximum carbon assimilation rate (Amax) to predict carbon fixation rates. An extensive overview of 3PG and BIOMASS is provided by Landsberg and others 2001 (3PG), Landsberg and Waring 1997 (3PG), McMurtie and Landsberg 1992 (BIOMASS). Solar radiation, atmospheric vapor pressure deficit (VPD), rainfall, frost days per month, and average temperature are input drivers used in 3PG calculations. Additionally, a fertility rating is used to adjust the simulated photosynthesis light-response curve in 3PG. BIOMASS uses shortwave radiation, VPD, minimum and maximum daily temperatures, and precipitation. BIOMASS and 3PG essentially calculate GPP based on the amount of absorbed PAR at the canopy level by converting light energy into carbon fixation potential. Other environmental inputs alter the efficiency and rate of carbon fixation at the canopy level.

Process models are rarely evaluated to determine if predicted GPPs reflect actual physiological data collected from a stand. The collection of gas exchange data over an entire year provided the unique opportunity to develop seasonal empirical photosynthesis models that could be used to validate process model GPP outputs. The two objectives of this study were (i) to compare monthly predicted GPP in a loblolly pine stand using two process models (3PG and BIOMASS) and an empirical model developed from gas exchange date collected from the same stand and (ii) to compare total yearly predicted GPP using the same models.

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METHODS

Study Site

Photosynthesis measurements for empirical model development were taken in Scotland County, North Carolina (35°N lat., 79°W long.) at the United States Forest Service (USFS) Southeastern Forest Tree Experiment and Education Site (SETRES). The stand consists of hand planted loblolly pine (2 x 3 m spacing) established in 1985 (14 years old at the beginning of the study). The site is flat, infertile, excessively drained, sandy, siliceous, and composed of thermic Psammentic Hapludult soil (Wakulla series). The average annual precipitation is 121 cm, but drought is common in the summer and early fall. The average summer temperature is 26°C and the winter average is 9°C. The average annual temperature is 17°C. The climate is humid and temperate with hot summers and mild winters, allowing for over a six month growing season. The native forest cover type is Longleaf Pine-Scrub Oak. The established site study design is a 2 x 2 factorial combination of fertilized and irrigated additions replicated four times. The plots consist of 30 x 30 m measurement plots within 50 x 50 m treatment plots. Interaction among below ground matter from adjacent plots is prevented by a 150 cm deep plastic liner that separates plots. Non-pine vegetation is controlled by mechanical and chemical (glyphosate) treatments such that no understory vegetation exists. Nutrient applications began in March 1992 and continued through March 1998. The total amount of each nutrient (in Kg/Ha) added over the six year period is as follows: N (777), P (151), K (337), Ca (168), Mg (164), S (208), and B (3.9). In the fertilized plots, crown closure is common. Total biomass accumulation at SETRES increased 91 percent four years after initial fertilization treatments began (Albaugh and others 1998).

Photosynthesis Measurements

Photosynthesis was measured monthly in fertilized plots from April 1999 to March 2000 at SETRES using the LiCor 6400 Portable Photosynthesis System (LiCor, Lincoln, NE). Fertilized plots were chosen over other treatments because the fertilized stands most closely represent intensively managed loblolly pine forests (since fertilization is common and irrigation is not). Photosynthesis rates from upper and lower crown cut foliage were measured (Ginn and others 1991) from a subsample of 2 trees per block for a total of 16 measurements (4 blocks x 2 crown positions x 2 subsamples). Gas exchange was measured in each block sequentially, and subsamples from each level were chosen randomly for sampling. Blocks were always measured in the same order. This sequence was repeated three times on each measurement day in order to capture an abbreviated diurnal response to daily environmental changes. Measurements included morning (9 AM), afternoon (11:30 AM), and late afternoon (1:30 PM) measurement periods. A total of 48 measurements (three sampling sequences) in fertilized plots were generally taken throughout the day.

