

Predicting leaf area index from scaling principles: corroboration and consequences

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Summary Leaf area index (LAI) is a key biophysical variable in most process-based forest-ecosystem models. However, most such models require LAI as an input, typically obtained from empirical observations. We tested whether scaling principles based on trade-offs between single leaf and canopy properties could be effectively used to model LAI, thereby obviating the need for empirical observations. To do so, we used the process-oriented model, PnET, configured to estimate LAI from these same scaling principles. We derived biologically based LAI predictions (LAI_{PnET}) for the Harvard Forest (Massachusetts, USA) eddy covariance tower site, a predominately mixed deciduous hardwood forest, using PnET, and compared these with a locally observed phenology record and with LAI estimates from both local (ground-based) photosynthetically active radiation transmittance (LAI_{TRANS}) and normalized difference vegetation index satellite data (LAI_{NDVI}). We generated the LAI_{PnET} trajectory by running the PnET model with meteorological observations from the flux tower as model drivers. We derived LAI_{TRANS} from measurements of above- and below-canopy photosynthetically active radiation at the flux tower, and LAI_{NDVI} from observations from the Advanced Very High Resolution Radiometer (AVHRR) satellite-borne sensor of surface greenness for the 1 km² cell containing the flux tower. Over a 5-year period, LAI_{PnET} and LAI_{TRANS} values were comparable intra- and interannually, with maximum values differing by less than 0.1 to 0.2 LAI units (m² m⁻²). Values of LAI_{NDVI} were similar to LAI_{PnET} and LAI_{TRANS} in midsummer, but higher LAI values were predicted in the early and late portions of the growing season.

In addition, we used the three alternative LAI trajectories in a modified version of the PnET model and compared the resulting outputs of gross primary production (GPP) with GPP estimates from the flux tower for 5 continuous years. The LAI_{PnET} and LAI_{TRANS} inputs resulted in a difference of less than 3% in mean annual GPP from 1995 to 1999, and these were within 7 and 9%, respectively, of the annual eddy flux-based estimates over the same time period. The results indicate that biologically based LAI scaling approaches can closely track temporal changes in a deciduous forest and have potential for spatial and temporal scaling of LAI.

Keywords: forest model, gross primary production, normalized difference vegetation index, phenology, photosynthetically active radiation transmittance, PnET.

Introduction

Considerable attention is focused on spatially distributed modeling of ecosystem variables such as net primary production (NPP) and net ecosystem production (NEP) (e.g., Cramer et al. 1999). These variables are of interest because of their relation to the global carbon (C) cycle (Schimel 1995) and their use in simulating potential effects of changing climate and atmospheric CO₂ on vegetation (VEMAP 1995), and mapping potential forest productivity (Milner et al. 1996). Because of the strong influence of leaf area on rates of canopy gas exchange and energy balance, efforts to model ecosystem metabolism and atmosphere–biosphere interactions using biophysically based algorithms often require estimates of leaf area. Thus, there is a clear need for methods to scale leaf area spatially and temporally under current conditions and environmental change scenarios.

The projected leaf area per unit ground surface area, or leaf area index (LAI), appears to be regulated at the ecosystem level such that discernible relationships between climate and maximum LAI are evident (Gholz 1982, Waring 1983, Woodward 1987). The timing of leaf emergence and leaf fall in temperate deciduous forests is also related in part to climate (Leith 1974). These relationships suggest the possibility of a biologically based scaling of LAI by reference to the plant carbon balance in an ecosystem simulation model driven by local climate. Given the difficulties inherent in empirically assessing LAI locally, regionally, or globally (Gower et al. 1999, Turner et al. 1999), biological understanding that could be used to improve LAI estimation would be valuable for assessment, monitoring and modeling. Several ecosystem models now simulate annual LAI trajectories in deciduous forests, but there has been relatively little comparison of model-generated LAI with phenological observations or with empirical LAI measures. In this study, we compared the biologically based scaling LAI trajectory from the PnET model (Aber et al. 1995,

1996) with a variety of observations at a temperate deciduous forest site, and assessed the consequential influences of alternative LAI formulations on gross primary production (GPP).

In theory, an ecosystem simulation model that incorporates leaf attributes, site quality and environmental constraints into its canopy size predictions should be able to make realistic LAI estimates. This would result from the trade-offs that exist between particular combinations of leaf traits and their associated shoot and canopy properties (Schoettle 1990, Reich et al. 1992, Gower et al. 1993). Species that produce leaves of high leaf mass per area (LMA) and long leaf life span tend to have low photosynthetic and respiration rates per unit mass (Reich et al. 1997, 1998). These same species produce dense canopies with large foliage mass compared with species with the opposite set of traits, and tend to be shade tolerant (Reich et al. 1992, 1995). The more shade tolerant the species, the greater the likelihood that a given leaf situated beneath a given (large) LAI (made up of higher positioned leaves and branches) will have a positive C balance. In addition, the number of shaded layers retained in a canopy (i.e., LAI) should be related to the number of layers with a positive C balance (Schoettle 1990). These ideas are consistent with data demonstrating that the transmittance of light decreases with the shade tolerance of the canopy species (Canham et al. 1994, Reich et al. 2003).

