

Influence of environmental variables on leaf area index in loblolly pine plantations

Stephen M. Kinane^{a,*}, Cristian R. Montes^b, Mauricio Zapata^c, Bronson P. Bullock^b, Rachel L. Cook^d, Deepak R. Mishra^e

^a Timberland Investment Resources, LLC, 115 Perimeter Center Pl #940, Atlanta 30346, GA, USA

^b Co-Director Plantation Management Research Cooperative (PMRC), Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green St, Athens 30602, GA, USA

^c Finite Carbon Corporation, 435 Devon Park Drive 700 Building, Wayne 19087, PA, USA

^d Department of Forestry and Natural Resources, North Carolina State University, 2820 Faucette Dr, Raleigh 27695, NC, USA

^e Department of Geography, University of Georgia, 210 Field St #204, Athens 30602, GA, USA

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ABSTRACT

The productivity of even-aged forest stands varies from one year to the next as a function of canopy size and its interaction with the effective radiation used for photosynthesis. To characterize this relation, ecologists use leaf area index (LAI), a metric that serves as an indicator of the photosynthetic capacity on a given site. In this research, we proposed a model describing leaf area index dynamics in loblolly pine plantations growing in the southeastern United States. The model implements a delayed differential equation using periodic coefficients that enforce the seasonality in resource availability. The equation was further expanded to accommodate climatic variables to evaluate their contribution in reducing the observed variability. The proposed model uses environmental modifiers to account for the changes in resource availability and to adjust the carrying capacity in forest stands. From a range of tested variables, we found monthly maximum temperature and monthly excess water to be the most influential on leaf area index dynamics. With the addition of environmental modifiers and a local carrying capacity parameter, root mean square error was reduced to 0.3802 units LAI (m^2/m^2) from a base model RMSE of 0.4427 units LAI (m^2/m^2). The results indicate that the delay component has a small 41-day effect in the model, which is contrary to our initial hypothesis that stored within-tree carbohydrates can be used for further seasons to build foliage.

1. Introduction

Variability in forest productivity has largely been attributed to the changes in radiation interception (Monteith, 1972; Grier and Running, 1977; Jarvis and Leverenz, 1983; Vose and Allen, 1988; Leverenz and Hinckley, 1990). Substantiating the variability in radiation interception is a multifaceted issue; with potential changes being driven by the environment (Vose et al., 1994; Dougherty et al., 1995), phenology (Vose et al., 1994), stand composition (Pretzsch, 2014), crown structure/architecture (Leverenz and Hinckley, 1990, 1994, 1998, 2003, 2004, 2010, 2012), species (Chmura and Tjoelker, 2008), genotype (Jayawickrama et al., 1998; Chmura and Tjoelker, 2008), or silvicultural practices (Vose and Allen, 1988; Zhang et al., 1997; Will et al., 2005; Chmura and Tjoelker, 2008; Campoe et al., 2013). While other factors,

such as light use efficiency and available photosynthetically active radiation, are necessary components in determining a forest's productivity (Martin and Jokela, 2004; Reich, 2012), leaf area index (LAI) is a popular surrogate for radiation interception due to its ecological significance as the representation of the surface where energy, carbon dioxide, and oxygen are exchanged between the environment (Grier and Running, 1977; Vose et al., 1994; Dougherty et al., 1995) and its ability to be estimated using readily available remotely sensed data (Badhwar and MacDonald, 1986; Spanner et al., 1990; Chen and Cihlar, 1996; Flores et al., 2006; Peduzzi et al., 2012; Savoy and Mackay, 2015; Blinn et al., 2019). LAI, defined as the single-sided sum of the leaf surface area per unit ground area (m^2/m^2), has been used as key driver in process based models to assist in determining energy fluxes, most successfully with physiological responses to climate (e.g. Running et al. (1989);

* Corresponding author.

E-mail address: kinane@tirlc.com (S.M. Kinane).

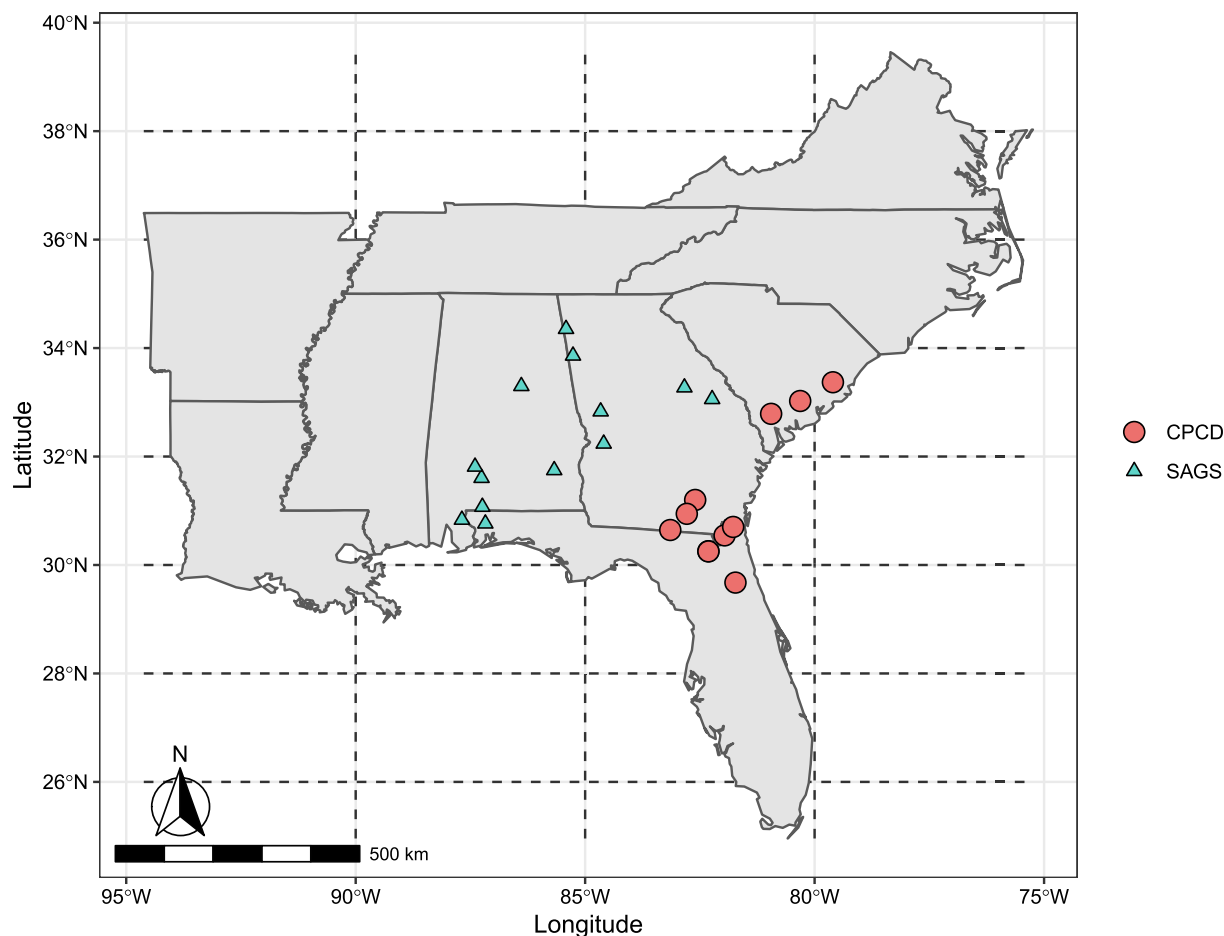


Fig. 1. Site locations for the Plantation Management Research Cooperative’s Coastal Plain Culture Density (CPCD) and South Atlantic Gulf Slopes (SAGS) installations used in analysis.

Table 1
Global parameter estimates and standard errors for the base leaf area index model (Eq. 4) fitted to 24 plots across the southeastern United States. Root mean square error (RMSE) was calculated across all observations.

Parameter	Estimate	Standard Error	Model Form	Environmental Variables
r	1.0750	0.0014	Base	N/A
τ	0.0002	0.0012		
L_{mx}	4.7760	0.0016		
A	3.1199	0.0036		
ω	6.2933	0.0012		
μ	-1.8875	0.0016		
h	0.0961	0.0004		
RMSE	0.4427			
AIC	12496.7			

Landsberg and Waring (1997); Sampson et al. (1997)).

1.1. Drivers of foliage display in loblolly pine

The concentration of leaf area in a canopy is a function of stand structure, nutrient availability, annual phenology, and environmental trends (Vose et al., 1994; Dougherty et al., 1995). These climate and soil variables are not only influencing the current year’s leaf biomass, but they also have an effect on the following year’s cohort due to the carryover of soluble carbohydrates that remain in the tree (Dougherty et al., 1995). The phenology of loblolly pine (*Pinus taeda* L.) needles is an environmentally driven process that represents a flux of nutrients within

a given tree and corresponds to changes in growth rates on an intra-annual seasonal basis (Dougherty et al., 1995; Jayawickrama et al., 1998; Albaugh et al., 2012). The phenological process relies on genetics, temperature, photoperiod, water availability, and nutrient availability to stimulate the hormones that spur physiological changes (Dougherty et al., 1994; Forrest and Miller-Rushing, 2010; Bahuguna and Jagadish, 2015; Quesada et al., 2017). The annual phenological trend of loblolly pine needles has been characterized as a system in three stages: 1) a period of rapid needle accretion, followed by 2) a reduction in growth in which the needles reach their final length, and 3) a period of needle abscission (Sampson et al., 2003). Needle elongation follows the onset of bud break and shoot elongation, which can be temporally related to thermal units (Teskey et al., 1987; Russell et al., 1989; Dougherty et al., 1994). Multiple flushes of foliage occur throughout the growing seasons for loblolly pine, with later flushes attaining similar elongation rates but not overall lengths as the first flushes (Dougherty et al., 1994). Nutritional status has been shown to affect needle elongation rates and overall needle length (Zhang et al., 1997). The overall lifetime of needles is a function of the environment, nutrition status, and genetics (Vose and Allen, 1988; Gholz et al., 1991; Hennessey et al., 1992; Dougherty et al., 1994; Zhang et al., 1997). Fertilized stands have been shown to retain foliage longer as compared to unfertilized stands (Zhang et al., 1997). Needle abscission introduces a higher degree of variability into the system as compared to accretion and has been shown to be affected by site nutritional and water status, stand density, and environmental variables (Vose and Allen, 1988; Hennessey et al., 1992). Longer growing seasons, a function of the number of frost-free days observed, provide more time for suitable growing conditions but may increase the

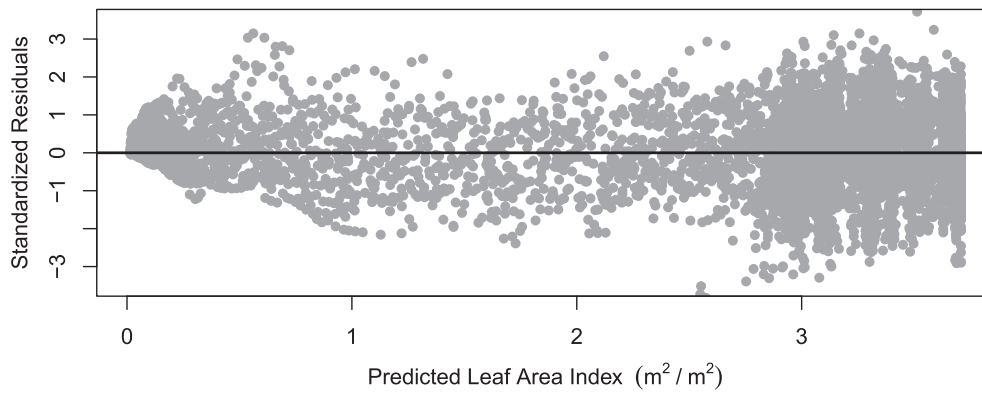


Fig. 2. Standardized residuals for the base model.