Shoots were cut using a pole pruner and measurements were taken immediately on a detached fascicle. All measurements were taken at the ambient temperature and humidity, and CO_2 concentrations were held constant in the chamber at 350 ppm. The average PAR was estimated for the upper and lower third of crowns and kept constant in the measurement chamber (using the LiCor's actinic source) for each crown level in the block throughout a measurement period. The PAR for each crown level was determined by evaluating the average PAR in full sunlight (for the upper third) and the average PAR in the understory (for the lower third) prior to the measurement period. The PAR was reassessed and adjusted for each measurement period according to the PAR levels immediately prior to sampling. Water potentials were determined for the same branch as the sample immediately after being cut using a field pressure chamber (PMS instrument Co., Corvallis, OR). All measurements were completed in one day. Needle diameter was immediately recorded and leaf area was later determined using the following equation (Ginn and others 1991):

$$LA_1 = (n * l * d) + (p * d * l)$$

where l = the length of the needle, d = fascicle diameter and n = number of needles in the fascicle. Values were adjusted to represent gas exchange on a per leaf area basis. Foliar nitrogen percentages of measured needles were obtained from pooled samples collected from each block/crown position combination during eight of the twelve months using a Carla ERBA (Raleigh, NC).

Empirical Model Development

Empirical models were developed using multiple linear regression techniques in SASä. (SAS Statistical Institute, Cary, NC). Common simplified gas exchange models for crown positions were developed for the growing (April – October) and non-growing (November – March) seasons. Common models include the variables PAR, ln(PAR), and VPD. Air temperature, stem water potential, relative humidity, and foliar nitrogen contents were not significant model variables. Statistical comparisons of seasonal and crown position model parameter estimates revealed that significant differences exist among all models. Therefore, models for the upper and lower crowns within the growing and non-growing seasons were used to estimate GPP.

GPP Analysis

Monthly GPP was predicted using the empirical models, 3PG, and BIOMASS. 3PG was originally calibrated for loblolly pine at SETRES (Landsberg and others 2001). Average environmental data for a 20-year period at SETRES was used to calculate GPP in 3PG, while BIOMASS utilized 1995-1996 environmental data from SETRES. 3PG outputs data in a monthly time-step while BIOMASS provides a daily time-step output. Daily BIOMASS outputs were summed for each month. Upper and lower PAR and leaf area index (LAI) for three canopy layers were estimated using BIOMASS. The middle layer was divided in half and added equally to both the upper and lower layers for the empirical estimates of GPP.

RESULTS AND DISCUSSION

Actual mean monthly photosynthesis measured at SETRES remained relatively high during the non-growing season with significantly greater rates occurring in the upper crown compared to the lower crown during all

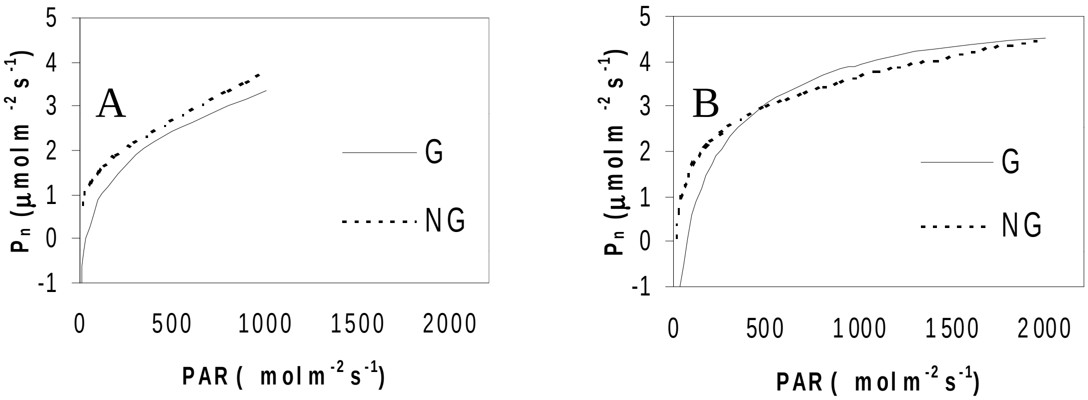

Figure 1—Simulated light response curves for the lower crown (A) and the upper crown (B) for both the growing and non-growing seasons.

months ($p<0.05$) (figure 1). Mean rates in January and February were higher than those recorded in June and largely reflect the cloudy conditions on the June measurement day. High photosynthesis rates at SETRESII (an adjacent sister experimental station) have been recorded during the non-growing season as well (unpublished data).