The PnET model (Aber et al. 1995, 1996) incorporates many of these basic assumptions. For a given combination of canopy properties and environmental constraints on those properties, PnET simulates its own canopy mass and LAI. At the end of each simulation year, PnET trims horizontal canopy layers that have a negative C balance and estimates the potential canopy mass (i.e., LAI) for the following year. In essence, the following year's canopy size is constrained by the amount of C gained from the number of layers in the present year's canopy that finish the year with a net positive C balance. In this way, PnET self-limits its canopy size based on each canopy layer's C balance. The PnET model uses a growing degree day and C balance algorithm to predict canopy phenology and uses these estimates in combination with its estimated canopy LAI maximum to develop a seasonal LAI trajectory. In some cases, PnET C flux and NPP estimates have been validated (Aber et al. 1995, 1996), but PnET LAI predictions have not been corroborated.

The possibilities for validating simulated LAI seasonal trajectories are constrained by the difficulty of measuring LAI. A number of direct and indirect approaches have been taken to assess forest LAI at the plot scale (Gower et al. 1999). Direct methods include destructive harvest, allometry, and leaf litter-fall. Leaf area index information for other ground-based methods rely on light sensing instruments (e.g., Decagon ceptometer (Decagon Devices, Pullman, WA) and the Li-Cor LAI-2000 (Li-Cor, Lincoln, NE)) and local calibration (Fassnacht et al. 1994, Chen et al. 1997). These instruments estimate LAI indirectly at the plot scale based on canopy light transmittance. As leaf emergence and leaf fall occur, there is typically a strong signal in the light transmitted through the canopy. Thus the continuous observations of above- and be-

low-canopy solar radiation made at the international network of eddy covariance flux towers (Baldocchi et al. 1996) contain useful information relevant to LAI and phenology.

The principal alternative to the ground-based LAI measurement is satellite imagery. Because of the difference in transmittance and reflectance of infrared and near-infrared energy between photosynthetic and non-photosynthetic plant material, there has been a great deal of interest in relating LAI to various spectral measurements that could be gathered by earth orbiting satellites. One of the more promising ratio-based indices is the normalized difference vegetation index (NDVI). For example, relationships between LAI and satellite-based measurements such as NDVI have been used to drive productivity models applied over large domains (Running et al. 1988, Hunt et al. 1996, Milner et al. 1996, Martin and Aber 1997). There are various concerns about scaling LAI by means of spectral vegetation indices (SVIs). These concerns include variation in background reflectance (such as soil and litter reflectance) (Huete 1988, Spanner et al. 1990, Huete and Tucker 1991), reflectance from understory vegetation (Spanner et al. 1990), the tendency of SVIs to asymptote at an LAI of around 5 (Turner et al. 1999), scaling issues such as the number and size of gap openings (Guyot et al. 1989, Cohen et al. 1990, Cohen and Spies 1992), leaf clumping (Guyot et al. 1989), and biological variation in leaf-level characteristics such as the amount and distribution of photosynthetic pigments. Nevertheless, the near daily coverage of the earth's surface provided by sensors such as the Advanced Very High Resolution Radiometer (AVHRR) and the Moderate Resolution Imaging Spectroradiometer (MODIS) has considerable potential for inferring spatial and temporal patterns in LAI (White et al. 1997).

In this study, we assessed the capacity of PnET to predict LAI in a temperate forest. Specifically, we compared the biologically scaled LAI trajectory estimated with the PnET model (LAI_{PnET}) with repeated ocular observations of leaf phenology, with an LAI trajectory calculated from photosynthetically active radiation (PAR) transmittance through the canopy (LAI_{TRANS}), and with a remotely sensed LAI trajectory derived from NDVI data (LAI_{NDVI}). In addition to direct comparison of LAI trajectories, we also investigated the potential influence of differences in the LAI trajectories on model C flux outputs. Typically LAI observations show variation of up to several weeks in leaf emergence and leaf fall dates in deciduous forests. Small variations in phenology can have large effects on carbon flux (Goulden et al. 1996, White et al. 1999) so it is important that they be successfully simulated in LAI scaling models. To assess such factors, we adapted PnET to run in a mode such that the LAI trajectories derived from PAR transmittance, NDVI, and the unmodified version of PnET could be used as model inputs. The daily GPP output by the model as driven by the alternative LAI trajectories was then compared with observations of GPP at the on-site eddy covariance flux tower (Wofsy et al. 1993, Goulden et al. 1996).