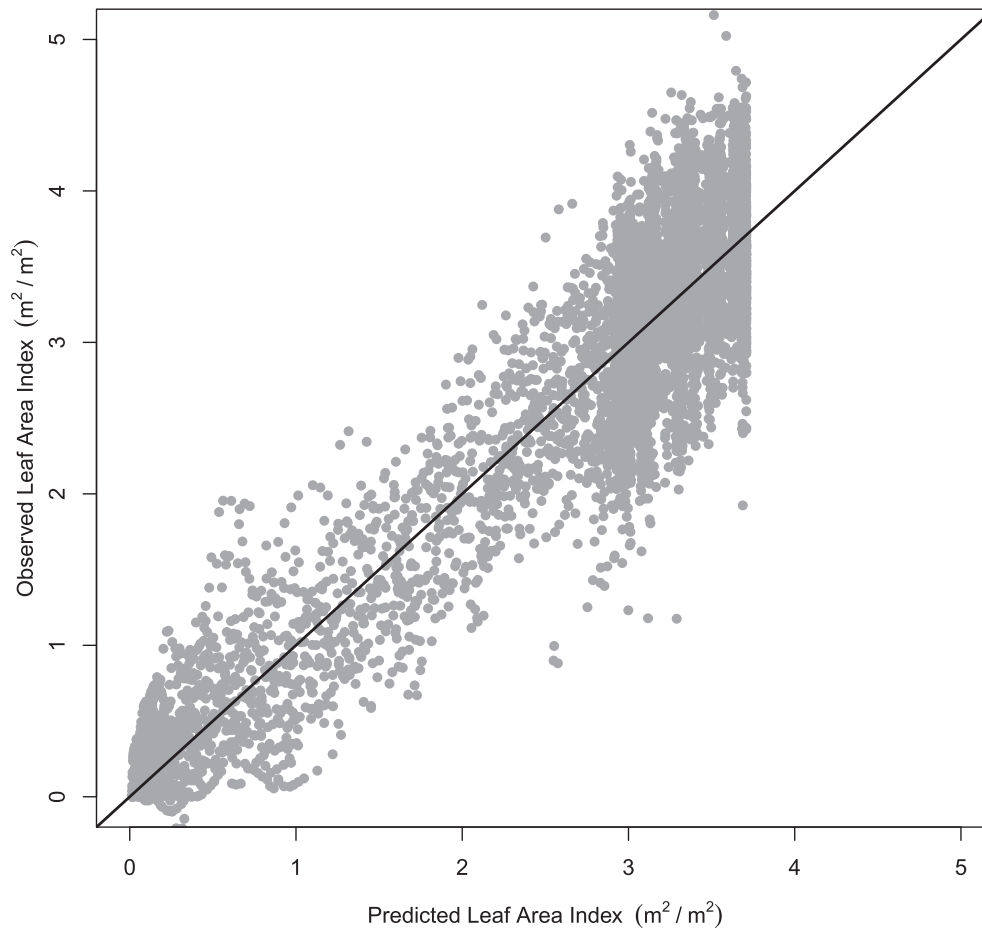


Fig. 3. Observations vs predictions for base model. The abrupt termination of predicted leaf area index values is due to the model reaching the estimated carrying capacity.

respiration losses due to higher temperatures (Teskey et al., 1987). Environmental regulation of leaf area has been reported to be influenced by temperature, water availability, and site available nutrients (Waring et al., 1978; Vose and Allen, 1988; Hennessey et al., 1992; Dougherty et al., 1995; Zhang et al., 1997; Savoy and Mackay, 2015). Understanding the environmental drivers of loblolly pine foliage provides a necessary understanding of the factors that promote or limit growth within and between years, and contribute to the variability observed in radiation interception.

1.2. Existing models for leaf area display

Leaf area display has been incorporated into process based and empirical models to simulate the ecophysiological processes that govern forest stand growth (Bossel and Schäfer, 1989; McMurtrie and Landsberg, 1992; Bossel, 1996; Landsberg and Waring, 1997; Sampson and Ceulemans, 1999; Battaglia et al., 2004; Sampson et al., 2006; Montes, 2012). Process based models, such as TREEDYN, BIOMASS, SECRETS, 3-PG, and CABALA, use the mathematical (functional) relationships between input state variables and parameterized ecophysiological equations to simulate the mechanistic behavior of the forest system in a

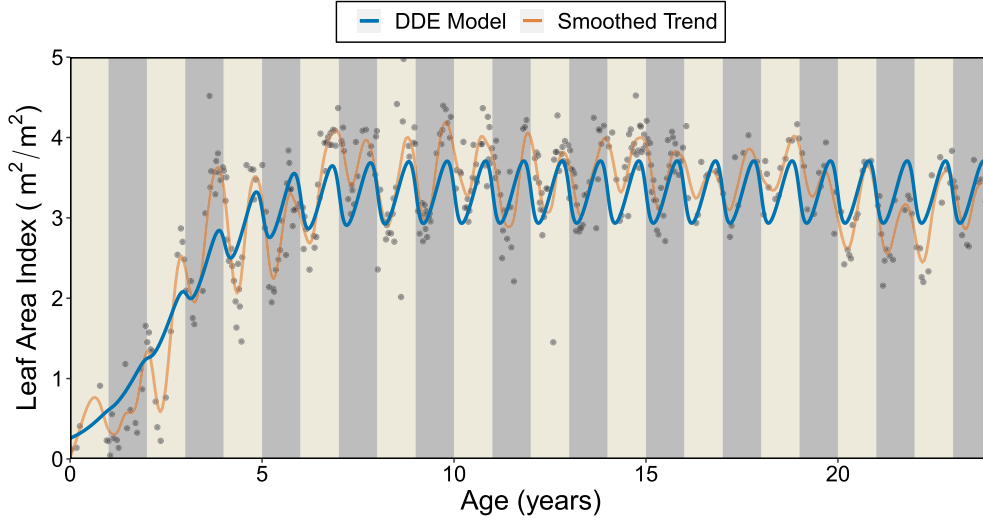


Fig. 4. Results for the base model compared to the smoothed trend and observations. Root mean square error for this observed plot was 0.3398.

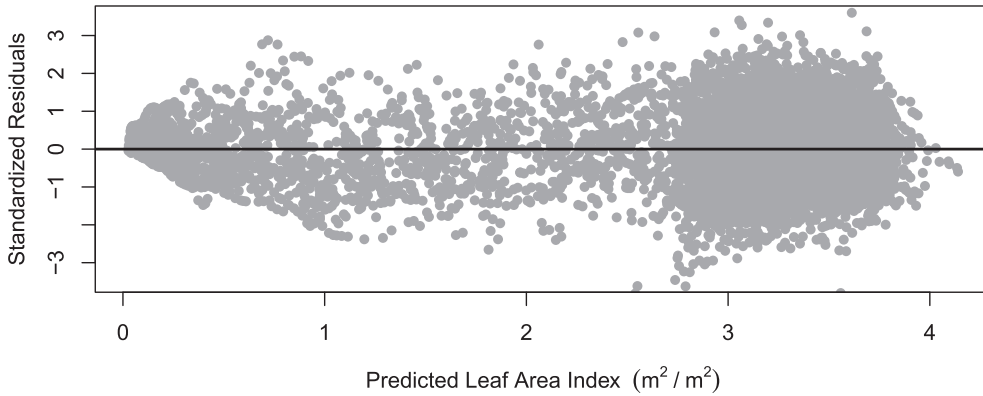


Fig. 5. Standardized residuals for the model parameterized in Table 2 using monthly maximum temperature (°C) in beta form as a modifier.

hierarchical fashion, including interaction and feedback relationships (Bossel and Schäfer, 1989; McMurtrie and Landsberg, 1992; Bossel, 1996; Landsberg and Waring, 1997; Sampson and Ceulemans, 1999; Battaglia et al., 2004; Sampson et al., 2006; Montes, 2012; Burkhart and Tomé, 2012). Using estimates of leaf area, these models simulate nutritional, water, and carbon fluxes and their interactions with meteorological and site conditions to provide stand growth estimates (McMurtrie and Landsberg, 1992; Landsberg and Waring, 1997; Sampson and Ceulemans, 1999; Sampson et al., 2006). Additional developments in the processed based models provided the ability to model silvicultural input effects on stand productivity (Battaglia et al., 2004).

Nevertheless, these models provide a complete overview of carbon capture using a single leaf approach, however, simpler but biologically meaningful models are needed to inform production models for intensively managed forest plantations. Differential equations have been used to model growth, among many other things, as a rate of change of one variable in relation to another, primarily time (Fulford et al., 1997). These equations provide a mechanistic hypothesis for how systems interact and their parameterization can provide biological interpretation, which is paramount to understanding the complex dynamics that factor into tree growth (Zeide, 1993; Garcia, 2001).

The objective of this research was to prove the differential equation modeling framework to model the phenological development and trends of LAI in loblolly pine stands in the southeastern United States. To account for the observed variability in LAI development we expanded the framework to include productivity modifiers based on temperature and

precipitation variables. We hypothesize that environmental variables have a direct effect on LAI dynamics in loblolly pine plantations and that the carry over effect from stored carbohydrates explains the current LAI state.

