



Assessing potential climate change effects on loblolly pine growth: A probabilistic regional modeling approach

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Abstract

Most models of the potential effects of climate change on forest growth have produced deterministic predictions. However, there are large uncertainties in data on regional forest condition, estimates of future climate, and quantitative relationships between environmental conditions and forest growth rate. We constructed a new model to analyze these uncertainties along with available experimental results to make probabilistic estimates of climate change effects on the growth of loblolly pine (*Pinus taeda* L.) throughout its range in the USA. Complete regional data sets were created by means of spatial interpolation, and uncertainties in these data were estimated. A geographic information system (GIS) was created to integrate current and predicted climate data with regional data including forest distribution, growth rate, and stand characteristics derived from USDA Forest Service data. A probabilistic climate change scenario was derived from the results of four different general circulation models (GCM). Probabilistic estimates of forest growth were produced by linking the GIS to a Latin Hypercube carbon (C) budget model of forest growth. The model estimated a greater than 50% chance of a decrease in loblolly pine growth throughout most of its range. The model also estimated a 10% chance that the total regional basal area growth will decrease by more than $24 \times 10^6 \text{ m}^2 \text{ yr}^{-1}$ (a 92% decrease), and a 10% chance that basal area growth will increase by more than $62 \times 10^6 \text{ m}^2 \text{ yr}^{-1}$ (a 142% increase above current rates). The most influential factor at all locations was the relative change in C assimilation. Of climatic factors, CO₂ concentration was found to be the most influential factor at all locations. Substantial regional variation in estimated growth was observed, and probably was due primarily to variation in historical growth rates and to the importance of historical growth in the model structure. © 1998 Elsevier Science B.V.

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1. Introduction

Pine forests of the southern USA are a crucial forest resource, producing more than half of the softwood forest products in the country (Powell et

al., 1993). Over the last two decades, increasing concern about the effects of anthropogenic stresses on forest ecosystems has resulted in the formation of coordinated research programs focused on acidic precipitation and ozone (Fox, 1996). Most recently, the potential effects of climate change on southern forests have been addressed by the Southern Global Change Program (SGCP) of the USDA Forest Ser-

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vice, a multi-year, multi-million dollar research program (Mickler and Fox, in press). In order to integrate the results of the diverse research conducted within this program, and to identify future research needs, an ecological regional assessment model is required.

Several types of models have been used previously to assess the potential effects of climate change on vegetation in the southern USA. At the global and continental scale, models of the biogeography and biogeochemistry of ecosystems have been used, for example in the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP, VEMAP Members, 1995). Biogeography models are best for examining broad-scale changes in vegetation type—for example, temperate deciduous forests and C₄ grasslands. Biogeochemistry models are designed to predict changes in nutrient cycling and primary productivity. Individual-based forest growth (gap) models such as FORET, FORENA and ZELIG have been used to predict changes in forest type throughout the eastern USA; the use of this type of model to assess climate change effects has been reviewed by Shugart et al. (1992). In general, this type of model is most useful for predicting broad-scale patterns in species associations over many centuries. To assess the risk posed by climate change within the next 100 yr for important species such as loblolly pine, there is a need to model not only such broad-scale patterns but also the direct effects of climatic change on tree growth rates.

A major limitation of existing ecological models is that they typically produce deterministic results, without any estimate of uncertainty. For issues such as climate change effects on forest growth, there are clearly large uncertainties in both the magnitude of future climate change, and the magnitude of various responses to a changed climate (Dixon and Wisniewski, 1995). Monte Carlo techniques have been used successfully to address uncertainties in the input values and parameters of forest growth models (e.g., van der Voet and Mohren, 1994). Regional ecological risk assessments must account for uncertainty in spatial data as well as uncertainty in the response of ecosystem components, such as the trees in a forest, to stresses. Several investigators, notably at the US Department of Energy's Oak Ridge Laboratory, have demonstrated over the last two decades that it is possible to use Monte Carlo techniques to

address these uncertainties quantitatively (e.g., Graham et al., 1991; Dale et al., 1988).

For regional assessments, there are often insufficient data to **parameterize** existing models. Conversely, there may be experimental data germane to the question that are not being used by an existing model. We developed a new modeling approach to analyze the potential effects of climate change on the growth of loblolly pine using available research and regional monitoring data. Our modeling system produces probabilistic estimates in order to account for important sources of uncertainty in the model. This task is accomplished by defining inputs to the model and functional relationships within the model as frequency distributions, and then using Monte Carlo-type techniques to sample from these distributions. The result is a frequency distribution of possible estimates. We refer to the model output as 'estimates' rather than 'predictions' because of the many sources of uncertainty in predicting climate change effects. This terminology is similar to that used by climate modelers, who use the term 'projection' for the output of general circulation models (GCMs).

2. Methods

Our modeling system is comprised of a geographic information system (GIS) and a probabilistic forest growth model. The GIS serves to integrate the regional data, facilitate the development of probabilistic inputs for the forest growth model, and display the probabilistic results of the forest growth model. The study area was the 12-state region of the USA where nearly all loblolly pine (*Pinus taeda* L.) occurs. This area includes Texas, Oklahoma, Louisiana, Arkansas, Mississippi, Alabama, Tennessee, Florida, Georgia, South Carolina, North Carolina, and Virginia. There is a small amount of loblolly pine in New Jersey and Maryland, but these regions were not included in our analysis. To produce regional probabilistic estimates of the effect of climate change, the forest growth model was run using Monte Carlo-type techniques (for a review of these techniques, see Morgan and Henrion (1990)). A total of 150 simulations were run for each of 1169 30 x 30 km grid cells in the 12-state region. The

major steps required to construct the GIS and the forest growth model are described below.

2.1. Regional data selection

2.1.1. Loblolly pine growth

Data on the growth rate of loblolly pine were obtained from the Forest Inventory and Analysis (FIA) survey (some details of these surveys can be found in Hansen et al. (1992)). Data were selected from survey plots consisting primarily of loblolly pine in stands that were not logged or otherwise substantially disturbed between consecutive surveys (Dr. Steven McNulty, personal communication). The most recent available survey data were selected for all states, growth rates were based on the last complete measurement interval available for a state (approximately 10 yr-exact dates differ among states). This selection regime resulted in 615 plots for the 12-state region. Growth rates, stand density and basal area were calculated.

2.1.2. Loblolly pine distribution

Data on the distribution of forest types were obtained from a digital version of a map that classifies forest types on a 1-km grid cell basis. This map was produced in support of the 1993 Resources Planning Act (RPA) update (Powell et al., 1993). The map is derived from Advanced Very High Resolution Radiometer data, FIA surveys, Thematic Mapper data, and other sources, using methods described by Zhu (1994) and Zhu and Evans (1992). For our investigation, we examined only grid cells classified as Loblolly-Shortleaf Pine.

2.1.3. Ozone exposure

Data on tropospheric ozone concentrations for May through September, 1988–1991, were obtained from the Aerometric Information and Retrieval System and represent nearly continuous measurements of known accuracy. Ozone exposure was expressed as 'SUM06', the sum of all hourly average concentrations greater than or equal to $0.06 \mu\text{l l}^{-1}$. Values were interpolated for the few days on which data were not collected (Herstrom, A., personal communication). Monitoring sites within the 12-state region and within neighboring states were used in order to avoid artifactual edge effects during spatial interpolation.