Materials and methods

Study site

The study site for these simulations was Harvard Forest. Located near Petersham, MA (42°32'30" N and 72°11'00" W), Harvard Forest is part of the US Long Term Ecological Research network (LTER, <http://lternet.edu/>). We utilized the Eastern hardwoods cover type (Campbell et al. 1999) for PnET model parameters. See Aber et al. (1995, 1996) for complete listings of model parameters. This is an "upland" community with an overstory dominated by sugar maple mixed with red oak, ash, basswood, and beech. The understory comprises saplings of shade-tolerant species and *Vaccinium* spp. Ground cover is made up of grasses and forbs which belong to the "Canadian carpet" community.

Phenology observations

We obtained phenology data for woody species from Harvard Forest, where it has been recorded since 1990 by J. O'Keefe and S. Johnson (unpublished data, <http://harvardforest.fas.harvard.edu/data/p00/hf003/hf003.html>). The dataset contains dates for observed bud break and leaf expansion on the same two to five individuals of 33 native woody taxa, at 3 to 7 day intervals from April through June. The dataset has recordings for fall color and leaf fall since 1991 from early September through leaf fall. All individuals are located along a 2 km loop near the Harvard Forest headquarters, which is approximately 1 km from the eddy covariance tower where a continuous sampling record of climate data and atmospheric fluxes are measured. We calculated means for the five most abundant tree species at the Harvard Forest eddy covariance tower site for bud break and leaf expansion (as a percent of observed maximum) to characterize canopy development in the spring, and means for observed color change and leaf fall (as a percent of observed maximum) to characterize the decline of the photosynthetic season.

Biologically scaled LAI

We derived temporal LAI estimates from PnET-II (Aber et al. 1995). The PnET family is a group of big-leaf forest ecosystem models that share the underlying assumption that a model with a minimum number of parameters can simulate the essential processes of forest ecosystem function (Aber and Federer 1992). In fact, it is the lumped parameter quality of PnET that allows it to be applied over broad spatial scales where detailed parameter information is difficult to come by. The canopy submodel of PnET is constructed around a group of central algorithms that take advantage of "quasi first principles" physiological relationships between foliar nitrogen, photosynthetic capacity, vertical scaling of leaf mass per area (LMA), and leaf life span (Reich et al. 1992, 1994, Ellsworth and Reich 1993, Gower et al. 1993).

The biologically scaled LAI version of PnET uses the Aber et al. (1996) algorithm that partitions the canopy into 50 layers, scales LMA with canopy depth, attenuates light vertically through the canopy, and calculates gross and net photosynthe-

sis for each layer. At the end of the growing season, the amount of C gained from canopy layers with a net positive carbon balance during the period of full canopy display (i.e., maximum LAI) is allocated to a bud carbon pool for use in constructing the following year's canopy. Canopy phenology is handled by a cumulative heat sum algorithm (Aber et al. 1996). The model adds foliage mass when parameterized growing degree day conditions are met. Leaf area index is calculated for each layer based on its foliage mass and scaled LMA. The model then sums LAI across layers to get a total canopy LAI at each timestep. Leaf off follows Aber et al. (1996), dropping leaves based on each canopy layer's C balance and a limit which prevents senescence from occurring before a particular day. For a thorough description of the PnET model, see Aber et al. (1995, 1996). To stabilize plant C pools, we ran the model with 50 years of climate data before we wrote any data to be used for LAI and GPP comparisons.

We derived daily climate data for maximum and minimum temperature, precipitation and PAR from half hourly meteorological observations at the flux tower (AmeriFlux 2001). We filled in data when necessary from observations at nearby meteorological stations. The meteorological data for 1995–1999 are available on the Internet (http://www.fsl.orst.edu/larse/bigfoot/data_data.html).

PAR Transmittance-based LAI

We derived temporal LAI estimates from light transmittance (LAI_{TRANS}) based on measurements of above- and below-canopy PAR at the flux tower and constrained by direct measurements of LAI at one time (see below). We estimated LAI by inverting the Beer-Lambert Law (Jarvis and Leverenz 1983):

$$LAI = \left(\frac{-1}{k} \right) \ln \left(\frac{I_z}{I_o} \right) \quad (1)$$

where k = radiation extinction coefficient, I_z = below-canopy PAR and I_o = incoming PAR.