2. Materials and Methods

2.1. Model Formulation

An initial model to explain leaf area increase between years was formulated as a logistic function expressed in its differential form:

$$\frac{dL}{dt} = rL \left(1 - \frac{L}{L_{mx}} \right), \quad (1)$$

with L the stand leaf area index, r the rate of increase in leaf area over time (t) and L_{mx} a theoretical maximum leaf area attainable on a given site. The equation presents a simple negative feedback relation between L and L_{mx} . As L approaches L_{mx} it is expected to see more competition for site resources among leaves, so the instantaneous LAI growth will tend to 0 (note: r is the proportional growth rate, which is constant). Throughout the year L_{mx} is expected to vary given resources that become more or less available (e.g. temperature, rainfall, and nutrients like nitrogen, phosphorus, potassium and boron). The effect was accounted for by adding a seasonal trend via a trigonometric function to the denominator of the L/L_{mx} term:

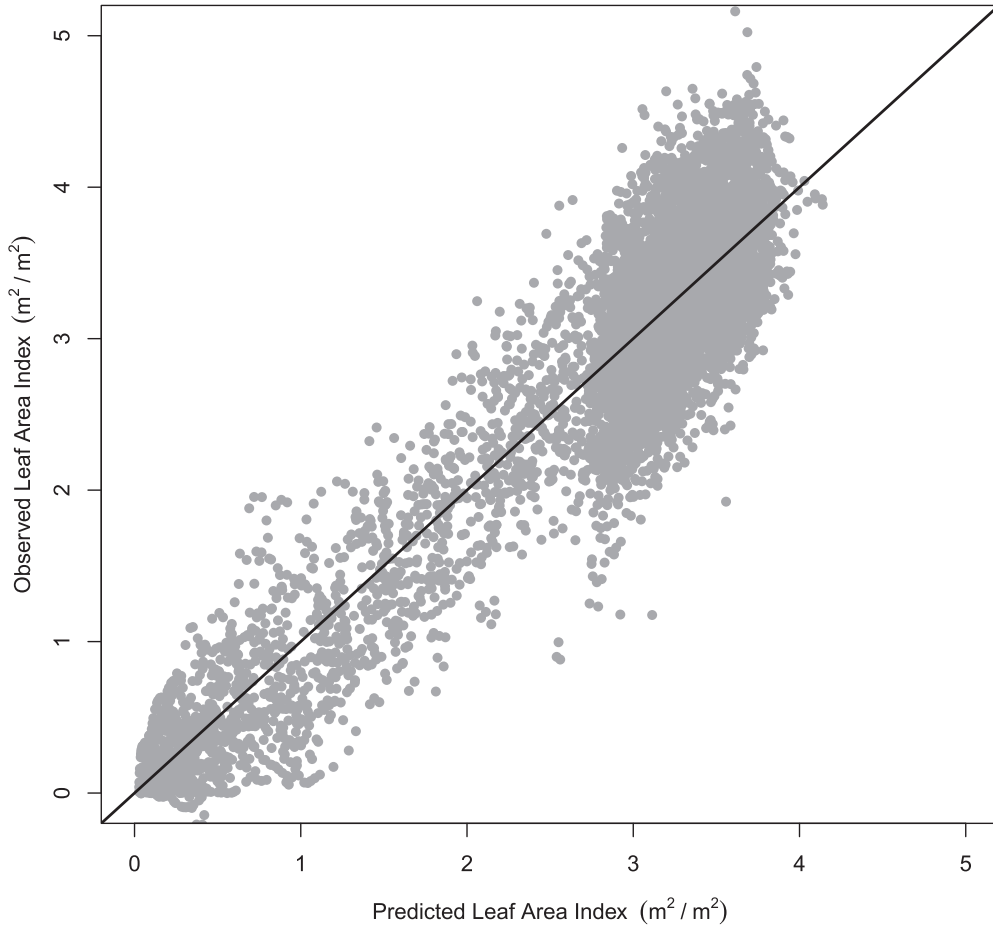


Fig. 6. Observations vs. predictions for the model parameterized in Table 2 using monthly maximum temperature (°C) in beta form as a modifier.

Table 2

Global parameter estimates and standard errors for the base leaf area index model (Eq. 4) with monthly maximum temperature (°C) as a beta modifier fitted to 24 plots across the southeastern United States. Root mean square error (RMSE) was calculated across all observations.

Parameter	Estimate	Standard Error	Model Form	Environmental Variables
r	1.1109	0.0006	Base	N/A
τ	0.1148	0.0004		
L_{mx}	4.5565	0.0010		
A	3.0997	0.0005		
ω	6.2948	0.0012		
μ	-1.8663	0.0009		
h	0.0885	0.0006	Beta	Monthly Maximum Temperature
μ_2	-5.7533	0.0009		
T_b	1.4255	0.0005		
α	1.4832	0.0006		
T_c	36.7020	0.0006		
β	0.3782	0.0011		
RMSE	0.4299			
AIC	11891.71			

$$\frac{dL}{dt} = rL \left(1 - \frac{L}{L_{mx} + A \sin(\omega t + \mu)} \right), \quad (2)$$

with A an amplitude term, ω the period and μ the phase of a seasonal function (Gopalsamy et al., 1990). With this formulation, L_{mx} serves as the vertical shift in the periodic function:

So far, this model assumes that production of new foliage will be solely determined by the existence of foliage in the current season. We

expanded this relation to include a delay effect, to reflect the impact of previous year photosynthetic capacity in the production of current year's foliage, leading to the following formulation using a delayed differential equation (DDE):

$$\frac{dL}{dt} = rL_t \left(1 - \frac{L_{t-\tau}}{L_{mx} + A \sin(\omega t + \mu)} \right), \quad (3)$$

where L_t is current leaf area index, $L_{t-\tau}$ is the leaf area index from previous state τ units ago. It is expected to see tree mortality on a given stand that will affect the amount of foliage present. This effect was added at the end of the base equation:

$$\frac{dL}{dt} = rL_t \left(1 - \frac{L_{t-\tau}}{L_{mx} + A \sin(\omega t + \mu)} \right) - hL_t, \quad (4)$$

with h a parameter to reflect the proportion expected L of mortality on a given site resulting from trees exhibiting competition. The final component, mortality, provides an accounting of additional biomass mortality that occurs independently of the seasonal leaf component.

2.1.1. Inclusion of Environmental Variables

Extendibility of the DDE to relate to environmental conditions that govern growth can be implemented by establishing the model parameters as functions of environmental variables (Kramer, 1994; Powers et al., 2003). It has been well established that environmental variables, such as temperature and water, are important drivers of loblolly pine productivity and regulate the annual phenological processes that determine the annual growth (Dougherty et al., 1994; Albaugh et al., 2012). To incorporate these environmental variables as growth regulators into the system, several model forms were evaluated for the

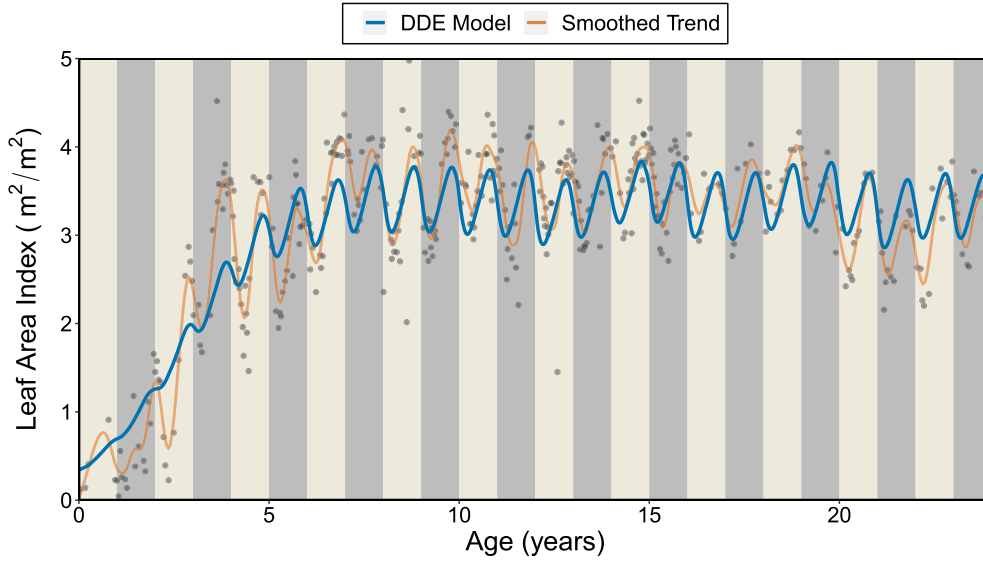


Fig. 7. Results for the model parameterized in Table 2 using monthly maximum temperature (°C) in beta form as a modifier compared to the smoothed trend and observations. Root mean square error for this plot was 0.3171.

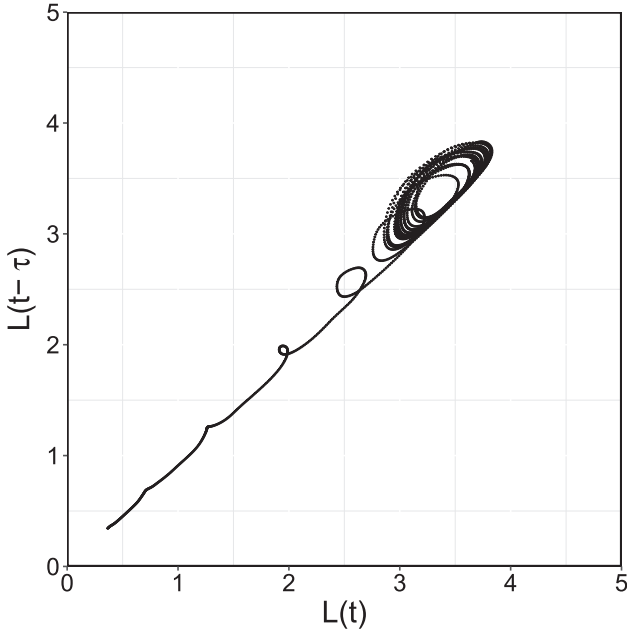


Fig. 8. Results for the maximum monthly temperature model lag history trend. The x-axis shows the current state $L(t)$ and its relationship with the historical state on the y-axis defined by τ , which was found to be 0.1148. State units are LAI m^2/m^2 .

individual components, including the beta equation (Eq. 5), the logistic equation (Eq. 6), the double logistic equation (Eq. 7), the Arrhenius equation (Eq. 8), the Heaviside equation (Eq. 9) simple linear equation (Eq. 10).

$$f(env(t)) = \exp(\mu) (env(t) - T_b)^\alpha (T_c - env(t))^\beta \quad (5)$$

$$f(env(t)) = \alpha \left(\frac{1}{1 + \exp(-b(env(t) - m))} \right) \quad (6)$$

$$f(env(t)) = \alpha \left(\frac{1}{(1 + \exp(-b(env(t) - m)))(1 + \exp(d(env(t) - n)))} \right) \quad (7)$$

$$f(env(t)) = \alpha \left(\frac{\exp(\frac{-b}{env(t)})}{1 + c \exp(\frac{-d}{env(t)})} \right) \quad (8)$$

$$f(env(t)) = \alpha(env(t) - T_b) H(env(t) - T_b) \quad (9)$$

where $H(env(t) - T_b) = \begin{cases} 1 & \text{if } env(t) \geq T_b \\ 0 & \text{if } env(t) < T_b \end{cases}$

$$f(env(t)) = \beta_0 + \beta_1 env(t) \quad (10)$$

The selected model form for the environmental modifier was incorporated into the base equation in a multiplicative fashion:

$$\frac{dL}{dt} = f\left(env\left(t\right)\right) \left(r L_t \left(1 - \frac{L_{t-\tau}}{L_{mx} + A \sin(\omega t + \mu)} \right) - h L_t \right) \quad (11)$$

To select the best model that represents the environmental effect on LAI growth dynamics, we used different statistics and criterion that measure the agreement between the model prediction and the training data.