As mentioned before, statistical tests revealed that significant differences exist among parameter estimates of photosynthesis prediction models developed for the growing and non-growing seasons and the upper and lower crowns (table 1). However, predicted light response curves for the growing and non-growing seasons within a crown level are similar, implying that the photosynthetic response to light and the ability to fix carbon does not greatly differ with season (figure 2). This is reflected in the monthly empirical GPP predictions for the upper and lower crowns (figure 3), which suggest that GPP is reduced by only a third in the winter months relative to the peak July rate. Monthly BIOMASS predictions exhibit a lower relative GPP accumulation during the winter months and a greater accumulation during the growing season (figure 4A), suggesting that BIOMASS is sensitive to low temperatures. This is reflected in daily BIOMASS outputs in which a GPP of zero was predicted for days below freezing (data not shown). 3PG predicts a rapid increase from January through May, followed by more erratic monthly values (figure 4B). This behavior is primarily due to the density induced mortality function incorporated into the process model (Landsberg and others 2001).

The BIOMASS and 3PG models predict that 80 percent of the yearly GPP accumulates during the growing season and 20 percent accumulates during the non-growing season. The empirical model predicts that 65 percent and 35 percent of the GPP is distributed between the growing and non-growing seasons, respectively (figure 5A).

Table 1—Significant variables, Parameter estimates, and total R^2 values for common photosynthesis prediction models developed for the upper and lower crowns and the growing and non-growing seasons in fertilized stands at SETRES. All parameter estimates were statistically different ($p<0.1$)

Lower Crown			Upper Crown		
Growing Season					
Parameter	Estimate	R^2	Parameter	Estimate	R^2
Intercept	-1.802	0.59	Intercept	-5.542	0.60
PAR	7.237×10^{-4}		PAR	5.477×10^{-4}	
Ln(PAR)	0.7912		Ln(PAR)	1.653	
VPD	-0.5238		VPD	-0.6983	
Non-Growing Season					
Intercept	-0.4707	0.63	Intercept	-2.048	0.62
PAR	0.001816		PAR	3.670×10^{-4}	
Ln(PAR)	0.2684		Ln(PAR)	0.7066	
VPD	0.2911		VPD	0.2356	

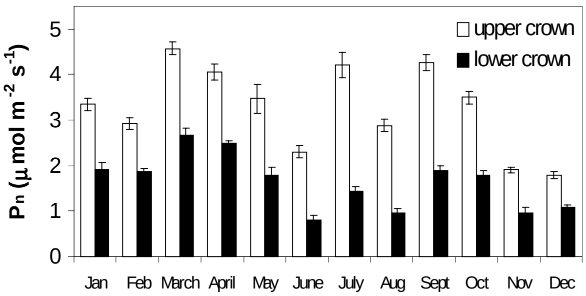

Figure 2—Mean monthly photosynthesis rates for 1999-2000 measurements in upper and lower crown foliage at SETRES. Photosynthesis was significantly greater in the upper crown for all months (p<0.1).

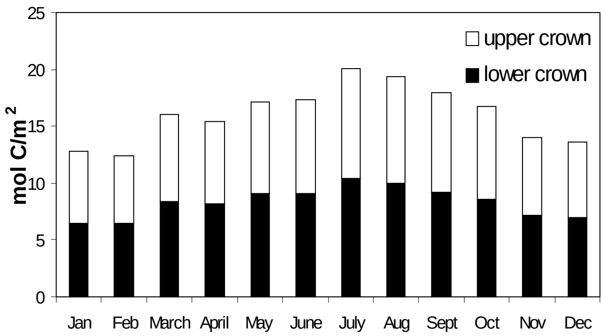

Figure 3—Empirically derived predictions of monthly GPP in the upper and lower crowns.