Continuous measurements of I_o (taken at 29.0 m) and I_z (taken at 12.7 m) were made at the Harvard Forest eddy covariance flux tower (Wofsy et al. 1993, Goulden et al. 1996) during the 1995 through 1999 study period (see AmeriFlux citation for data access) with a Li-Cor silicon quantum sensor, and a mean value was reported for each half-hourly period. Measurements of I_z/I_o for the estimation of LAI are typically made under clear sky conditions (Fassnacht et al. 1994) when the diffuse proportion of PAR is relatively small and I_z/I_o is relatively large (Hutchinson and Matt 1977), thus the maximum value of I_z/I_o at noon during each week was selected to calculate an LAI value for that week. Optimally, I_z is averaged over an array of quantum sensors (Fassnacht et al. 1994) or for different positions from a moving sensor mounted on a track (Chason et al. 1991). However, data were available for only one fixed pair of sensors. Nonetheless, the integration of sunflecks over the half-hour periods, and the shifting solar angle over the growing season, helped to increase the effective canopy area sampled. Noon I_z/I_o fell from about 0.6 in the win-

ter to about 0.1 in the summer, with a standard deviation across days in a week of about 0.02.

The radiation extinction coefficient varies depending on sun angle and leaf orientation. However, 0.58 is commonly used by PnET to model this type of forest (Aber et al. 1995, 1996) and was adopted for this study. Transmittance is affected by branches and stems to a varying degree. To partly account for this time varying factor, the transmittance-based LAIs were constrained and calibrated to the assumed range of LAI_g using a simple proportionality:

$$\text{LAI}_g = \text{mLAI}_g + \text{rLAI}_g \left(\frac{\text{LAI}_t - \text{mLAI}_t}{\text{rLAI}_t} \right) \quad (2)$$

where LAI_g = green LAI, mLAI_g = annual minimum for LAI_g, LAI_t = LAI estimate for transmittance, mLAI_t = annual minimum for LAI_t, rLAI_t = annual range for LAI_t and rLAI_g = annual range for LAI_g. Values are mLAI_g = 0.2, mLAI_t = 0.8, rLAI_t = 3.6 and rLAI_g = 4.4.

These parameters are based on previous work that documented a low percent (7%) conifer cover at the tower site (Waring et al. 1995), and recent maximum growing season LAI measurements (S.T. Gower, University of Wisconsin, personal communication). After reaching maximum seasonal LAI in early June, temperate broadleaf forest canopies generally change minimally until leaf abscission (Baldocchi and Collineau 1994). Therefore, to remove transient dips in predicted LAI_{TRANS} during the full canopy display period, which probably reflected measurement error, not LAI changes (see Baldocchi and Collineau 1994), we held LAI_{TRANS} constant once LAI_{TRANS} reached a sustained plateau during the mid-growing season until the autumn decline. The result of the above constraints was a consistently low LAI in winter and early spring, until a sustained increase above 0.2 after approximately day 100, then a rapid increase to the full canopy display value of about 4.5, followed by an end of growing-season decline.

NDVI based LAI

We also derived estimates of LAI and its phenology from remote sensing (LAI_{NDVI}). Our calculations were based on a bi-weekly time series of NDVI from the AVHRR sensor. We extracted the NDVIs for 1999 at the 1 km² grid cell associated with the Harvard Forest eddy covariance tower for this analysis from a national NDVI database (Brad Reed, USGS EROS Data Center, personal communication, see Reed et al. 1994). Normalized difference vegetation index has been shown in theoretical (Sellers 1985, 1987) and empirical (Goetz and Prince 1996) studies to be nearly linearly related to the fraction of incident PAR that is absorbed by the canopy (f_{APAR}). For this sensitivity analysis, we interpolated the biweekly NDVI values to obtain a daily record. We then fit a least squares linear regression between NDVI and the weekly measured transmittances described earlier. Canopy PAR reflectance is relatively small (Gower et al. 1999) and was not treated here, thus the NDVI/transmittance relationship directly related to

the NDVI/ f_{APAR} relationship. We converted the daily transmittances to LAIs using the same procedure as was described for the PAR transmittances.

Observed and modeled GPP

To evaluate the effect of the alternative LAI trajectory formulations on simulated GPP, we modified the PnET model to permit LAI to be prescribed from an external input file. We substituted the following for the original Aber et al. (1996) canopy expansion algorithm:

$$\text{Folmass}_j = \sum (\text{LAI}_{ij})(\text{LMA}_{ij}) \quad (3)$$

Where Folmass_j is foliage mass at each day *j*, LAI_{ij} is the LAI for each layer *i*, at each day *j*, and LMA_{ij} is vertically scaled leaf mass area for each layer *i*, at each day *j* (source code available on request).