2.2. Data

Data for this analysis came from a time series of satellite reflectance values extracted from two long-term spacing studies installed and maintained by the Plantation Management Research Cooperative (PMRC). The Coastal Plain Culture Density (CPCD) and South Atlantic Gulf Slopes (SAGS) studies were installed between 1995 and 1996, and between 1996 and 1997 respectively. The SAGS study comprised 23 sites throughout the Piedmont/Upper Coastal Plain physiographic region across five southeastern states (Zhao et al., 2010). The CPCD study consisted of seventeen installations throughout the lower coastal plain of Florida, Georgia, and South Carolina (Zhao et al., 2011).

2.2.1. Plot layout

The design of each study corresponds to a split-plot design that study the effects of two cultural regimes (main plot) across a range of planting densities (subplot) (Zhao et al., 2011). The cultural regimes for the either study included two levels of silviculture: 1) operational, consisting of bedding and banded chemical site preparation, herbaceous weed control after the first growing season, and fertilization at planting,

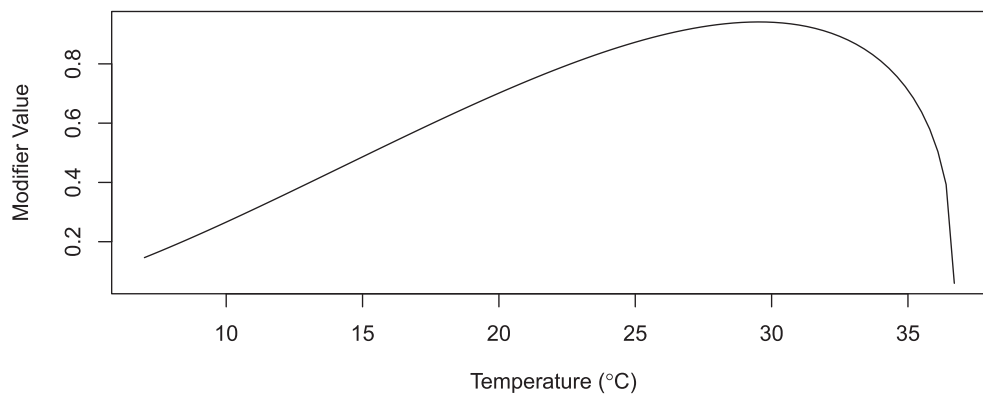


Fig. 9. Evaluation of the parameterized monthly maximum temperature beta modifier.

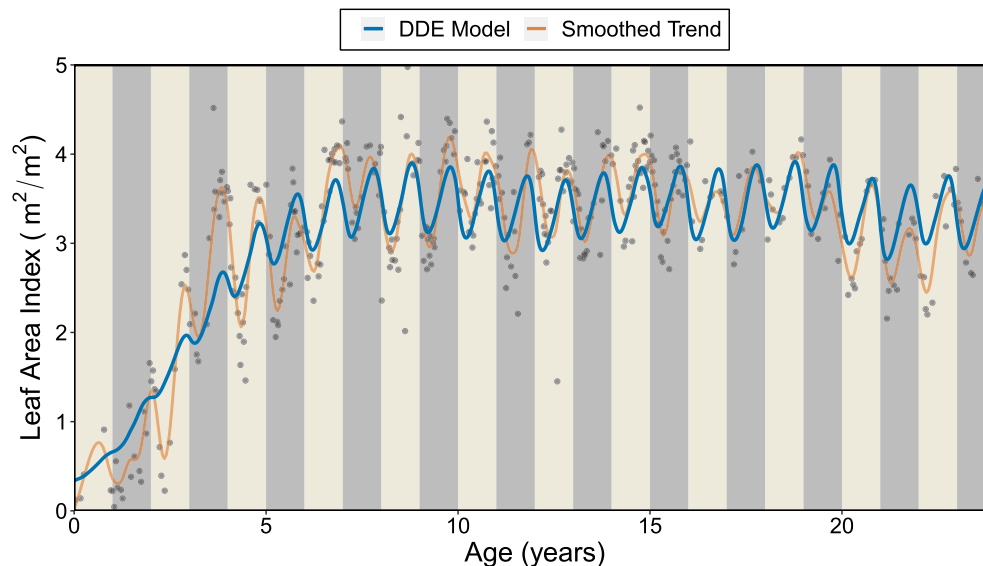


Fig. 10. Results for the model parameterized in Table 3 using monthly maximum temperature ($^{\circ}\text{C}$) in beta form and monthly excess water in double logistic form as modifiers compared to the smoothed trend and observations. Root mean square error for this plot was 0.3096.

before the 8th growing season, and before the 12th growing season and 2) intensive, consisting of bedding and broadcast chemical site preparation, tip moth control, complete vegetation control, and multiple fertilization treatments throughout the first twelve growing seasons (Zhao et al., 2011). The planting densities ranged from 741 to 4448 trees per hectare on study plots sized from 0.12 to 0.23 hectares to accommodate the minimum number of measurement trees. Further details for the CPCD study can be seen in (Harrison and Kane, 2008). For further details on the SAGS experimental design and treatments, see (Zhao et al., 2008). A total of 24 sites, 11 from the CPCD study and 13 from the SAGS study were selected for analysis (Fig. 1). Only plots under the intensive treatment were selected to remove potential sources of variability associated from differing treatment responses.

2.2.2. Satellite data

Due to the range of subplot size in the CPCD and SAGS studies, subplots from the 741 trees per hectare planting density (3.66 m x 3.66 m spacing) receiving intensive treatments were selected to maximize the subplot size (0.23 hectares) to increase the geographic footprint for remotely sensed data acquisition. All available surface reflectance scenes from the Landsat 5 TM and Landsat 7 ETM+ sensors were pre-processed and extracted using the Google Earth Engine platform from time of establishment to end of year 2019, masked for clouds, and exported as individual band values averaged for the subplot (Gorelick

et al., 2017). Data were further filtered based upon cloud quality attributes, pixel quality attributes, and radiometric saturation. Using near-infrared (band 4) and short-wave infrared (band 5) bands, the normalized difference moisture index (NDMI) was calculated. Estimates of LAI were produced from an empirical model using the NDMI values (Kinane et al., 2021). The number of available scene observations per study plot ranged from 334 to 1005 from plot establishment to December 31, 2019. Additionally, erroneous and outlying observations within the first five years of development were removed to reduce the amount of noise observed in the time series. The time series of individual plots were shortened to remove any observations that included post-thinning or increased mortality to insects. To provide increased temporal consistency and determine the underlying LAI development trend and seasonality, a thin plate spline (TPS) from the *ffds* package was used to smooth the observed data (Savoy and Mackay, 2015; Nychka et al., 2017). LAI time series for each plot were fitted using the TPS function with the cost function set to 1.2. Using the fitted TPS model, a new time series for each plot was created on a 0.05 year time step for the age range observed at each plot.

2.2.3. Environmental data

Environmental variables for the individual study sites were interpolated using the data from the University of East Anglia's Climate Research Unit (CRU) (Harris et al., 2020). Using CRU's TS v. 4.04

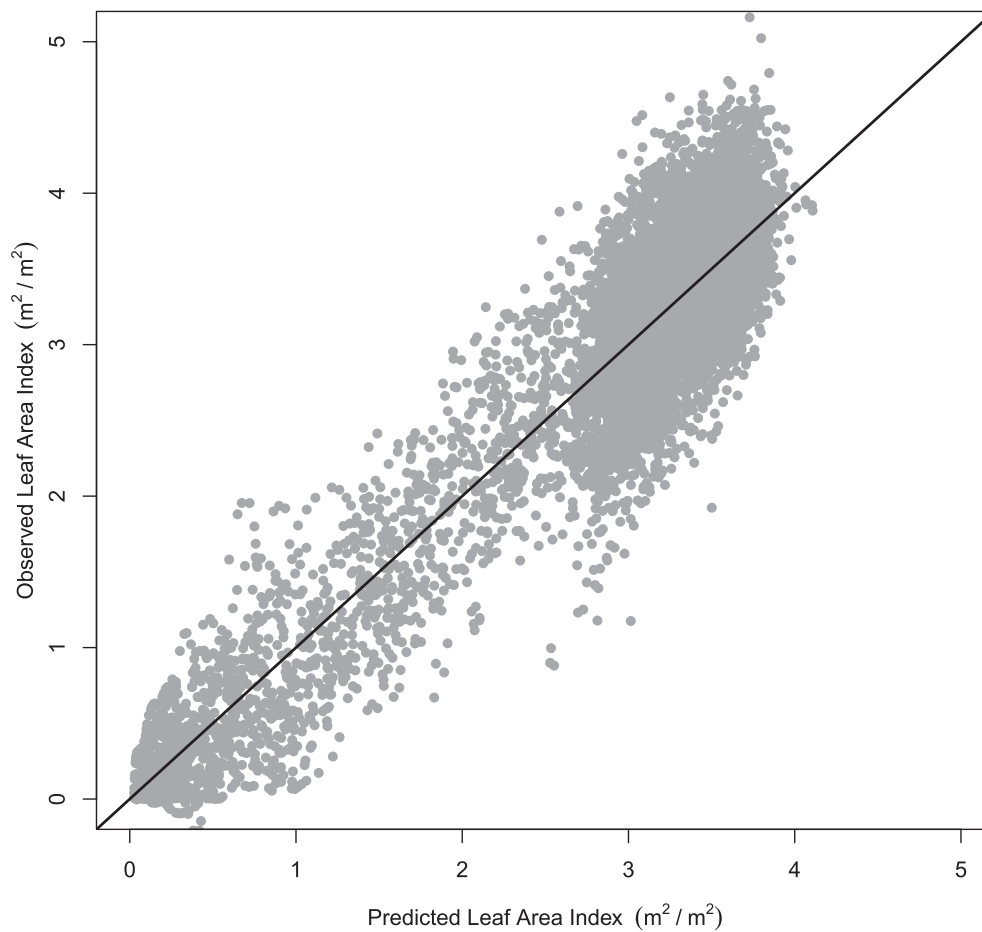


Fig. 11. Observations vs. predictions for the model parameterized in Table 3 using monthly maximum temperature ($^{\circ}\text{C}$) in logistic form and monthly excess water (mm) in double logistic form as modifiers.