2.1.4. Climate scenarios

In order to meet the needs of forest growth models, regional scenarios of climate change should meet several criteria. Estimates of precipitation, temperature, and other climatic variables should be produced for all locations in the region. These estimates should account for topographical effects, and physical consistency should be maintained among climatic variables. All data should be interpolated to a single grid cell size, including climate change projections from GCMs that operate at different spatial resolutions. The SGCP (among others) supported an effort to produce such a data set in the VEMAP. The methods used to develop this data set have been described previously (Kittel et al., 1995). The VEMAP database contains single-year steady-state climate scenarios based on the results of four GCMs. These four GCMs are: United Kingdom Meteorological Office (UKMO, Wilson and Mitchell, 1987), NASA Goddard Institute for Space Science (GISS, Hansen et al., 1984), Oregon State University (OSU, Schlesinger and Zhao, 1989), and Geophysical Dynamics Laboratory R30 [GFDL, Manabe and Wetherald in Mitchell et al. (1990); Wetherald and Manabe in Cubasch and Cess (1990)]. The rationale for the use of these GCMs for this study region is discussed by Cooter et al. (1993). In brief, they were well documented model runs available at the time of database construction. We selected this data set for use in our modeling effort because it met the above criteria.

Because GCMs are designed to study global rather than regional processes, there is greater uncertainty in their projections for regions such as the southern USA (Sulzman et al., 1995; Trenberth, 1997). Our use of a stochastic scenario helps to account for some of this uncertainty by using the projections from several GCMs simultaneously. According to the 1995 Intergovernmental Panel on Climate Change (Houghton et al., 1996), recent projections of global temperature increase with a doubling of CO₂ are approximately one-third lower than the best estimate in 1990. This is due in part to improvements in modeling the radiative effects of clouds and the effects of sulfate aerosols (Houghton et al., 1996). Because the GCM model runs on which our scenario is based were published in or before 1990, the projected temperature increase may be somewhat

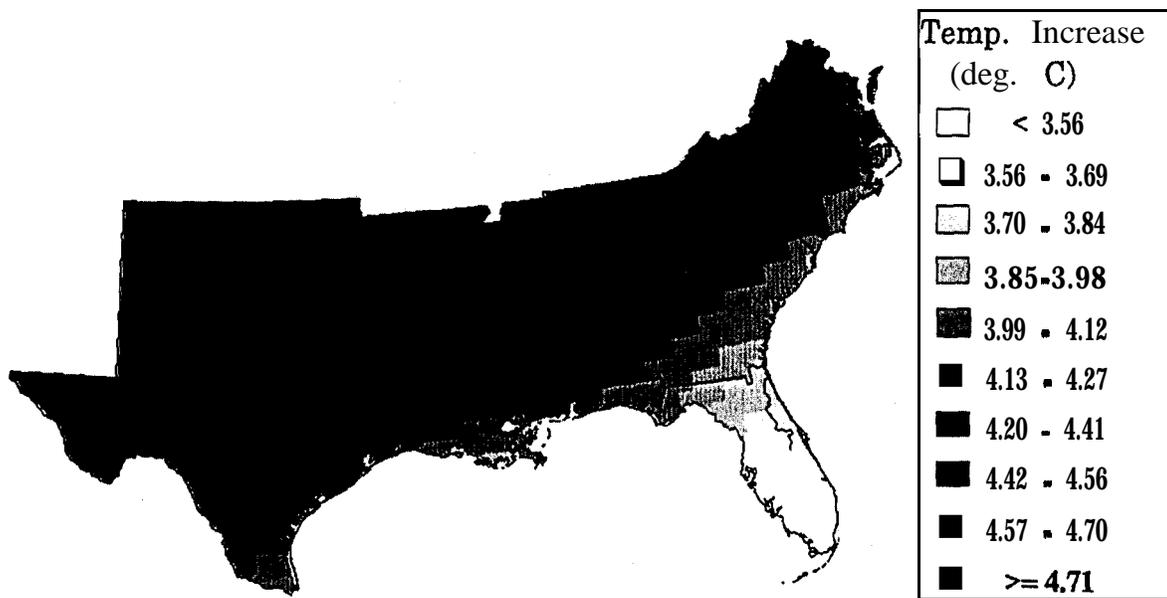


Fig. 1. Estimated modal increase in mean annual temperature with doubled CO_2 . For future temperature, we used a probabilistic scenario defined as a frequency distribution for each analysis cell. The modal value for each cell is shown. The regional average is 4.3°C and the range is 3.0 to 6.3°C (see text for details).

overestimated. However, the consistent regional scenarios developed by the VEMAP were the best ones for our purpose for the reasons mentioned above.

For our investigation, we constructed a probabilistic future climate scenario based on four VEMAP scenarios derived from the four GCM model runs cited above. For each location in the study region, the lowest, highest and middle (average of the remaining two values) ranked values were used to create a triangular frequency distribution describing estimated climate. Monthly data on precipitation, solar radiation, and maximum and minimum air temperature were obtained from the VEMAP database for the base case (no climate change) and for the climate change scenario. All VEMAP data are calculated for a grid cell size of 0.5×0.5 degrees latitude and longitude. The mode of the temperature increase for the climate change scenario is shown in Fig. 1.

2.2. Creation of geographic information system

All data were imported into a single database using Arc/Info software (ESRI, Redlands, CA). Data were converted to a common projection (Lambert

equal azimuthal). This projection was selected to minimize the generation of errors in the area of data features. The forest distribution data were already in this projection, and other data were either in a geographic (latitude and longitude) projection or were point locations, so there was little distortion when converting them to another projection. For each type of data, a grid with a cell size of 1 km was created. Additional grids were created to represent the uncertainty of each of several data types, as described below. To supply data to the forest growth model, data were aggregated into 30-km analysis cells. However, data are stored at the 1 km resolution in order that smaller analysis cells could be used in the future if they are required.

2.3. Interpolation and uncertainty estimation

Our modeling strategy required that complete regional data sets with estimated uncertainties be generated for each type of data. These data sets were obtained by means of spatial interpolation, when required. Methods of interpolation and estimation of uncertainty in data are described below for each data type.

2.3.1. Loblolly pine growth

Growth at locations between FIA plots was assumed to equal that of the nearest plot. No attempt was made to use distance-weighted averages or other spatial methods because examination of the data did not suggest strong spatial auto-correlation in the growth rate of loblolly pine among this subset of FIA plots. Uncertainty was assumed to increase as a linear function of distance from the nearest FIA plot. We believe that this is a reasonable model, since it is likely that spatial auto-correlation occurs at a scale too small to be detected by the course scale of the selected FIA plots.

2.3.2. Loblolly pine distribution

Since the forest distribution data provided complete coverage of the region, no interpolation was required. While some classification error may be expected to occur with such a data set, we had no estimate of such error and did not include it in this analysis.