Tower GPP estimates for comparison with the model outputs were from the Harvard Forest eddy covariance flux tower (Wofsy et al. 1993). Gross primary production is estimated as the daytime sum of net ecosystem exchange (NEE) minus ecosystem respiration, with ecosystem respiration derived from soil temperature and the relationship of NEE to soil temperature at night (Goulden et al. 1996). We used data recorded from 1995 through 1999 (see AmeriFlux citation for data access). In the source data, GPP estimates were aggregated on a 5-day bin period. We binned daily model output to correspond to the bin periods of the flux data so as to permit direct comparisons with the tower data.

Results and discussion

LAI and phenology comparisons

Observed phenology data showed rapid leaf expansion in the spring, reaching 100% by late May in all 5 years (Figure 1a). The observed phenology data indicated that color change was initiated in September and reached 100% by October in all 5 years, with leaf fall following by about a week across all years. There was interannual variation on the order of a week or two on either end of the growing season. Variation among tree species was evident (e.g., Lechowicz 1984) but not dramatic.

The LAI_{TRANS} trajectory closely matched the visually observed leaf development points during the leaf expansion phase, as would be expected. There was a lag in LAI_{TRANS} relative to the phenology observations of a week or so at the end of the growing season in some years. Phenology estimates calculated from 1999 NDVI data predicted higher LAI values both in the early and late portions of the growing season compared with the observed phenology record, LAI_{TRANS} and LAI_{PnET}. These differences suggest an error in the LAI_{NDVI} data. However, the dynamics of the LAI_{NDVI} trajectory in the periods before canopy leaf out and after canopy leaf off may be tracking changes in understory and ground cover LAI. The relative contributions of actual changes in below-canopy LAI and possible artifacts from variation in the solar zenith angle (Spanner