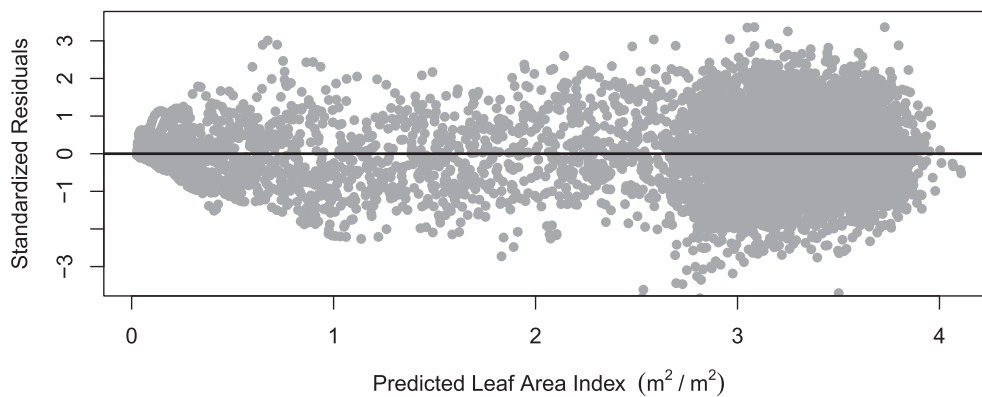


Fig. 12. Results for the model parameterized in Table 3 using monthly maximum temperature ($^{\circ}\text{C}$) in beta form and monthly excess water in double logistic form as modifiers compared to the smoothed trend and observations.

NetCDF product, monthly values at the individual study plots were acquired from establishment to December 2019. These variables include precipitation, monthly mean temperature, monthly maximum temperature, monthly minimum temperature, and vapor pressure (Harris et al., 2020). Water storage capacity for the first 1.5 meters of soil was estimated at the individual site using data from SSURGO spatial data base (Soil Survey Staff, 2017). Additional indices, including water deficit, water deficit index, excess water, and excess water index were calculated from the CRU environmental variables in association with water storage capacity at the individual study plots. Water deficit for the site is

calculated by subtracting the monthly precipitation from the monthly estimated potential evapotranspiration. Conversion of water deficit to water deficit index incorporates subtracting out the water storage capacity and summing the water deficits (Ojeda et al., 2018). Excess water and its index are calculated in similar fashion by subtracting the monthly potential evapotranspiration from the monthly precipitation.

2.3. Model Parameterization

The DDE model proposed was parameterized using maximum like-

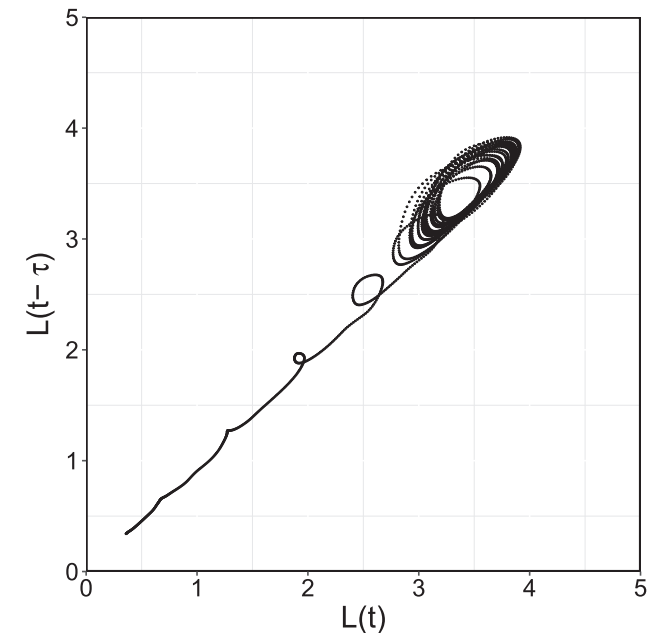


Fig. 13. Results for the maximum monthly temperature and excess water interaction model lag history trend. The x-axis shows the current state $L(t)$ and its relationship with the historical state on the y-axis defined by τ , which was found to be 0.1148. State units are LAI m^2/m^2 .

likelihood estimation. To account for differences between the individual plots, parameterization included global variables for the base model and modifier components and local variables for initial starting values at the

individual plot level. The model relied on 33 parameters: eight for the LAI equation, one for the standard deviation for the maximum likelihood procedure, and 24 local variables describing the starting points for each time series. Using the environmental modifiers to calculate a productivity adjustment factor for the base model, the relationship was

Table 3
Global parameter estimates and standard errors for the base leaf area index model (Eq. 4) fitted to 24 plots across the southeastern United States with the monthly maximum temperature ($^{\circ}\text{C}$) included as a beta function and monthly excess water (mm) included as a double logistic function. Root mean square error (RMSE) was calculated across all observations.

Parameter	Estimate	SE	Model Form	Environmental Variable
r	1.1175	0.0060	Base	N/A
τ	0.1148	0.0011		
L_{mx}	4.5535	0.0073		
A	3.1052	0.0004		
ω	6.2973	0.0061		
μ	-1.8661	0.0457		
h	0.08848	0.0024	Beta	Monthly Maximum Temperature
μ_2	-5.5757	0.0876		
T_b	1.4248	0.1920		
α	1.5219	0.0185		
T_c	37.01863	0.2095		
β	0.3799	0.0045		
α	1.5082	0.0007	Double Logistic	Monthly Excess Water
β	0.0067	0.0004		
δ	0.0072	0.0004		
T_b	-0.0005	0.00004		
T_c	320.0497	0.0359		
RMSE	0.4257			
AIC	11684.19			

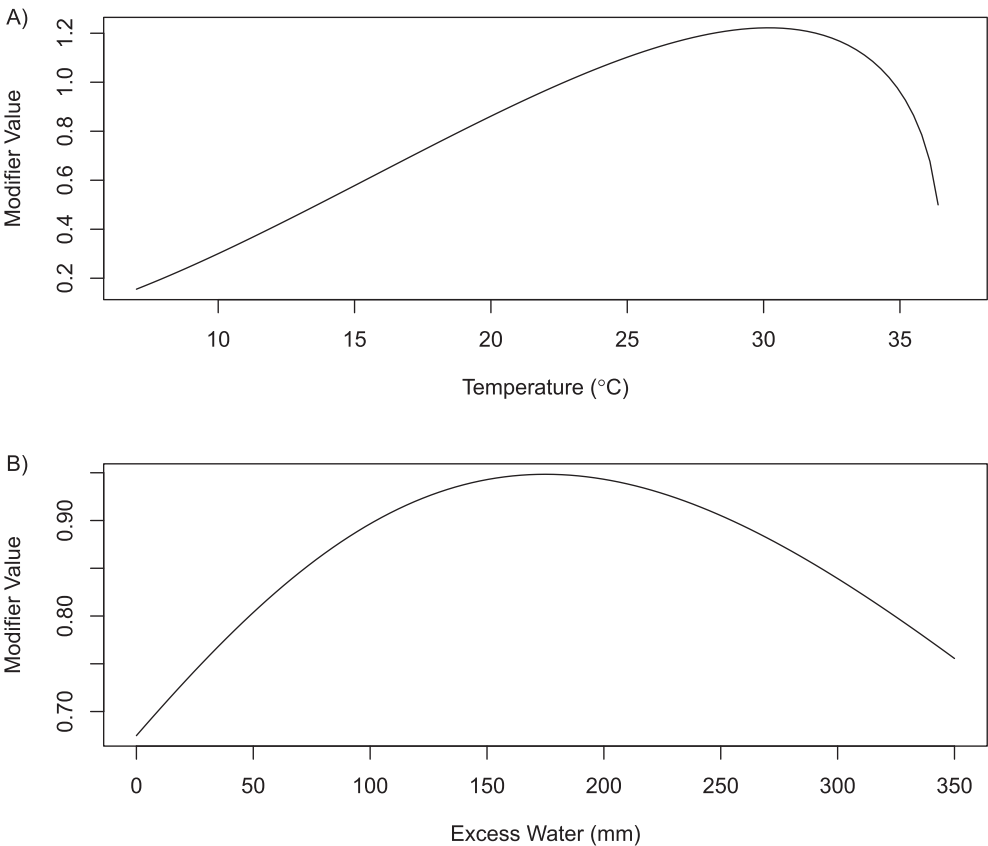


Fig. 14. Evaluation of the parameterized modifiers for A) monthly maximum temperature ($^{\circ}\text{C}$) in beta form and B) monthly excess water (mm) double logistic form across the ranges of observed values for the individual variable.

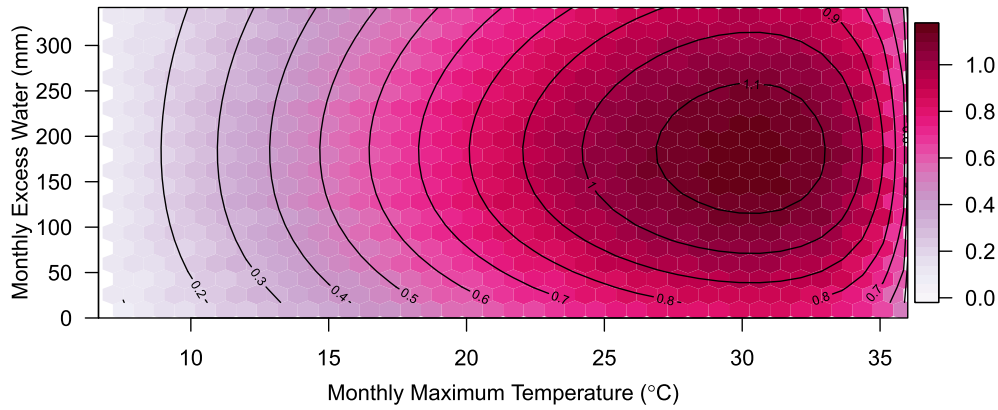


Fig. 15. Resulting interaction modifier between the monthly maximum temperature beta modifier and the monthly excess water double logistic modifier across the ranges of observed values for the 24 study plot across the southeastern United States. Contour lines show the resulting modifier value to be imposed on the LAI model.