2.3.3. Ozone exposure

Ozone values were interpolated as the weighted average of values from all monitoring stations within 300 km of each analysis cell. Weighting decreased with the square of the distance from the station. For the model presented here, interpolated ozone SUM06 values for each year from 1988–1991 were averaged to obtain a value for current exposure. Ozone concentrations are likely to increase with climatic change (Ashmore and Bell, 1991). Because data on the magnitude of this increase were not available, we defined it to be uniformly distributed (to avoid more stringent distributional assumptions) with endpoints of a 20% to a 60% increase above current concentrations.

2.3.4. Climate scenarios

No spatial interpolation was required since these data provided complete coverage. Uncertainties in weather data exist due to interpolation and averaging error, yearly variation, and, particularly, uncertainties in predicting climate change. We incorporated uncertainty in climate change estimates by using a combination of output from four different GCM model runs as discussed above. The VEMAP scenarios are based on a doubling of tropospheric CO₂ concentra-

tion. We used a value of 360 $\mu\text{l l}^{-1}$ CO₂ for the base case (current) condition. In order to include some uncertainty in the estimate of future CO₂ concentration, we defined it to be uniformly distributed between 648 and 792 $\mu\text{l l}^{-1}$ (i.e., a doubling plus or minus 10%).

2.4. Forest growth simulation

We created a simple annual Latin Hypercube carbon (C) budget model in order to estimate changes in forest growth rate. Because many investigations of the effects of climate change are conducted at a single tree scale (or smaller), we judged that an individual-tree C budget would be the most tractable means for integrating a variety of experimental results. Each result could be interpreted as influencing the rate of some portion of annual C gain or loss. For this reason, stand basal area growth data from the FIA were transformed into values of C gain, loss, and allocation for individual trees, as described be-

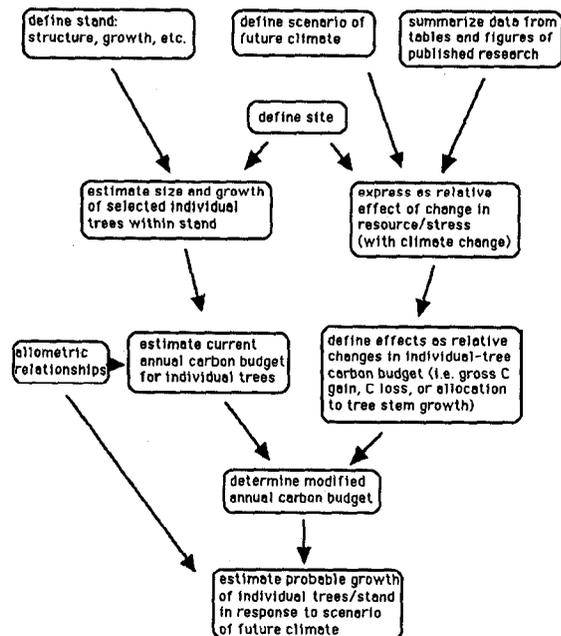


Fig. 2. Flow chart of probabilistic forest growth model. Probabilistic estimates of current carbon gain, loss, and allocation for individual loblolly pine trees are modified by functions describing the effects of changes in CO₂, air temperature, and other factors to produce probabilistic estimates of growth under a climate change scenario. The inputs to the model are maintained in a geographical information system, and the results are sent to this system to generate a regional analysis.

low. Then, experimental data were transformed to stochastic functional relationships describing the effect of climatic factors such as air temperature and CO₂ concentrations on C gain, loss and allocation for individual trees.

We implicitly incorporated the effects of competition and mortality in individual tree performance by using the historical rate of growth. Hence, our approach assumes that the influence of these factors on growth will not change with alterations in climate. This approach is reasonable because we are integrating experimental data on the physiological responses of trees to climate change to produce an estimate of the change in the instantaneous growth rate of monospecific stands, or stands with small amounts of other conifers present. The overall organization of the forest growth model is shown in Fig. 2.

2.4. 1. Historical *growth*

We assumed that without climate change, future growth would be the same as has been measured recently. For each of the selected stands in the region, the following FIA stand-level data were used: basal area, basal area growth rate, number of stems in each of two size classes (less than or equal to 12.7 cm in diameter at breast height (DBH), or greater than 12.7 cm DBH), height of the largest size class, and stand quadratic mean stem diameter. Because trees of different sizes allocate carbon differently, we modeled five size classes for each stand. For modeling purposes, an individual tree (henceforth 'representative tree') was used to represent each size class. The historical growth rates of each size class within each stand were estimated from total stand growth based on an estimated distribution of stem basal areas. These distributions were skewed; they had ends based on likely size extremes (from stand height); and had a central values based on average stem area (from the quadratic mean diameter). Based on preliminary results, extremely skewed distributions, such as the log-normal, can introduce bias in the model. Therefore, for each stand we selected a normal distribution with a standard deviation set as one-quarter of the size range. Extreme values were truncated from this distribution so that it would match the mean stem diameter specified by the FIA data. We assumed that the diameter growth rate (not basal area growth rate) was constant among size

classes, and selected a single diameter growth rate value such that the sum of individual tree basal area growth rates within a stand matched that of the FIA data. The simulated responses for each representative tree were then extrapolated to all trees of the stand in the corresponding size class.

2.4.2. C budget

We assumed that climate change effects could be expressed as alterations in the annual flux of C into and out of individual trees. The annual individual tree C budgets for the base climate scenario were based on the relationship: (annual growth) = (gross assimilation) - (leaf and root turnover) - (maintenance + growth respiration). Total above-ground growth (bole, leaves, and branches) was estimated from the basal area growth data by means of published allometric equations (Shelton et al., 1984; Van Lear et al., 1984; Gower et al., 1994). Root biomass was defined as a fixed value of 20% of shoot biomass. Fine roots (2 mm or less) were estimated to be a fixed value of 15% of root biomass. Fine roots were assumed to turn over twice yearly (Schoettle and Fahey, 1994) and leaves were assumed to be held for 2 yr. To account for the loss of organs due to wind, diseases, etc., we increased the estimated net carbon gain required to produce coarse roots, branches, and leaves by 5%. Half of the biomass was assumed to be C. Hence the net annual growth on a C basis could be calculated for fine roots, coarse roots, bole, branches, and leaves for representative trees. To estimate gross C allocation to growing structures, growth respiration was assumed to be a stochastic function of biomass. Specifically, growth respiration was defined as a uniform distribution between one-quarter to one-third of the carbon content of biomass (Waring and Schlesinger, 1985; Ryan et al., 1994, 1995).

Gross annual assimilation was defined as the sum of net daytime C uptake at the leaf level. Annual maintenance respiration was defined as a function of temperature, biomass, and plant part, using published temperature response functions and respiration rates (Ryan et al., 1994). Maintenance respiration was assumed to be 33 to 67% of gross annual assimilation (Ryan et al., 1994, 1995). Because larger trees have proportionately more tissue to maintain, they were assumed to have proportionately greater main-

tenance respiration (Ryan et al., 1994). If the bole represented more than 80% of aboveground biomass, maintenance respiration was defined as a uniform distribution between 45 and 67% of gross annual assimilation. If the bole represented less than 80% of aboveground biomass, these values were 33 and 55%. The total annual C budget was calculated as the sum of each of these pools of expended carbon. To estimate the effects of climatic variables, the C budget was then modified by project summary functions as described in Section 2.4.3.