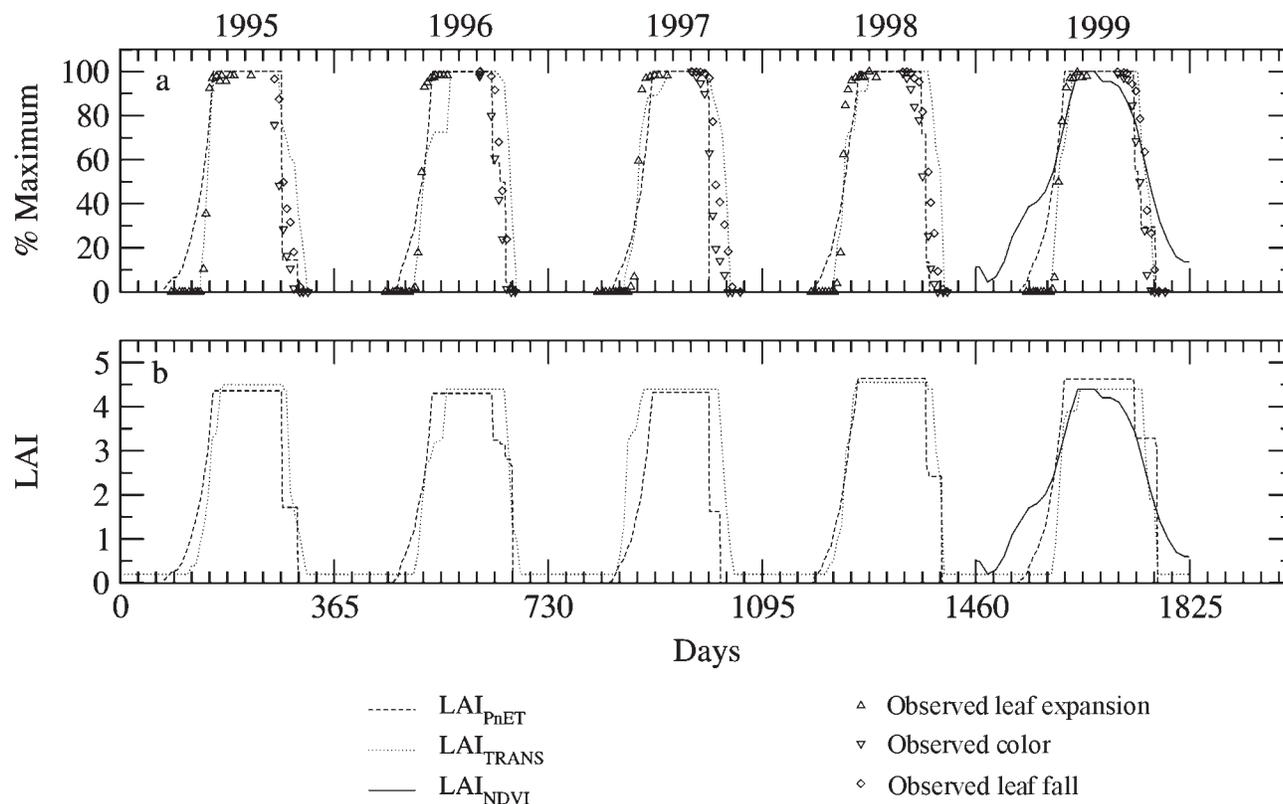


Figure 1. Phenology and leaf area index (LAI) data from Harvard Forest for 1995–1999. (a) Relativized LAI as a percentage of maximum for LAI estimates calculated with PnET's internal canopy display algorithms (LAI_{PnET}), LAI calculated from photosynthetically active radiation (PAR) transmittance (LAI_{TRANS}) and LAI calculated from the normalized difference vegetation index (LAI_{NDVI}). Symbols: Δ = observed foliar expansion, ∇ = observed color change, and \diamond = observed leaf fall, all as a percent of maximum. (b) Actual LAI estimated from PnET, PAR transmittance and NDVI.

et al. 1990) are not well understood. The seasonal NDVI signal is probably a function of both. Leaf area index trajectories based on the Moderate Resolution Imaging Spectroradiometer (MODIS), which is much improved relative to AVHRR in terms of georeferencing, atmospheric corrections and sensor calibration (Justice et al. 1998), are now being produced operationally every 8 days, and will be a stimulus to resolving these issues (e.g., Privette et al. 2002).

Estimates from PnET's phenology algorithms are reasonably consistent with the timing of leaf emergence, expansion and senescence from the observed record. However, LAI_{PnET} tends to start leaf expansion a few weeks earlier than the observed phenology record, and misses some of the interannual variation observed in the ground based phenology data and LAI_{TRANS} trajectories. Several factors may contribute to these differences. PnET's phenology algorithm is based on air-temperature-driven cumulative heat sums. It is widely accepted that tree phenology responds to a variety of environmental factors such as photoperiod, temporal variability in air temperature, soil temperature and soil water, any of which have the potential to nudge actual phenology away from the model predicted phenology (Jackson et al. 2001). For example, years for which there is a larger than "average" lag between an air-tem-

perature-based growing degree sum and soil temperatures that are favorable to leaf out, are likely to be years when PnET's growing degree day drivers miss the timing of leaf emergence and expansion as a result of a delay in belowground xylem activity relative to an air-temperature-based heat sum. Also, because a growing degree day sum simply accumulates favorable days, irregularities in the temporal dynamics of these same environmental factors (such as early warming followed by a period of cold) could also induce a disconnect between PnET's growing degree day estimates of leaf out and observed phenology (Schwartz and Marotz 1986).

The absolute LAI trajectories across all 5 years (Figure 1b) are quite similar. Differences among annual maximum LAI estimates from LAI_{PnET} and LAI_{TRANS} during the peak growing season are less than 0.2 LAI units in all 5 years (Table 1). These differences are within the potential associated measurement error limits. Given that LAI estimates from PnET are constrained by leaf traits and physiologically based canopy-level carbon balance and not empirical measurements, the close agreement between maximum LAI predicted by PnET and empirically based LAI estimates is noteworthy. Values of LAI_{NDVI} from 1999 show a comparable maximum LAI relative to LAI_{PnET} and LAI_{TRANS} , but note that LAI_{NDVI} and LAI_{TRANS}

Table 1. Estimates from three leaf area index (LAI) characterization methods for the years 1995–1999. See Figure 1 for LAI acronyms. Abbreviations: FCD is the period (day of the year) for which the full canopy is displayed and LAI is the LAI during that period.

Year	LAI _{PnET}		LAI _{TRANS}		LAI _{NDVI}	
	FCD	LAI	FCD	LAI	FCD	LAI
1995	159–275	4.4	175–277	4.5	–	–
1996	168–268	4.3	192–290	4.4	–	–
1997	179–274	4.3	164–290	4.4	–	–
1998	165–271	4.6	163–282	4.6	–	–
1999	152–269	4.6	178–283	4.4	174–202	4.4

were constrained to the same maximum LAI, albeit that constraint (4.6) was higher than either predicted estimate and therefore did not suppress either estimate.

The interannual range of estimated maximum LAI_{PnET} was 0.3 LAI units. This variation reflects the constraint on the current-year LAI by the amount of C gained from the previous year's canopy, and the incorporation of algorithms that scale leaf attributes to the canopy level. The idea that foliage dis-

played is linked to the carbon balance of an earlier time period is well grounded in forest ecological theory (Kozlowski 1992). Available carbon is a source not only for foliage display, but also for foliage redisplay in the event of a sudden loss of foliage as a result of disturbance. However, the time period of 1 year (last year's C gain) as incorporated in PnET is arbitrary. It is equally likely that a tree's available carbon may well be integrated over longer time periods (Fritts et al. 1999). Aber et al. (1996) reported that the lack of a discernable signal in tower flux measurements during dry periods in 1991 and 1993 seemed to indicate that water stress at this site is not a controlling factor.