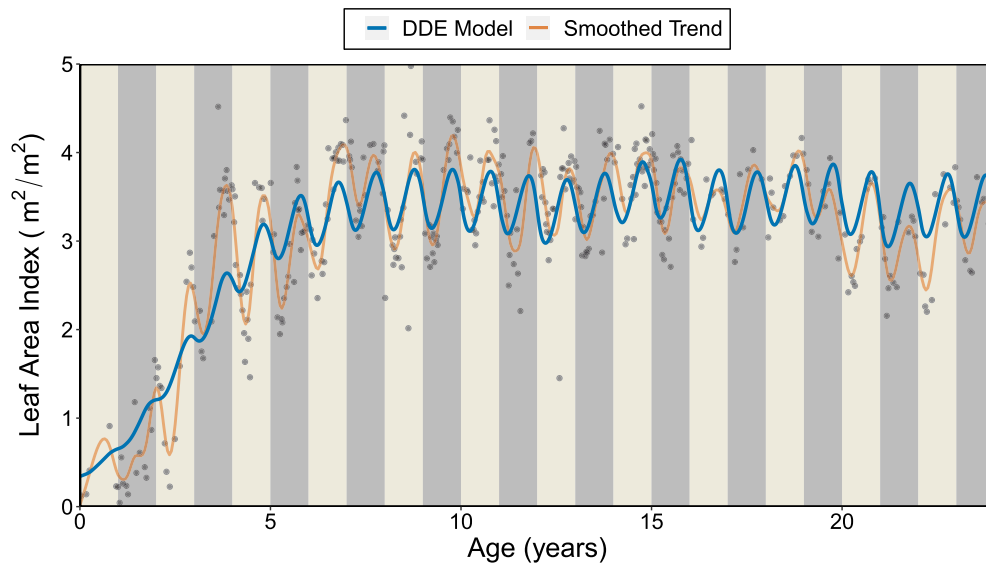


Fig. 16. Results for the model parameterized in Table 4 using monthly maximum temperature (°C) in beta form, monthly excess water in double logistic form as modifiers and a local LAI carrying capacity parameter compared to the smoothed trend and observations. Root mean square error for this plot was 0.3096.

assumed to be interactive, so the base model and environmental models were formulated in a multiplicative fashion. The *dede* function in the *deSolve* package was used to solve the DDE model and the conjugate gradient (CG) method was used as the optimization method to maximize the log likelihood of the functions as implemented in the *optimx* package (Soetaert et al., 2010; Nash and Varadhan, 2011). Starting values for the local parameters were defined by the first observations of LAI at the individual plot level. For the models using local L_{mx} values, starting values were the global L_{mx} parameterized in the model fitting procedure. Global parameters starting values were selected through a trial-and-error approach to define the model form and starting values for the environmental modifiers were selected based on the response between the environment and loblolly pine reported in the literature (Albaugh et al., 2004; Teskey et al., 1987; Nedlo et al., 2009). Addition of the environmental variables and their subsequent model form were evaluated on reductions of root mean square error (RMSE) and Akaike's Information Criterion (AIC) to account for the additional parameters for the given model. Evaluations for parameter uncertainty estimates required the fixing of local variables to allow for the final standard error calculations. To evaluate model robustness, k-fold ($k = 9$) cross validation was used. The 24 plots were randomly assigned to one of nine groups. For each of the nine groups, the plots in the group were withheld from the training data set, the model was fit on the training data set and

then evaluated on the withheld group. The process was repeated for each group.

3. Results

3.1. Base Model Parameterization

Parameterization of the base model (Eq. 4) resulted in an overall root mean square error (RMSE) for the 24 sites of 0.4427 and an AIC of 12496.7 (Table 1). Estimated standard errors for the individual parameter estimates indicate little variability with the exception of the L_{mx} parameter. At the individual plot level, RMSE ranged from 0.2594 to 0.6158 LAI m^2/m^2 . Inspection of the residuals showed little evidence of heteroscedacity (Fig. 2) and comparison of the observations to predictions showed an adequate 1:1 relationship (Fig. 3). Model predictions show a defined upper limit at approximately 3.72 m^2/m^2 , where the base model limits the overall LAI production (Fig. 3). This limitation is a result of how Eq. 4 is structured. Annual seasonality was adequately captured by the trigonometric portion of the base model, with peak LAI occurring in September/October every year (Fig. 4). The τ estimate indicated little importance of the prior state, with a value of 0.0002 (Table 1). Without a considerable lag effect, the relationship between the current and prior state maintained linearity. The L_{mx} parameter

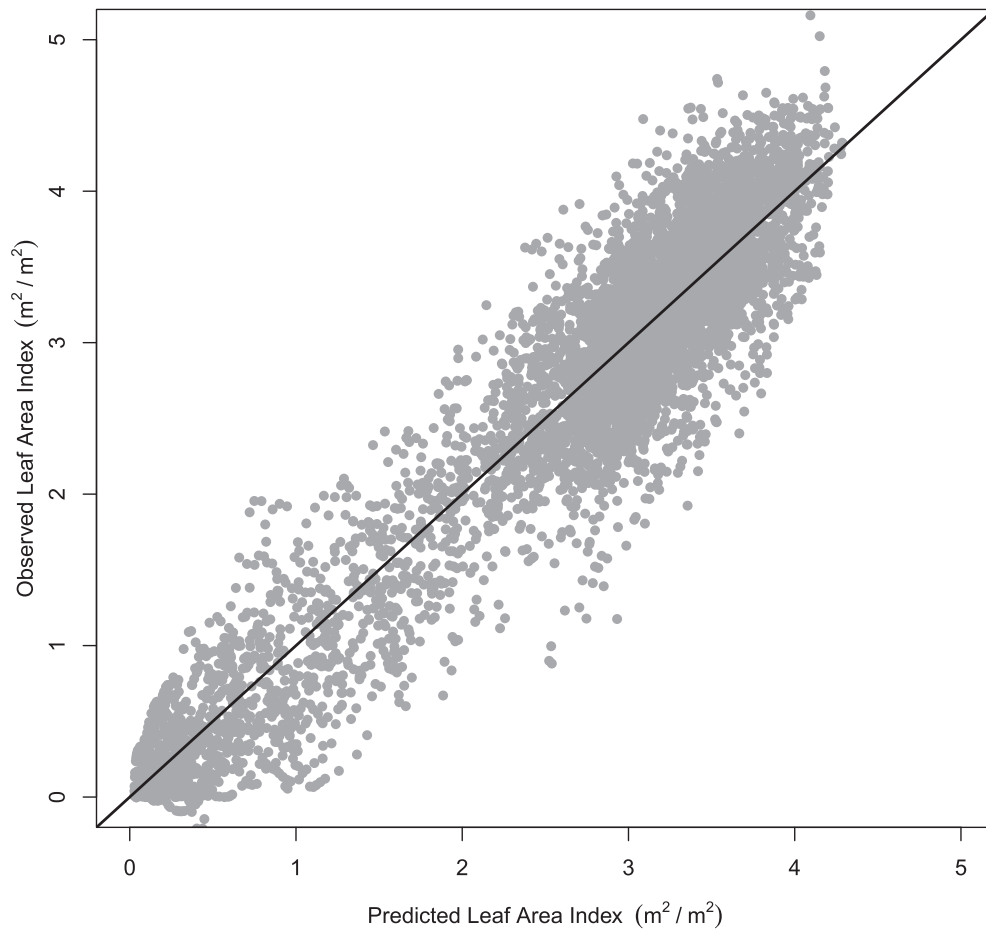


Fig. 17. Observations vs. predictions for the model parameterized in Table 4 using monthly maximum temperature (°C) in logistic form, monthly excess water (mm) in double logistic form as modifiers and a local LAI carrying capacity parameter.

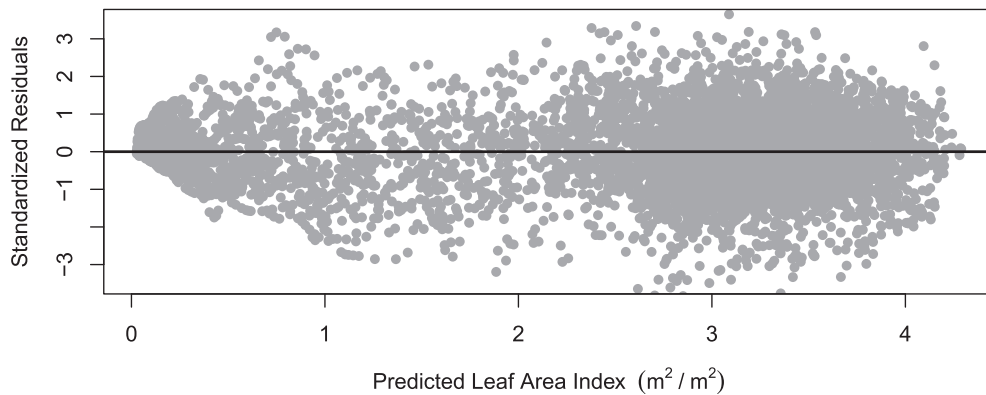


Fig. 18. Results for the model parameterized in Table 4 using monthly maximum temperature (°C) in beta form and monthly excess water in double logistic form as modifiers and a local LAI carrying capacity parameter compared to the smoothed trend and observations.

showed an overall estimated carrying capacity for LAI at $4.7760 \text{ m}^2/\text{m}^2$, subject to the model formulated constraints and imposed seasonality. Systematic patterns were observed in the residuals as LAI increased, an artefact of the model reaching a global steady state with no outside forces imposing individuality at the plot level (Fig. 2). The base level model was inadequate in capturing the seasonality and trend of LAI in the formative years of stand development, common to all observed plots (Fig. 4). While the underlying development trend was captured with the inclusion of the local initial value at the individual plot level, the base model provided a gross simplification of the system. The amplitude of

seasonality in the parameterized model showed large variations as compared to amplitude of seasonality in the observed plots and their subsequent smoothed spline time series. (Figs. 5 and 6).

3.2. Inclusion of Environmental Variables

Temperature was found to be the most influential on improving the LAI, with monthly maximum temperature having the greatest effect. The logistic, double logistic, and beta model forms proved to be the most flexible in parameterizing for inclusion of the environmental variables.