Absolute predicted GPPs during the growing season are fairly similar for the empirical model and BIOMASS (about 120 mol C/m^2), while 3PG predicts a much higher value (160 mol C/m^2) (figure 5B). During the non-growing season, both 3PG and BIOMASS predict lower actual values compared with the empirical model. Thus, in relative terms (figure 5A) the process models may overpredict GPP during the growing season and underpredict GPP during the non-growing season. In absolute terms (figure 5B), only 3PG predicts greater GPP during the growing season when compared with the empirical predictions. 3PG is calibrated using field growth and biomass measurements; therefore, the model may not accurately account for the potential carbon gain in the winter if photosynthate does not immediately contribute to growth. Evidence exists that labile carbon pools accumulate in loblolly pine during the winter and are utilized during high stress situations in the summer when carbon fixation is limited and does not meet the metabolic or growth requirements of the tree (Sampson and others 2001).

Thus, winter GPP may not result in immediate measurable growth. Seasonal 3PG estimates probably more closely parallel growth data while the empirical analysis directly reflects carbon fixation estimates. This is consistent with growth data collected from SETRES in which a majority of measurable stem wood production is observed during the growing season (unpublished data).

Interestingly, the cumulative predicted GPPs for the year are fairly similar among the empirical (192.8 mol C/m^2), BIOMASS (142.9 mol C/m^2), and 3PG (192.4 mol C/m^2) models. Again, 3PG was calibrated for loblolly pine at SETRES, which is where data was collected for empirical model development. This may explain why the yearly total is similar for the two models since 3PG was calibrated against actual field biomass data and the empirical model is likely a good estimate of GPP based on actual physiological measurements of carbon fixation on the site over a year. 3PG and the empirical models used different data collected at SETRES and represent two modeling approaches. The fact that they arrive at similar cumulative predicted GPPs validates both models on a yearly scale.

These results indicate that the process models do not fully account for winter acclimation and summer declines. 3PG

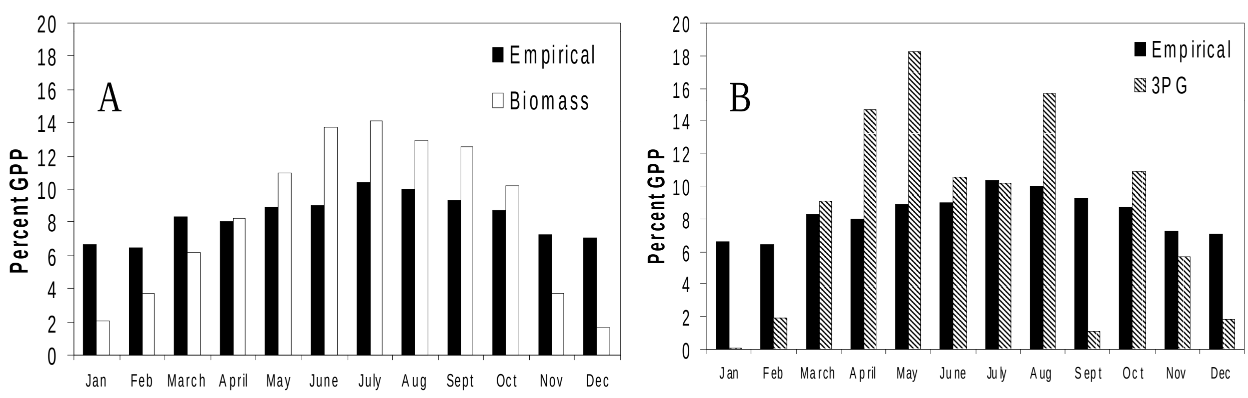

Figure 4—Percent monthly GPP contributions relative to yearlong totals for empirical and BIOMASS predictions (A) and empirical and 3PG predictions (B).