Observed and modeled GPP

Gross primary production estimates from LAI_{PnET} indicate appreciable photosynthetic start-up close in time to the eddy flux estimates (Figure 2). In general, GPP estimates from LAI_{PnET} ramp down close to the eddy flux GPP estimates at the end of the growing season. In four of the five years examined, GPP from LAI_{PnET} underestimated the mid-season GPP values calculated from eddy flux data. The differences were approximately 1.5–2.0, 1.0–1.5, 1.5–2.0 and 1.0–1.5 g C m⁻² day⁻¹ in

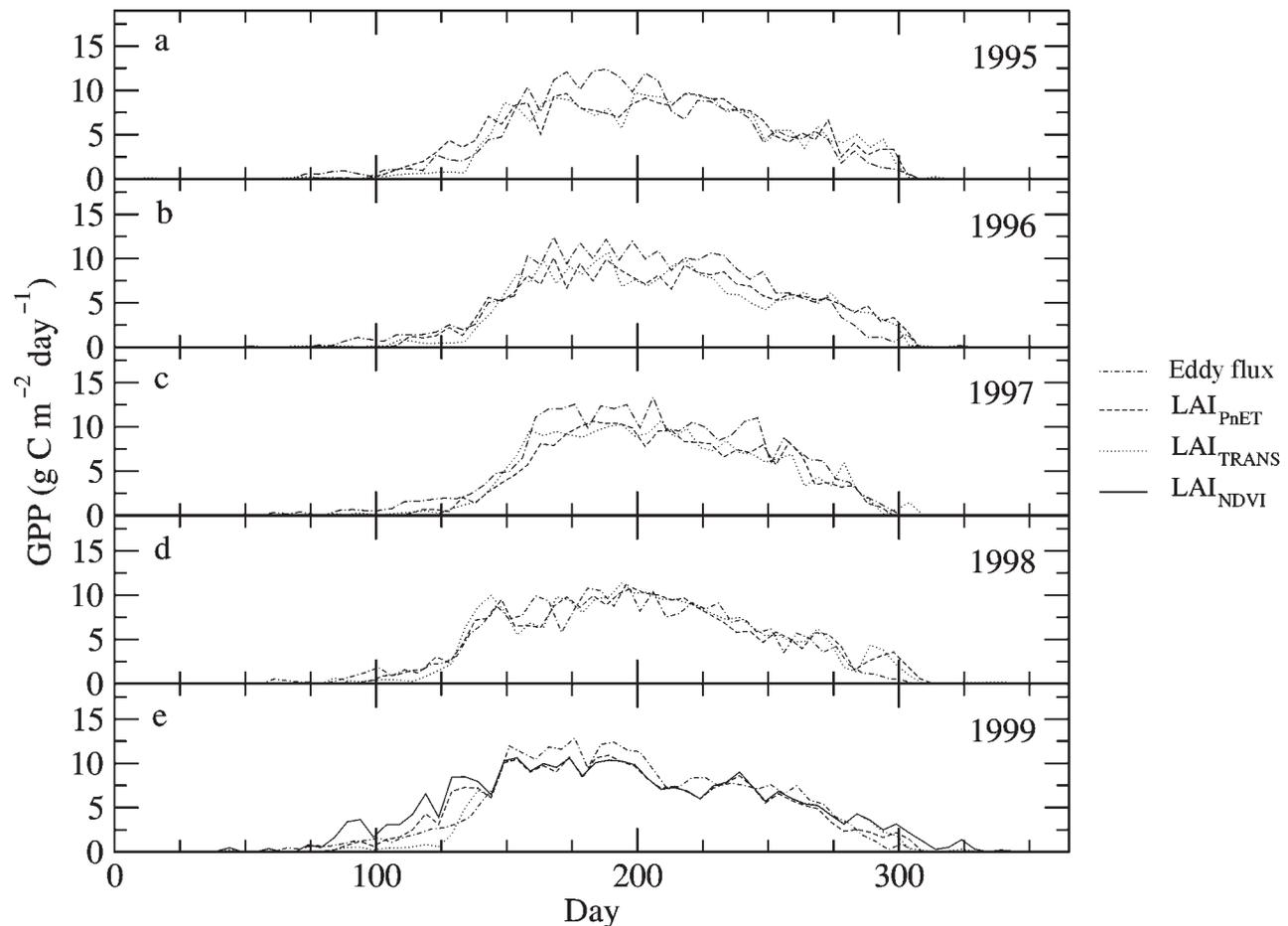


Figure 2. Gross primary production (GPP) estimates from eddy covariance data and 3 PnET model runs at Harvard Forest. See Figure 1 for legend and LAI acronyms.