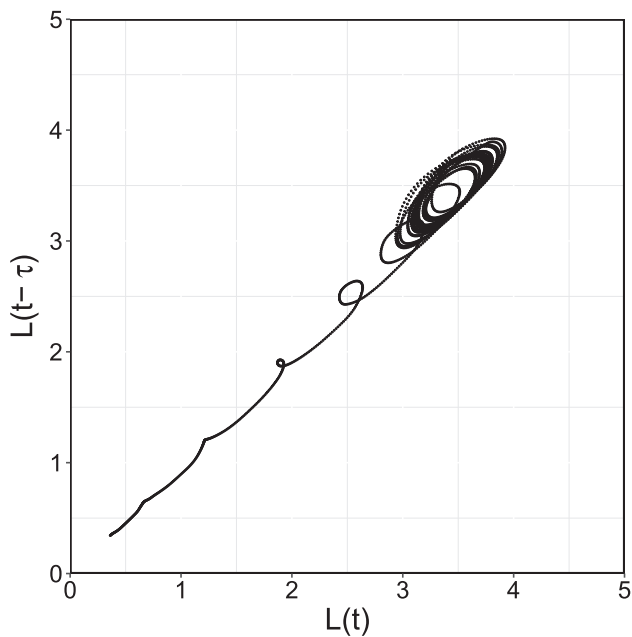


Fig. 19. Results for the maximum monthly temperature and excess water interaction model with local LAI carrying capacity parameter lag history trend. The x-axis shows the current state $L(t)$ and its relationship with the historical state on the y-axis defined by τ , which was found to be 0.1143. State units are LAI m^2/m^2 .

Maximum monthly temperature in the beta form showed the greatest increase in model performance when included as a modifier to the base LAI model. RMSE decreased to 0.4299 and AIC decreased to 11891.71. Addition of the environmental modifier increased τ to 0.1148, or approximately 41 days, indication of past state dependency and a delayed reaction in physiological response to temperature (Table 2). Base level carrying capacity (L_{mx}) decreased from 4.7760 to 4.5565 while the rate parameter (r) showed a slight increase from 1.0750 to 1.1109, a result of the modifier imposing changes to the base level productivity at the individual sites (Table 2). Across the individual plots, inclusion of the temperature modifier produced a range of 0.2616 to 0.5846 RMSEs, indicating adverse effects on some plots and benefits to others. Comparisons between the trend and the model showed an increase in the model's ability to react to environmental conditions, capturing some of the changes in the observed points and smooth trend (Fig. 7). The resulting parameterized beta monthly maximum temperature modifier showed an asymmetrical modifier across the range of observed monthly maximum temperatures, displaying a slow modifier rate increase from the lower bound ($\approx 10^\circ\text{C}$) to a peak of approximately 30°C , and a sharp decline in modifier value following the peak as temperature increased to beyond 35°C (Fig. 9). Increase of the τ parameter provided a relatively stable limit cycle relating the current and past states as LAI developed and reached its upper asymptote (Fig. 8). Cycles around a central point, ≈ 3.1 LAI m^2/m^2 showed slight temperature induced deviations but an overall stable process.

Evaluation of additional modifiers and their interactions with the beta monthly maximum temperature modifier focused primarily on water relations variables to reduce the collinearity between monthly maximum temperature and the other temperature variables under consideration. Examination of the water relations variables and their interactions with the monthly maximum temperature modifier found that monthly excess water in the double logistic model form to be the

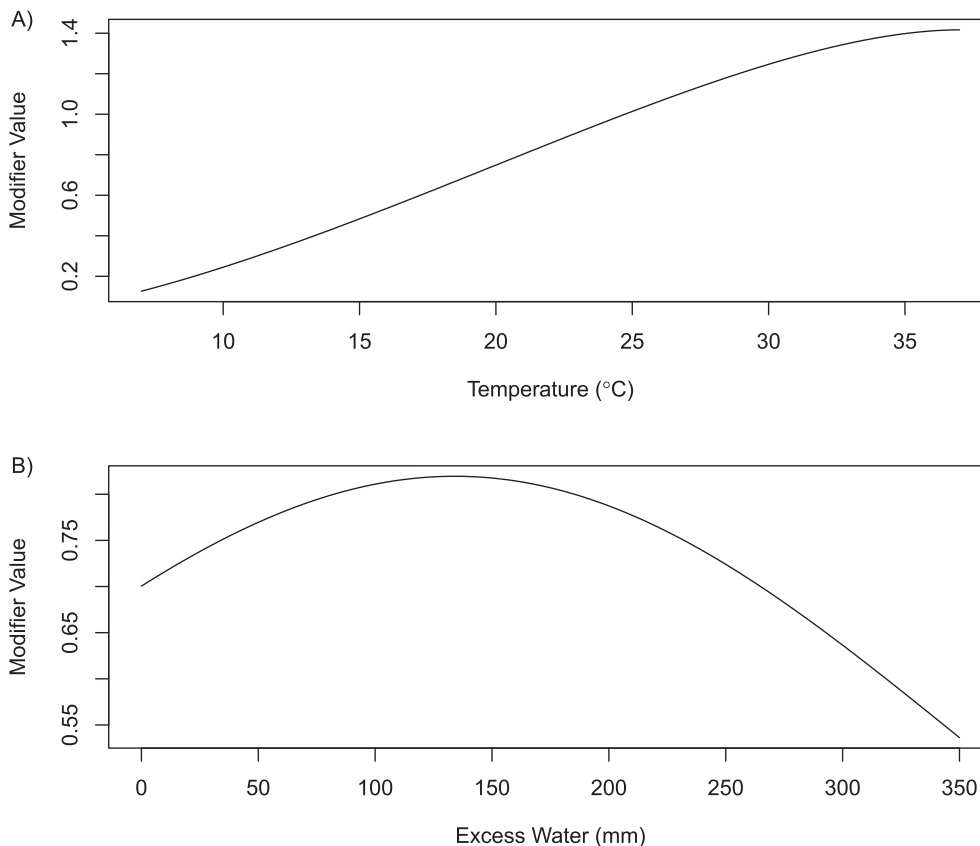


Fig. 20. Evaluation of the parameterized modifiers for A) monthly maximum temperature ($^\circ\text{C}$) in beta form and B) monthly excess water (mm) double logistic form across the ranges of observed values for the individual variable for the model fitted with a local LAI carrying capacity parameter.

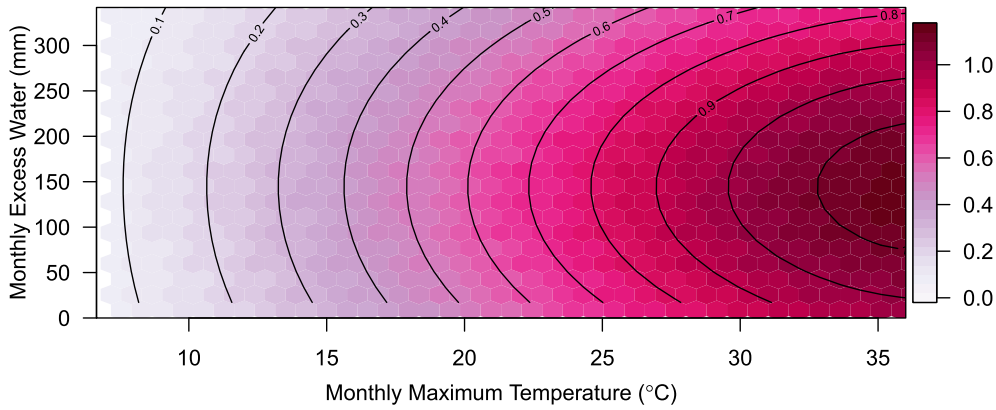


Fig. 21. Resulting interaction modifier between the monthly maximum temperature beta modifier and the monthly excess water double logistic modifier across the ranges of observed values for the 24 study plot across the southeastern United States fitted with a local LAI carrying capacity parameter. Contour lines show the resulting modifier value to be imposed on the LAI model.

Table 4

Global parameter estimates and standard errors for the leaf area index model (Eq. 4) fitted to 24 plots across the southeastern United States with the environmental variables included as a beta and double logistic function, and a local carrying capacity parameter (L_{mx}). Root mean square error (RMSE) was calculated across all observations.

Parameter	Estimate	SE	Model Form	Environmental Variable
r	1.1968	0.0181	Base	N/A
τ	0.1143	0.0080		
A	2.6254	0.0237		
ω	6.2877	0.0009		
μ	-1.7420	0.0062		
h	0.0647	0.0041		
μ_2	-6.0359	0.0324	Beta	Monthly Maximum Temperature
T_b	1.4592	0.0093		
α	1.5984	0.0081		
T_c	44.69	0.0197		
β	0.3419	0.0103		
α	1.5984	0.0081	Double Logistic	Monthly Excess Water
β	0.0063	0.0004		
δ	0.0071	0.0006		
T_b	-0.0004	0.00004		
T_c	276.3619	0.0166		
RMSE	0.3802			
AIC	9383.04			

most influential for improving the model fit. Inclusion of excess water as an additional modifier had modest improvements in model fit as compared to monthly maximum temperature's effect on the base model, with the largest decrease of RMSE at the individual plot being 0.03 units

of LAI. The updated parameter values for the base model and beta monthly maximum temperature modifier showed slight changes as compared to the temperature - modifier only model, and a slight overall decrease in RMSE to 0.4257 and AIC to 11684.19. The newly parameterized monthly maximum temperature modifier displayed a similar trend as the previous model (Fig. 14, Table 3). The excess water modifier, formulated as a double logistic model, displayed a symmetrical shape centered about approximately 175 mm of excess water (Fig. 14). As excess water increased from 0 mm to the peak, the modifier increased from a baseline of approximately 0.70 to approximately 0.9. Following the peak, the modifier value began to decline to approximately 0.75 as the excess water value reached the end of its natural range of 350 mm observed in the data. When the two environmental modifiers'

Table 5

Root mean square error (RMSE) results from the k-fold ($k = 9$) cross validations performed on the four models. Base indicates base model, Env1 indicates the inclusion of monthly maximum temperature as a beta function, Env2 indicates monthly excess water as a double logistic function, and Local L_{mx} indicates the use of a local leaf area index carrying capacity parameter.

Model	Training			Validation		
	Min	Max	Avg	Min	Max	Avg
Base	0.4270	0.4544	0.4422	0.3161	0.5508	0.4367
Base + Env1	0.4056	0.4489	0.4285	0.2885	0.5210	0.4283
Base + Env1 + Env2	0.4082	0.4419	0.4265	0.3209	0.5801	0.4319
Base + Env1 + Env2 + Local L_{mx}	0.3658	0.3886	0.3796	0.3237	0.4709	0.3819

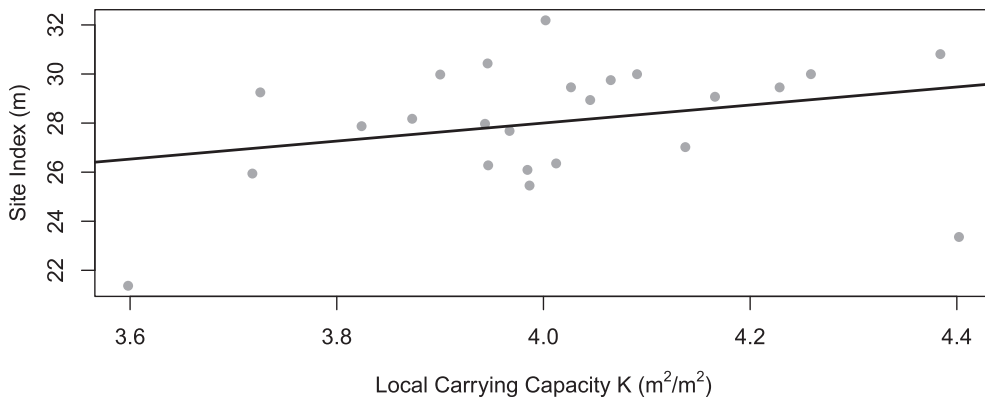


Fig. 22. Comparison between the fitted local L_{mx} LAI carrying capacity parameter and estimated site index (base age = 25) for the 24 sites.

interactions were calculated, a defined area of increased productivity above the baseline model (modifier > 1) was observed at the peaks of temperature and excess water (Fig. 15). A large area within the interaction plot indicates that a wide range of conditions can satisfy the conditions necessary for peak LAI growth. (see Figs. 16–21).