2.4.3. Project summary functions

The primary experimental data were from a number of investigations sponsored by the SGCP. A few data from the literature were selected to fill gaps in the results from the SGCP, primarily with respect to allometry and respiration rates. Experimental measurements of responses to climatic factors ranged from CO₂ uptake of leaves to bole growth in mature stands. Each selected experimental result was reduced to a function describing the effect of one or more climatic factors on annual C gain, loss, or allocation to bole growth (Table 1). These effects were defined as probability density functions (PDFs). Data from eight SGCP experimental research projects were included in this model, but some projects examined more than one climatic factor (Table 1). Literature data on base respiration rates and Q_{10} values for various parts of the tree were used to create a summary function describing the effect of temperature on maintenance respiration (Ryan et al., 1994).

Summary functions were developed from research results based on three simplifying assumptions. First, we assumed that changes in response variables such as biomass or growth rate could be attributed to annual C gain, loss, or altered allocation. Second, we assumed that results collected at the branch or tree scale could be extrapolated to the monospecific (or nearly monospecific) stands and to a regional scale. Third, we assumed that the effects of all climatic factors (e.g., temperature and CO₂) were independent because the SGCP data that we used provided no evidence of interactions. These assumptions were consistent with our goal of integrating the results of a group of diverse experimental results to produce a regional assessment. The functions are summarized

in Table 1. The four general steps taken to produce each summary function are presented below.

2.4.3.1. Step a. Identify appropriate data. We identified data in a publication that: (1) examined the effects of climatic factors available in our regional GIS, and (2) could be related to the C budget framework of the model.

2.4.3.2. Step b. Transform climatic inputs. Data available in the regional GIS were not always in the same format as those used in an experiment. When necessary, we developed functions to estimate, for example, from SUM04 to SUM06. In such cases, we increased the variability in the definition of input values to reflect the uncertainty of such transformations.

2.4.3.3. Step c. Convert research result into a function. This was done in two steps. First, response variables were transformed into an expression of C gain, loss, or allocation to boles. Second, frequency distributions were defined by including error terms presented with the data. In general, normal distributions were used, although other distributions were used as shown in Table 1.

2.4.3.4. Step d. Convert climate response into a function. Steps a-c were repeated to produce frequency distributions representing the effects of current and future climate scenarios. The ratio of these two distributions was used to define the relative effect of climate change on each component of the C budget. When sampling from the two distributions, we assumed a moderate positive correlation between the two distributions ($r = 0.5$). In some cases, data were most appropriately summarized as a ratio before extrapolating to the C budget (step d before step c).

We present below detailed descriptions of two of these summary functions as examples.

2.4.3.5. Summary function for Murthy et al. (1996). Some of the following steps are shown diagrammatically in Fig. 3.

The proportional increase in CO₂ uptake with an addition of 175 ppm to the base climate (360 ppm) was defined as a normal distribution with mean = 1.6

Table 1

Data sources used in functions relating climate factors to loblolly pine growth

Portion of carbon budget	Type of results	Inputs to function	Components of summary function	Source of data
Gain	leaf CO ₂ uptake	CO ₂	at base [CO ₂] ^a ; uptake $\sim N(7.2, 0.9)^b$; at base [CO ₂] + 150, uptake $\sim N(9.2, 1.1)$; at base [CO ₂] + 300, uptake $\sim N(10.9, 1.3)$	Alemayehu et al. (in press)
Gain	seedling-stand CO ₂ uptake	CO ₂	at [CO ₂] ~ 400 , relative uptake ~ 1 ; at [CO ₂] = 800, rel. uptake $\sim N(2.23, 0.35)$	Groninger et al. (1996)
Gain	leaf CO ₂ uptake	CO ₂ , H ₂ O	at base [CO ₂], uptake $\sim N(3.1, 1)$; at base [CO ₂] + 175, uptake $\sim N(5.2, 2)$; at base [CO ₂] + 350, uptake $\sim N(5.9, 1.3)$	Hennessey and Harinath (in press)
Gain	leaf CO ₂ uptake	CO ₂	at base [CO ₂] + 175, relative uptake $\sim N(1.6, 0.461)$; at base [CO ₂] + 350, rel. uptake $\sim N(2.28, 0.594)$	Murthy et al. (1996)
Gain	leaf CO ₂ uptake	CO ₂	at [CO ₂] = 174, uptake $\sim N(2.6, 1.03)$; at [CO ₂] = 363, uptake $\sim N(6.98, 1.6)$; at [CO ₂] = 501, uptake $\sim N(9.98, 2.13)$; at [CO ₂] = 690, uptake $\sim N(13.31, 2.6)$; at [CO ₂] = 910, uptake $\sim N(16.48, 2.96)$	Teskey (1995)
Gain, loss to R _m ^c	tree diameter growth	O ₃	for proportions of ambient O ₃ of 0.5, 1, 1.7, and 2.5, seedling diameter growth was N (60.7, 4.7), N (58.3, 4), N (53.4, 4), N (49.3, 4.7) mm, respectively	Flagler et al. (1998)
Gain, loss to R _m	circumference growth	O ₃ , rain, temperature	stem circumference growth = (slope of annual growth) × (days since mid-May) + 0.0036 × (3 days SUM04 [O ₃]) × (moisture supply index) + 0.0471 × (3 days ave. rainfall in mm) + 0.0458 × (3 days ave. max temp. 0900 to 2100) – (0.0000454 × 3 days SUM04 [O ₃]) × (3 days ave. max. temp. 0900 to 2100)	McLaughlin and Downing (1996)
Loss to R _m	respiration rates	temperature	respiration was calculated using these uniform distributions representing R ₁₅ and Q ₁₀ values, respectively: leaf $\sim U(20,70)$, $U(2,2.3)$; branch $\sim U(2,37)$, $U(1.9,2.2)$; stem $\sim U(1.8,8)$, $U(1.9,2.2)$; coarse root $\sim U(4.2,29)$, $U(1.9,2.2)$; fine root $\sim U(23,240)$, $U(1.8,2.1)$	Ryan et al. (1994)
Loss to R _m	stand volume	temperature	change in growth (%), where AT = change in temperature from base case to climate change scenario, equals a normal distribution with mean = 2.81 × AT - 0.3 × ΔT ² and SD = 1.3 × ΔT + 2	Schmidting (1994)

^aBase concentration of CO₂ = 360 ppm. All other CO₂ concentration values are expressed in ppm.

^bThe notation N (7.2, 0.9) signifies a normal distribution with a mean of 7.2 and a standard deviation of 0.9. When similar summary functions exist for multiple research projects, composite summary functions were produced by pooling through Monte Carlo sampling. For detailed examples of how these distributions were used to represent experimental results, please refer to Section 2 and to Fig. 3Fig. 4. All rates of uptake of CO₂ are in $\mu\text{mol m}^{-2} \text{s}^{-1}$, unless they are expressed as a proportion of uptake at the ambient concentration of CO₂.