1995, 1996, 1997 and 1999, respectively. Given similar underestimates for GPP based on LAI_{TRANS}, these differences were probably related to ecophysiological parameterizations in the model rather than to the LAI values. There was also general agreement in PnET between modeled and measured GPP for the 1990–1994 period at Harvard Forest (Aber et al. 1996).

In each of the 5 years examined, GPP estimates based on LAI_{TRANS} showed a delay in the start-up of appreciable photosynthetic activity relative to the eddy flux estimates. These delays ranged from approximately one and a half weeks in 1997 to about 4 weeks in 1995. The later than expected seasonal start-up of GPP that we observed in the model runs, based on LAI_{TRANS} relative to the eddy flux data, may be because the LAI_{TRANS} trajectory was based on PAR transmittance through the overstory. It is likely that the eddy covariance-based GPP estimates captured some photosynthetic activity in the understory and ground cover that flourish temporally in the early part of the growing season (Braun 1950, Harrington et al. 1989). The fact that the GPP estimates from the LAI_{PnET} profile capture the early season increase seen in the tower-based GPP data is consistent with PnET's theoretical underpinnings as a big-leaf ecosystem model.

Although the general profile of daily GPP modeled from the LAI trajectory follows the GPP profile from LAI_{PnET} and LAI_{TRANS} trajectories, daily GPP modeled from the LAI_{NDVI} trajectory tends to be higher in early and late portions of the 1999 growing season. Daily GPP estimates calculated from the LAI_{NDVI} trajectory for 1999 extended the growing season in both the spring and fall, overestimating tower-based GPP by about 1.5–2.5 g m⁻² day⁻¹ in those periods. In addition, daily GPP estimates from LAI_{NDVI} underestimated the mid-season maximum GPPs by about 1.0–1.5 g C m⁻² day⁻¹ relative to the eddy flux data. As with LAI_{PnET}, the LAI_{NDVI}-based GPP estimates may have captured early-season photosynthetic activity. Like the late-season extension of GPP, this may in part be an artifact associated with varying solar zenith angle (Spanner et al. 1990), or another error source.

Cumulative GPP

There was reasonably good long-term (1995–1999) agreement between eddy flux-derived GPP totals and GPP estimates derived from LAI_{PnET} and LAI_{TRANS} (Table 2). Annual GPP estimates averaged over the 5-year period for LAI_{PnET} and LAI_{TRANS} were within 7 and 9%, respectively, of eddy flux data. For the period from 1991 to 1994, LAI_{PnET} GPP estimates were within 2% of average annual GPP estimates from eddy flux data (Aber et al. 1996). However, the correspondence of annual GPP among models and eddy flux data was more variable on a year-by-year basis. Compared with flux data, annual GPP from LAI_{PnET} model output ranged from 22% less in 1997 to 8% more in 1998, and was not consistently an over- or underestimate. The LAI_{TRANS} output ranged from 19% less to 8% more than the eddy flux GPP estimates. Although the empirically derived LAI_{TRANS} model output should hypothetically be more accurate than GPP estimated from biologically modeled LAI_{PnET} (because site-specific observations were used in

Table 2. Annual gross primary production (GPP; g C m⁻² year⁻¹) estimates for Harvard Forest for 1995–1999. See Figure 1 for leaf area index (LAI) acronyms. Eddy flux estimates are from the Harvard Forest eddy covariance tower. Annual totals are calculated from 5-day bins.

Year	LAI _{PnET}	LAI _{TRANS}	LAI _{NDVI}	Eddy flux
1995	1204	1144	–	1240
1996	1142	1095	–	1324
1997	1079	1124	–	1382
1998	1242	1249	–	1145
1999	1311	1256	1487	1347
\bar{x}	1195	1174	–	1287

the development of LAI trajectories), the differences in GPP between the two predictions were small. Given that the GPP estimates from LAI_{PnET} were as close to the annual eddy flux GPP estimates as the empirical LAI_{TRANS} estimates, biologically based LAI predictions offer promise as part of a modeling strategy.

Conclusions

A process-based ecosystem model that predicts LAI based on constraints due to leaf-level ecophysiology, light response characteristics, intra-canopy light attenuation, and available C for canopy construction was able to predict LAI values and phenology patterns that closely match intensive empirical observations. This “quasi first principles” approach to canopy construction allows models such as PnET to simulate LAI seasonal trajectories without a priori knowledge of LAI. Such models could be particularly useful if the goal were to make predictions into the future or for sites where LAI estimates would be difficult. Furthermore, these results are an affirmative test of our integrated understanding of canopy dynamics and make the linkage of leaf phenology to plant carbon balance in such models particularly appropriate for evaluating potential effects of environmental change.

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