3.3. Addition of Local Carrying Capacity

To test the effect of a local carrying capacity parameter compared with a global parameter, the final model was refitted with the addition of a local L_{mx} parameter for each individual plot and dropping the global L_{mx} , increasing the number of parameters by 23. RMSE across all observations decreased to 0.3802 accompanied by a decrease in AIC to 9383.04 (Table 4. Values for L_{mx} ranged from 3.59 to 4.40, which had a weak positive relationship with estimated site index (Fig. 22). As compared to the base model, the largest decrease in RMSE due to the local L_{mx} parameter was a 0.29 reduction.

Model validation through k-fold ($k = 9$) cross validation showed overall support for the proposed models (Table 5). Improvement was made with the inclusion of environmental variables as compared to the base model, while the addition of a second environmental variable showed minimal declines in RMSE in training and validation data sets (Table 5). Inclusion of the local parameter L_{mx} showed a considerable decline in RMSE for both the training and validation data sets, indicating the importance of local features on LAI growth and development and its overall interaction with environmental variables.

4. Discussion

Dependency of the future state based on the current and prior states, denoted by τ , showed varying conditions based on whether additional information, such as temperature, was provided in terms of a productivity modifier. In the base model, τ proved to be quite small, an indication that, as modeled, LAI followed the development and seasonal trend defined by the periodic and rate parameters and didn't require further information from prior states. It has been shown that at sufficiently small τ , the Hutchinson model is equivalent to the traditional logistic, providing a simplified model (Gopalsamy, 1992). As additional variability in the modeled system was introduced by the environmental modifiers, a dependence on those prior states proved influential, indicating that the state at time $t - \tau$ is necessary in determining the future state. These larger lags produce a feedback loop, which can be visualized in Figs. 8 and 13, where oscillations about the equilibrium point of the solution for the individual parameterized equations occurs as t increases and the population (LAI) reaches steady state (Gopalsamy, 1992). Fluctuations in the oscillations about the equilibrium point indicate the influence of the environment, but overall LAI shows to be a relatively stable variable, or one that is able to return to its equilibrium (May, 1973).

Differences in the observed equilibrium point in the two models incorporating environmental effects and their individual parameterized L_{mx} values shows a defined difference, with the equilibrium point far below the L_{mx} . This difference is likely due to the fluctuations in L_{mx} , which is representative of the carrying capacity but now defined as the vertical shift in our periodic coefficient, a representation of the changing resource availability and additionally influenced by the environmental variables, which has been reported to be the case in other population studies (May, 1973; Roff, 1974). Stability and persistence of a given population has been shown to have direct correlations with the heterogeneity of the population's environment, with the probability of persistence decreasing with increased environmental variability (Levins, 1969; Roff, 1974).

While the base model overall has adequate fit and conceptually represents LAI growth, the steady state reached does not provide an accurate understanding of the observed LAI dynamics, as once net growth for a period is zero, we see no changes to the dynamics, which is

unlikely in any ecosystem. The mechanisms proposed to model LAI development were not able to fully capture the observed dynamics, especially in the early stages prior to reaching steady state (Figs. 4, 7, and 10). Large changes between years in the seasonality, peak, and minima observed were oversimplified by the proposed model form, with poor representation of those early stand dynamics. From the remote sensing and LAI estimation standpoint, this portion of the individual time series proved difficult to provide a smooth seasonal trend due to a large number of erratic and outlying estimates from the Landsat 5 and 7 ETM + imagery. Potential sources of this variability may be from pixel level saturation of neighboring plots, large amounts of competing vegetation present in the stand prior to treatment, among others. (Figs. 11 and 12).

Monthly maximum temperature provided the greatest increase in model performance for capturing the dynamics of loblolly pine LAI. Similar to the results presented in (Savoy and Mackay, 2015), many of the sites evaluated in this study were highly influenced by the temperature modifier. Increased temperatures at the cellular level have been reported to provide increases in photosynthesis and respiration, leading to greater increase of carbon assimilation rates (Way and Oren, 2010). More specifically, Way and Oren (2010) found that evergreens increased leaf mass, among other allometric changes, when temperatures were increased. This change may be driven by greater leaf elongation rates from increases in division and expansion at the cellular level (Ryan, 2010).

DDEs are a common way of modeling biological systems that tend to rely on past states due to delays in development, such as sexual maturity, energy fluxes, overlapping populations, or predator/prey dynamics (Hutchinson, 1948; Wright, 1955; Nisbet and Gurney, 1976; Gopalsamy et al., 1990; Gopalsamy, 1992; Gallegos et al., 2008; Ghil et al., 2008; Keane et al., 2017). The common theme for use of DDEs is the understanding that feedback mechanisms that occur in nature typically come with some delay. In our case of modeling loblolly pine LAI, DDEs provide the ability to model the effect of prior and current leaf area states on future states, an important feature since loblolly pine canopies feature delays in physiological and phenological processes. Furthermore, historical trends provide influence on current canopy dynamics due to foliage in loblolly pines typically last for two years, providing up to two concurrent age classes of needles occupying the canopy at any given time, and a cause of great variability observed in canopies (Dougherty et al., 1995; Sampson et al., 2003). An effective DDE provides a glimpse into the dynamics of a given population, which in this case is leaf area, and can provide a cause and effect analysis into the factors determining growth (Kuang, 1993).

Large decreases observed in the time series data at individual plots may have been caused by interaction effects of environmental stress with disease or pests, clearly not captured in the models proposed here. While these biotic effects can cause large variations in observed leaf area, further modeling developments can be used to incorporate the probability of these interactions affecting the system given environmental inputs and the magnitude of their potential effects. Providing insight on the conditions that cause fluctuations of LAI outside of the base model, shown here with maximum temperature and excess water, allows for a more systematic understanding of forest productivity and provide tools for management planning to account for potential disturbances to the population (Gopalsamy, 1992).

Further analysis into periodic coefficients may provide additional insight into the seasonality of growth, the effects of the environment on the fluctuations of growth and its effects on individual model parameters (Gopalsamy et al., 1990; Lisena, 2007). Additionally, periodic coefficients may provide the necessary switching of the modifier to correctly adjust the growth given the forced seasonality of the model, i. e., promote growth when conditions are adequate and restrict declines in growth when the seasonality begins its annual decline. Potential improvements in model and computation efficiency may be obtained from implementing neural or universal ordinary differential equations

to handle the various data on different time steps to provide a better adapting system (Rackauckas et al., 2020). Examining the lag component as a neutral DDE, where τ is used to define historical derivatives as opposed to past states may increase the ability to adequately capture the changes imposed by environmental modifiers. Following the methodology used by Powers et al. (2003), we incorporated our environmental variable modifier on the entire state rather than individual parameters. While future work will investigate the environmental influences individually on the parameters, earlier work has shown that in the logistic model form, the current state will follow a weighted harmonic mean of L_{mx} (Levins, 1969). Further inquiries into the effect of additional delays ($n \geq 2$) and combinations of positive and negative feedback may provide a more thorough investigation into environmental induced dynamics of the LAI system on an annual and lifespan basis (Keane et al., 2017).

A sensitivity analysis into the size of time step selected in the splined LAI and environmental variables used for the modeling purposes should be undertaken to verify that the underlying system being modeled isn't affected by the timing and amount of observations (Powers et al., 2003). Splining the data and providing a discrete time step between interpolated observations improved the model fitting procedure by ensuring adequate observations across the time interval. LAI observations proved to be quite noisy and provide a suitable medium for future improvements by incorporating stochastic methods to handle the erratic time series observed. Additionally, using annual peaks and minima may provide an alternative to capture the true amplitude of the seasonality component.

Interpretability of the formulated model allows for our increased understanding of the dynamics that govern forest productivity and how they interact with resource availability, which is observed in annual seasonal cycles and interactions with the local environment. Here we defined the carrying capacity of our system as a periodic coefficient to represent the changes in available resources throughout the year. When imposed, environmental modifiers retard annual growth of the system and we see an overall decline in the carrying capacity, which may affect other physiological changes associated with forest growth. When defining the carrying capacity of a forested stand, using shorter-term phenomena that pair resource availability and consumption, such as leaf area index, as opposed to cumulative basal area yield or stand density index that is typically reported, may provide a better biological representation of a dynamic system. Further investigations into the regional effects of different environmental variables may provide more insight into the factors limiting growth across the loblolly pine spatial extent. Additionally, understanding the sensitivity of loblolly pine vegetation to extreme temporal variation in biogeochemical processes (hot moments) may improve our understanding of LAI dynamics (McClain et al., 2003).

5. Conclusions

Overall, it was shown that a mechanistic derived model can describe aspects of the growth and development of LAI in loblolly pine plantations and provide additional insight into the seasonal and environmental dynamics that affect the current state. We were able to provide improvements in a base loblolly pine LAI model by incorporating environmental variables for 24 sites across a wide geographic range in the southeastern United States. Monthly maximum temperature and monthly excess water were shown to be influential in the development and long-term trends of loblolly pine LAI in the southeastern United States.

By using the environmental modifiers to adjust the system, we are accounting for the changes in resource availability due to the stochastic environment, resulting in changes to the carrying capacity. As resources and conditions becoming limiting to the biological processes, we are able to model the effects on how much leaf area a stand can support at any given time. Interactions between environmental modifiers indicate that peak LAI growth in loblolly pine plantations can occur across a

range of conditions across the southeastern United States. The results demonstrate that for our available data, incorporating a lag effect was influential in modeling LAI along with environmental modifiers. Periodicity was imposed by the inclusion of a periodic coefficient for the L_{mx} parameter, resulting in forced oscillations based on seasonally limited resources, affecting overall carrying capacity and driving the modeled patterns. Future work will aim to improve the understanding of local conditions on the LAI carrying capacity and to provide estimates of L_{mx} when data is not available.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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