^cMaintenance respiration.

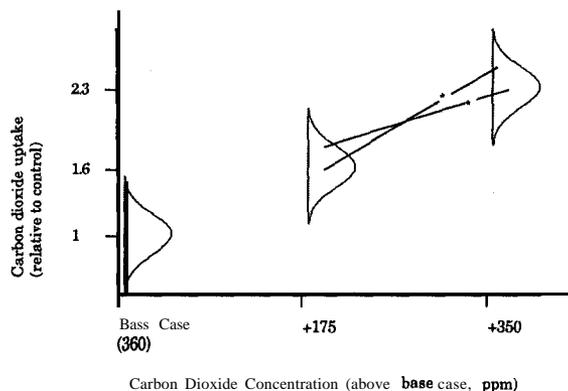


Fig. 3. Summary function data from Murthy et al. (1996). To estimate uptake for carbon dioxide concentrations between + 175 and + 350 (above the base case), a sample was taken from each distribution, and a linear interpolation was performed between these two samples. The two lines in the figure represent two such interpolations representing two iterations of the Monte Carlo procedure.

and standard deviation (SD) = 0.461. Uptake at an addition of 350 ppm was defined as a normal distribution with mean = 2.28 and SD = 0.594. The uncertainties in uptake at different CO₂ concentrations were likely correlated. Therefore, we specified a correlation coefficient of $r = 0.5$ between these two distributions so that samples drawn from them (in the next step) would be correlated. Relative CO₂ uptake was determined for each Monte Carlo iteration by sampling a value for CO₂ concentration from the climate change scenario and linearly interpolating between samples from the CO₂ uptake distributions described above. If the climate change scenario specified a CO₂ concentration of greater than 710, uptake was determined from the distribution representing an addition of 350 ppm.

2.4.3.6. *Summary function for Flagler et al. (1998).* Some of the following steps are shown diagrammatically in Fig. 4.

Experimentally elevated O₃ concentrations were multiples of ambient concentration, including: 0.5, 1, 1.7, and 2.5. For each of these treatments, we defined a normal distribution of seedling diameter (in mm) with the following means and standard deviations, respectively: (60.7, 4.7), (58.3, 4), (53.4, 4), and (49.3, 4.7). As discussed in the description of the project of Murthy et al. (1996), adjacent pairs of

distributions were defined with correlation coefficients of $r = 0.5$. Response to ozone was derived from linear interpolation between samples from the two distributions that bracketed the sample value. The ozone response distribution was then divided by the distribution of diameter growth with ambient ozone to estimate relative diameter growth. Total biomass growth was then estimated for each representative tree from basal area growth using the same allometric relationships used to establish the base C budget. Total C gain for the ozone-exposed tree was calculated by adding maintenance and growth respiration as described above in Section 2.4.2 on base C budget. The amount of gross C gain that was not realized due to above-ambient ozone exposure was calculated as the difference between the gross C gain of a tree exposed to ambient ozone and that of a tree exposed to elevated ozone. The amount of this unrealized gross C gain that represented increased maintenance respiration vs. decreased gross C gain was specified as a beta distribution with parameters (6, 4): that is, a mean of 60% due to increased maintenance respiration, and the balance due to decreased gross C gain. The absolute values of growth were then converted to relative values to produce a summary distribution of the effect of ozone on basal area growth.

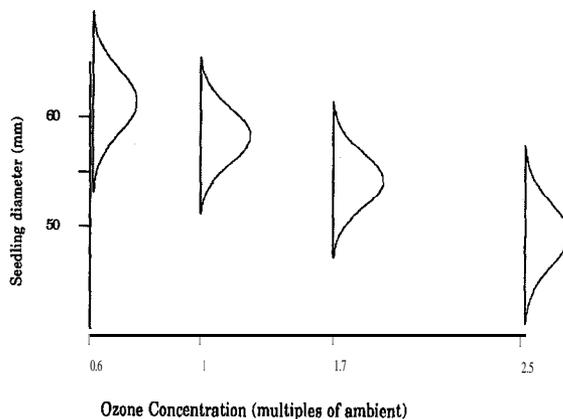


Fig. 4. Summary function data from Flagler et al. (1998). To estimate the effect of ozone for intermediate values of ozone concentration, linear interpolation was performed between the closest two response distributions as shown in Fig. 3.

2.4.4. Future forest growth

The growth rate of individual trees in response to a changed climate was estimated by multiplying components of the current C budget by the changes estimated by the project summary functions. In some cases, more than one function produced an estimate of the relationship between a climatic factor and a portion of the C budget. In such cases, a single pooled estimate was produced by randomly sampling among frequency distributions representing the different estimates. This process resulted in a single frequency distribution describing the estimated relationship between each climatic factor and each portion of the C budget. After any such pooling of results, each function was applied to modify a portion of the C budget. Values of annual maintenance respiration and gross annual assimilation from the base climate scenario were multiplied by the appropriate response functions, and were then summed to give a new value for C allocated to growth under the future climate scenario. This value was then multiplied by the distribution describing allocation to bole growth. If any of the experimental data had indicated a change in C allocation to the bole vs. other organs, they would have been used here, but there were no such data. Total growth was then reduced to account for growth respiration, as described above for the base C budget. Finally, the bole growth rate was transformed to basal area growth rate via the allometric equations cited above. Because the model estimates the growth of individual representative trees, we constrained the growth estimates to positive values; i.e., negative growth rates were not allowed, and small positive values were substituted instead.

2.4.5. Modeling uncertainty

A probabilistic estimate of growth rate was generated by selecting one value from the frequency distribution of each variable for each iteration of the simulation. The results of a number of such iterations form a frequency distribution that is a probabilistic estimate of the effect of a climate change scenario on forest growth rate. The relative influences of model inputs or intermediate values (such as expected relative change in C budget) on model output were determined by means of partial non-parametric correlation coefficients (Morgan and Henrion, 1990). Because we determine influence in this manner, it

incorporates the effect of both the median value and the dispersion of each stochastic function. Model results were produced using a stratified sampling method known as Latin Hypercube that systematically samples from all parts of the distribution. This method has the advantage of requiring fewer repetitions of sampling before achieving a stable output distribution (Morgan and Henrion, 1990). The software used to create the forest model and perform Monte Carlo simulations was Analytica (release 1.0, Lumina Decision Systems, Los Gatos, CA).

2.5. Regional analysis

The forest growth model produced estimates on a 30 X 30 km cell basis, as described above. These results were then applied to each 1 km² cell within the 30 X 30 km cell that contained growing loblolly pine stands. Based on the RPA map, there were 230,106 1-km grid cells of loblolly-shortleaf pine in the USA, nearly all of which lie within our 12-state analysis region. Estimates were made for nearly all of these 1-km² cells (226,390). For some cells, no estimate was made due to missing data, location outside the study region, or a record of a zero growth for loblolly pine from the nearest FIA plot.