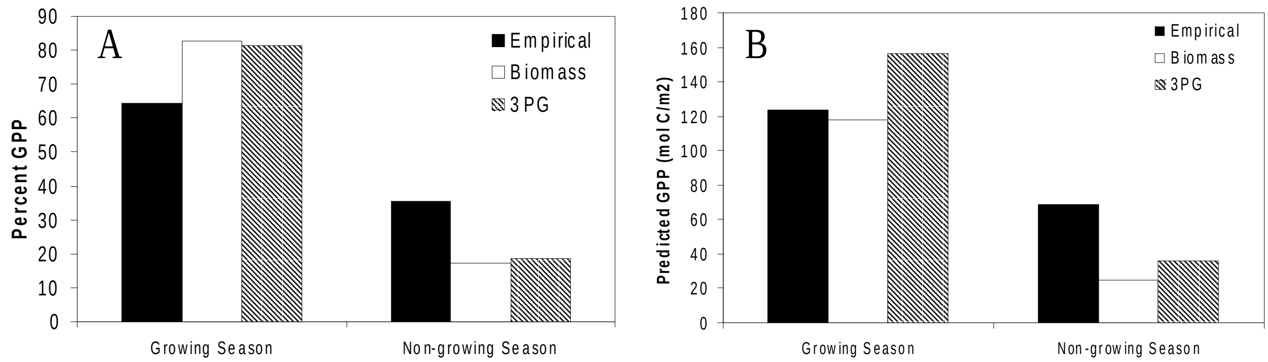

Figure 5—Empirical, BIOMASS, and 3PG estimates of percent GPP contribution (A) and actual predicted GPP (B) for the growing (April-October) and non-growing (November-March) seasons.

and BIOMASS have critical temperature thresholds (Landsberg and others 2001 (3PG), McMurtie and Landsberg 1992), which may result in oversensitivity when the environmental data are averaged, especially when average temperatures are skewed by a few instances of extremely low or high temperatures. During the summer, higher predicted GPPs by process models relative to the empirical model could be explained by a lower sensitivity to VPD. The empirical estimates show approximately a 25 percent decline due to high VPDs in the summer (figure 6), which is similar to the actual difference in predicted GPPs between the empirical and process models during the growing season (figure 5B).

The empirical approach to predicting GPP provides reasonable estimates - at least for SETRES. Scaling up of the empirical model to the stand level at other locations may possibly be achieved by taking into account factors that drive total carbon fixation and ultimately GPP. LAI is an excellent indicator of potential productivity (Teskey and others 1987, Teskey and others 1994, Vose and Allen 1988) and highly reflective of site fertility (Gillespie and others 1994, Albaugh and others 1998). Reported crown leaf area estimates for loblolly pine in Hawaii were five times greater than stands examined in coastal South Carolina at 25 years (Harms and others 1994). Greater crown leaf areas paralleled higher total biomass estimates

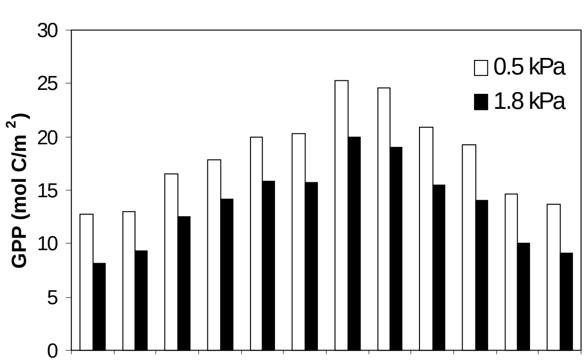

Figure 6—The effect of high and low VPD on empirically predicted GPP. The selected VPDs represent the high and low monthly averages recorded at SETRES.

in Hawaiian loblolly pine. Therefore, leaf area may be an excellent indicator of site productivity and substitute for fertility ratings that are required inputs in process models and are often difficult to determine (Landsberg and others 2001). Leaf area is directly related to GPP since total crown carbon fixation is enhanced with the increase in photosynthetic machinery. This of course is only the case when the assumption is made that greater fertility does not directly affect the photosynthetic capacity or efficiency of an individual leaf. Incident radiation and day-length, and density-induced mortality would also have to be accounted for in order to expand the inference space of empirical estimates to include other sites.

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