3. Results and discussion

3.1. Estimates of future growth

We used several approaches to present the probabilistic results from the forest growth model on a regional scale, as shown in Figs. 5 and 6 and Table 2. Fig. 5 shows the likelihood-expressed as a percent chance-that loblolly pine growth rate will be decreased by climate change. These results indicate a high likelihood of decreased growth, ranging from 19 to 95%, throughout the 12-state region. Growth is particularly likely to decrease in some portions of the region, such as northeastern Georgia and northwestern Louisiana.

While Fig. 5 shows the likelihood of a growth decrease, it does not indicate the magnitude of this effect; such results are shown in Fig. 6. Since the estimates are probabilistic, there is no single estimated value for any particular location that contains

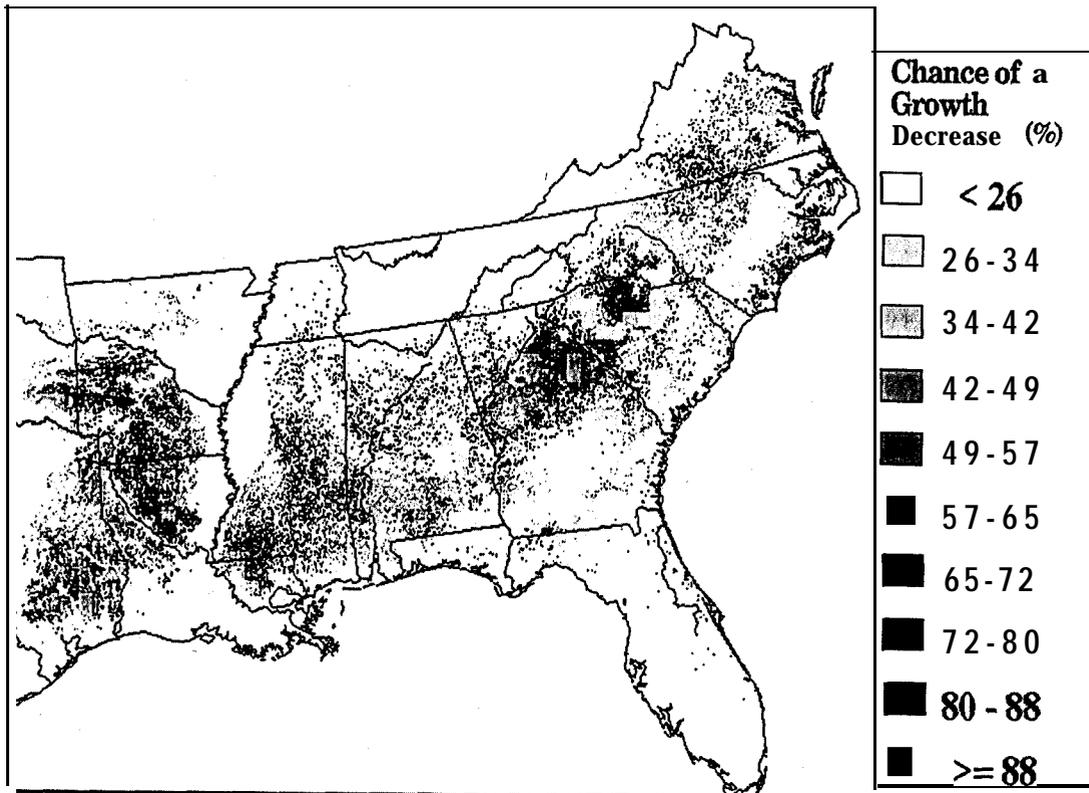


Fig. 5. Chance that climate change will decrease loblolly pine growth. The prediction for each 30 X 30 km cell is applied to all locations (1 X 1 km) where loblolly pine forest occurs within that cell, resulting in a pattern of squares and rectangles apparent in the map.

loblolly pine forest. Fig. 6 shows three possible effects of the climate scenario on loblolly pine basal area growth as a percentage of the historical growth rate. The three histograms show a worst case, most likely case, and a best case estimate for all loblolly pine throughout the region. These three histograms represent the 10th, 50th, and 90th percentiles of the frequency distribution representing the model estimate for each location where loblolly pine occurs. In the worst case estimate, climate change reduces loblolly pine basal area growth substantially throughout the region. There were no negative values for estimated basal area growth because we constrained the forest growth model to avoid such estimates, as discussed above. In the most likely estimate, growth would decrease in about half the locations, but would increase substantially in the other half. The distribution appears to be bimodal—a large number of stands would grow much more slowly (less than half

the historical rate) under the climate change scenario. This bimodal distribution is probably due to the large number of locations for which growth estimates were constrained to positive values, resulting in a large number of values just above zero.

In the best case estimate, the climate change scenario would increase loblolly pine growth substantially in nearly all locations throughout the region. In many locations, growth rates were estimated to double, triple or even quadruple. Such large increases in growth may be unrealistic, even with a low probability of occurrence. We did not constrain the estimates of growth increases because there is not an obvious choice of a cut-off point for defining 'unrealistically' rapid growth. The wide dispersion of values of estimated 'best case' estimates are due to the multiplication of uncertainties in the model and the lack of constraint on these estimates. Hence the 'best case' estimates should be interpreted as

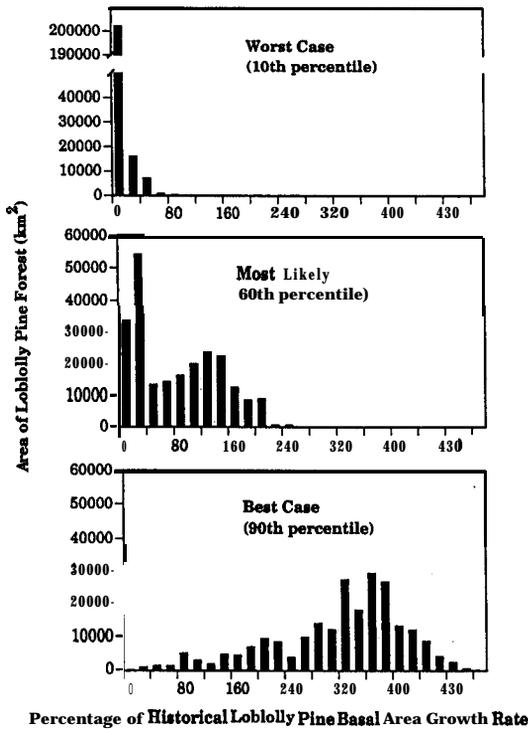


Fig. 6. Estimated change in loblolly pine basal area growth rate. For each of the 1169 analysis cells in the region, the model produced a probabilistic estimate (in the form of a frequency distribution) of loblolly pine basal area growth rate under a climate change scenario. These histograms show selected percentiles from the frequency distributions for each of the analysis cells.

indicating that there is some chance of a substantial increase in loblolly pine growth throughout much of its range, but that there is much uncertainty about the magnitude of such an increase.

In addition to relative changes in growth rates, it is useful to examine the regional sums of the estimated change in total annual basal area growth as shown in Table 2. These results indicate that under

the most likely case, there will be a slight decrease in growth throughout the region as a whole. Although the most likely effect of climate change will be a slight decrease in growth, there is a chance of either a large decrease in basal area growth, or a large increase in growth, as discussed above, and shown in Table 2.

Most of the experimental data used in the forest growth model (Table 1) showed increases in C assimilation due to increased CO₂, or increases in maintenance respiration due to increased temperature. Hence, this model represents a balance between increased growth due to CO₂, and decreased growth due to temperature. This balance is the reason for the lack of a large effect of climate change on the midpoint of the distribution of estimated growth rate. In previous analyses of a climate change scenario with a larger temperature increase, our model estimated a greater likelihood of growth declines (Smith et al., 1998). The importance of these two responses has been found in other models: changes in CO₂, and temperature were estimated by several diverse models to be important direct influences of climate change on forest productivity in the southern USA, as reviewed by Weinstein et al. (1998).

The wide range of possible effects shown in Fig. 6 and Table 2 is a result of including in our model estimates of uncertainty in measurements of regional factors such as air temperature, as well as uncertainty in the effects of climate change on loblolly pine growth. Areas such as southcentral Alabama and eastern Texas have some of the lowest estimated growth rates in the worst-case result, as well as some of the highest estimated growth in the best-case result (Fig. 7). These results indicate that uncertainty about the effect of climate change on basal area growth rate is greater in these portions of the region. The locations that are most likely to experience a decline in growth are not entirely coincident

Table 2
Predicted change in regional loblolly pine basal area growth

Type of prediction	Percentile of distribution of predicted values	Change in growth rate (10 ³ m ² yr ⁻¹)	Percent change in growth rate
Worst case	10th	- 24,000	-9.2
Most likely	50th	-60	-0.2
Best case	90th	+ 63,000	+ 14.2

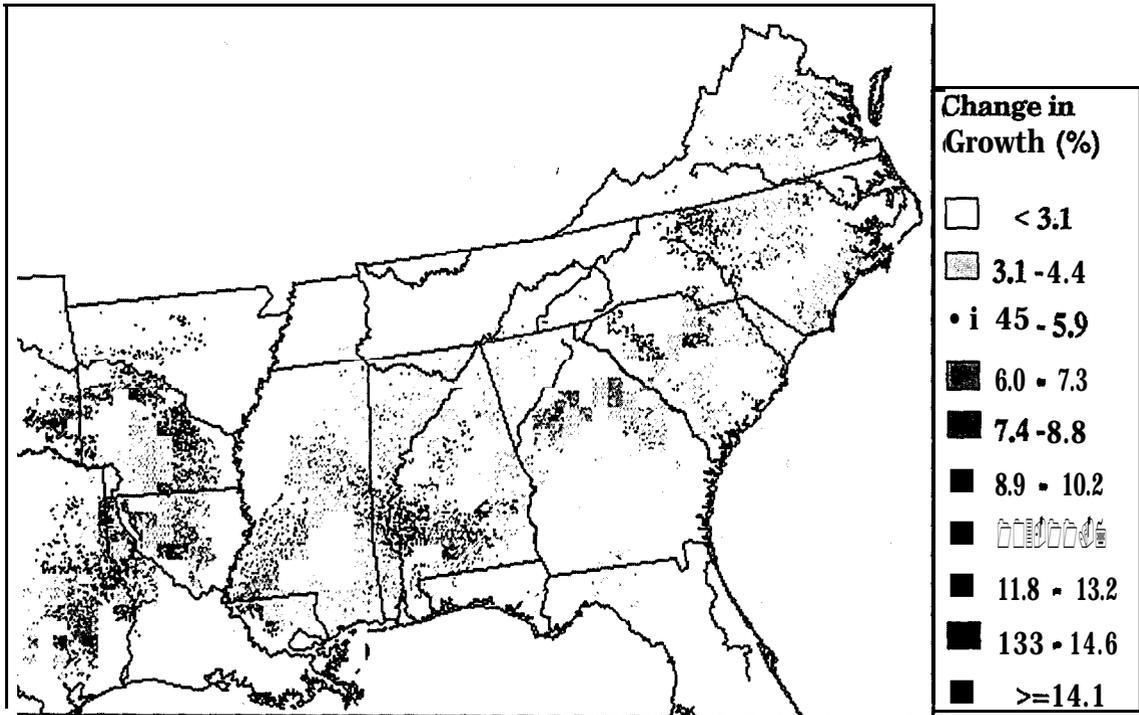


Fig. 7. Uncertainty in estimated loblolly pine growth rate. This map shows the uncertainty in basal area growth rate calculated as the difference between the 90th and 10th percentiles of predicted growth after climate change ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$).

with those that have the greatest uncertainty in the estimated growth rate. For example, there is substantial uncertainty about the effect of climate change on loblolly pine growth rate in southcentral Alabama, but this area is not one of those most likely to experience a growth decrease (Figs. 5 and 7). Fig. 7 demonstrates a benefit of combining probabilistic and regional analyses—it may be useful to identify locations for which our ability to estimate the effects of a **stressor** are most limited.

3.2. Factors influencing estimated growth

The above tables and figures illustrate the estimated effect of a climate change scenario on loblolly growth rate. An equally important goal of our modeling approach is to identify the climatic factors that have the greatest influence on the estimated growth rate at each location throughout the region. Before discussion of these results, it may be helpful to point out how our approach differs from sensitivity analy-

sis, which is also used to examine the influence of model input values and parameters. While sensitivity and uncertainty analyses are both concerned with uncertainty in model parameters; they focus on different issues. Sensitivity analysis is concerned with the propagation of errors due to deterministic, but unknown, model parameters. Uncertainty analysis treats selected parameters as uncertain, and examines the influence of this uncertainty on model predictions. Sensitivity analysis is commonly used to assess the importance of model parameters. However, sensitivity analysis typically modifies a single parameter at a time, failing to address interactions of different factors within the model, although this technique has been extended to examine changes in several parameters simultaneously, and interactions among them (e.g., Williams and Yanai, 1996). Uncertainty analysis has the advantage of simultaneously treating a large number of parameters as stochastic, and hence all possible interactions among stochastic variables are examined. Additionally, because appropriate frequency distributions are se-

Table 3
Influence of climatic variables and model summary functions

Description of probabilistic ^a variable	Rank of influence ^b (high value = more influence)	Number of probabilistic influences ^c
<i>Climatic factors</i>		
Future CO ₂	7.2	1
Future precipitation	3.9	1
Future temperature	2.2	1
Future ozone	2.1	1
<i>Summary model functions</i>		
Future carbon assimilation	9.0	31
Current carbon assimilation	7.0	14
Future respiration	6.8	15
Current respiration	4.2	14
Future carbon allocation	2.7	2

^aProbabilistic variables are those represented by probability density functions.

^bInfluence was measured as the rank correlation coefficient between the PDFs representing a climatic factor or a function and the PDF representing the predicted loblolly pine growth rate. Thus 'influence' incorporates the effect of both the median value and the dispersion of the climatic factor or the summary model function. The data in this column are the average rank values throughout the range of loblolly pine.

^cAll climatic factors are model inputs, therefore they cannot incorporate other probabilistic influence. However, summary model functions include the influence of multiple model inputs and other model functions. Variables may influence more than one summary model function, hence they may be counted more than once in this column.

lected for each stochastic variable, the 'parameter space' of the model is explored more appropriately than even in a multiple-factor sensitivity analysis, in which typically all values within a range are equally likely to be used. Our model is unusual in that we perform the analysis for a large number of grid cells throughout the region of interest. Hence we produce a probabilistic analysis in two dimensions, in the same spirit as has been recommended for 'state of the art' risk assessments (Hoffman and Hammonds, 1994). For each individual cell in the region, an uncertainty analysis is performed. All of these analysis cells together form another distribution, analogous to a population of individuals. This approach allows us to examine spatial patterns in the influence of different climatic factors as well as functional relationships within the model.

We examined the influence of uncertainty in two types of variables: (1) climatic factors such as future estimates of CO₂, precipitation, ozone, and temperature, and (2) summary functions within the forest growth model. Summary functions are those that may incorporate the results of multiple research projects, which may also be represented as stochastic functions. These summary functions, along with the number of stochastic functional relationships that

influence these summary functions, are shown in Table 3. By examining the influence of these summary functions, we can determine which functional relationships within the model are most important. The capability to examine the influence of uncertainty in defining functional relationships between climatic factors and forest growth response is particularly important for modeling the effects of climate change, for which thorough validation of any model will not be possible until after climate change has occurred. Inclusion of uncertainty into the model structure in this fashion promotes insight into which uncertainties are most important, and hence should be targets of future experimental and modeling investigations.

The most influential factor for all locations was the relative change in C assimilation under the climate change scenario (Table 3). As mentioned above, we used our model in a previous investigation to examine the effects of a more extreme temperature increase (5 to 8°C, UKMO model) throughout the region (Smith et al., 1998). In this high-temperature scenario, we found respiration to be the most influential summary function in many locations throughout the region. With the less extreme temperature increase in the current scenario, respiration had much

less influence, as indicated in Table 3, and C assimilation was the most influential factor.

Although we can examine the influence of uncertainty in many of the assumptions within the model, we cannot examine factors that are not included in the model. As mentioned above, inter-tree competition and mortality are included implicitly by means of historical growth rates, but possible influences of climate change on these factors are not modeled. Similarly, the model neither addresses the influence of changes in radiation on regional water balance, nor changes in pest population dynamics. Hence, we cannot determine from our analysis how important such factors may be in estimating the response of loblolly pine to a changed climate. Changes in competition, mortality, and species migration will be important over centuries. However, as discussed above, our goal was to integrate the results of a specific body of research, which focused primarily on physiological responses of a single species rather than population dynamics. Hence, we chose to model effects on instantaneous growth rate after a doubling of CO₂, and to model monospecific stands, or those with relatively small amounts of other pine species, which may be expected as a first approximation to have similar physiological responses as loblolly pine.

As shown in Figs. 5 and 6, and Table 2, there is substantial regional variability in the estimated effects of climate change on loblolly pine growth. Uncertainty in estimated growth is quantified as the difference between the best case and worst case

estimates. As shown in Fig. 8, loblolly pine stands with greater historical growth rates tended to have greater uncertainty in the estimated growth rate under climate change. The relationship shown in Fig. 8 suggests that historical growth rate is quite influential in the model. Such influence is to be expected since the model is based on modifying historical growth rate by means of functions describing climate change effects.

The task of estimating climate change effects on forest growth is complex due to the numbers of ecological interactions, the long time period of effects, and uncertainties about both future climate and ecological effects. In the model described here, we extrapolated from a body of experimental data using a C budget approach to produce probabilistic regional estimates. As mentioned above, we assumed that short-term, tissue-specific measurements could be extrapolated to estimate the annual growth trees and stands. Our goal was to create a tractable model structure that would focus attention on quantifying the uncertainties in estimating the regional effects of multiple climatic factors on forest growth based on a select body of experimental research. As in any modeling effort, we were not able to represent all of the potentially important processes. By focusing our efforts on C, we did not incorporate possible changes in other factors such as nitrogen and water availability in forest soils. Nitrogen deposition, transformation, and uptake are likely to change under future climatic conditions, and may affect the response of forests to increased CO₂ and temperature. Total annual precipitation and its distribution through the year, especially late in the growing season, affect loblolly pine productivity. By focusing on estimating the growth rate of a single species, we did not examine interactions with other plant or pest species. We did not incorporate genetic variation, except indirectly if such variation was included in the experimental data. We also did not attempt to model the migration of loblolly pine over decades and centuries in response to a changed climate. Despite such limitations, we propose that this methodology can focus an assessment on the most important issues in a complex system. For example, while ozone has been demonstrated to decrease loblolly pine growth, our results suggest that its effect is much less than that of other climatic factors.

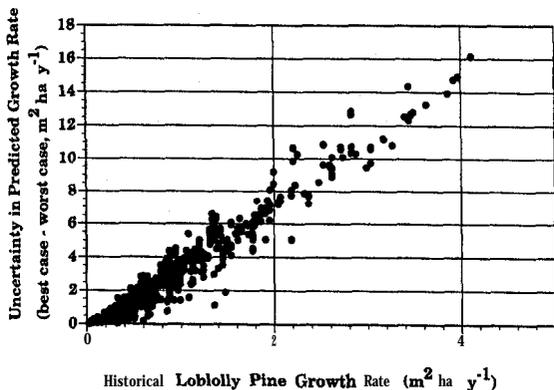


Fig. 8. Estimation uncertainty increases with historical growth rate. Uncertainty in estimated growth is quantified as the difference between the best case and worst case estimates.

Models of forest growth may be constructed at many scales for many purposes, ranging from detailed physiological models that describe a single tree, to global vegetation models. We believe that the type of model we have constructed is useful for integrating existing information from regional surveys and experimental investigations to produce ecological risk assessments that are useful to policy and decision makers. Historically, assessments of the effects of stresses on forests have often taken the form of a lengthy report delivered to policy makers. However, such an approach was criticized when used in the National Acidic Precipitation Assessment Program (for example, Loucks, 1992; Russell, 1992; Schindler, 1992). Such an approach does not guarantee that research results have been synthesized, nor that uncertainties in scientific understanding have been systematically addressed. For such complex topics, we believe that modeling approaches such as the one we have described can improve assessments by integrating pertinent experimental research findings, summarizing what is known, and identifying key scientific uncertainties.

4. Conclusions

Based on a climate change scenario derived from the results of four GCMs, our model estimated that loblolly growth will likely decrease slightly throughout its 12-state range. However, due to large uncertainties in both climate factors and the influence of these factors on forest growth, there is a substantial chance of either a large decrease or a large increase in loblolly pine basal area growth rate under future climate conditions. We also determined which climatic factors and components of tree growth had the most influence on the predicted growth rate. The most influential factor at all locations was the relative change in C assimilation. Of climatic factors, CO₂ concentration was found to be the most influential factor at all locations. Substantial regional variation in estimated growth was observed, and was probably due primarily to variation in historical growth rates and to the importance of historical growth in our model structure. The estimate of future

loblolly pine growth rate was more uncertain for stands with historically rapid growth rates.

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