CHARACTERIZATION OF OPTIMUM PHYSIOLOGICAL RESPONSES OF FIELD-GROWN LOBLOLLY PINE[1]

Zhenmin Tang, Jim L. Chambers, and James P. Barnett[2]

Abstract-Photosynthetic photon flux density (PPFD), air temperature (Ta), needle net photosynthesis (Pn), vapor pressure difference (VPD), stomatal conductance (gw), transpiration (E), and predawn and daytime xylem pressure potentials (XPP) were measured in a loblolly pine (*Pinus taeda* L.) plantation in 1995 and 1996. Boundary-line analyses were conducted to determine optimum physiological responses and critical levels of Ta, PPFD, VPD, and XPP that restricted gas exchange. Our results showed that under field conditions, the maximum Pn, gw and E were 6.0 μmol m^{-2} s^{-1}, 180 mmol m^{-2} s^{-1} and 3.5 mmol m^{-2} s^{-1}, respectively. Irradiance less than 1100 μmol m^{-2} s^{-1} was the most significant variable limiting Pn. Threshold values of Ta, VPD and XPP that resulted in a decrease in Pn and gw were 33 ^{0}C, 1.3 KPa and -1.3 MPa, respectively. Our findings suggest that the boundary-line technique is an alternative for assessing and predicting responsive physiology of trees without artificial constraints on the environment.

INTRODUCTION

It is predicted that global climate is changing, with a rise in ambient CO$_2$ concentration, an increase in annual mean temperature, and more fluctuation inseasonal precipitation (Cooter 1998, Hansen and others 1988). Global climate change may increase the variability of stand resource availability and cause stresses that will impact the growth and productivity of southern pine forests (Peters 1990). Long-term studies of trees larger than seedlings are needed to understand how foliage physiology, crown development and tree growth respond to microclimate variation in forest stands. Such studies also will provide data to develop process models for predicting the effects of global climate change on leaf gas exchange, root growth, tree size and stand productivity.

Recent ecophysiological research suggests that foliage production, needle physiology and shoot growth are closely correlated with variation in stand environment (Gravatt and others 1997, Leverenz and Hinckley 1990, Sword and others 1998, Tang and others 1999b, Teskey and others 1994). These studies also indicate that there is great variability in canopy and soil factors, which makes it difficult to assess stand responses to environmental changes. Interpretation of the impacts of silvicultural treatments and global climate change on tree growth and stand productivity hinge on our ability to correctly determine and model the tree physiological responses under field conditions. Often, forest scientists, working in the field, impose artificial constraints on the tree environment to reduce variability and thus increase the resolution of statistical significance. An alternative known as boundary-line analysis can be use to study relationships between plant and environmental variables without artificial restrictions on the tree environment (Chambers and others 1985, Webb 1972). Researchers have used this technique to model and predict physiological responses of forest species in the field and found reasonable agreement between prediction models and field data (Chambers and others 1985, Reed and others 1978). The objectives of this paper are to: (1) characterize optimum responses of physiological variables of field-grown loblolly pine associated with independent environmental and plant variables, and (2) examine these dependent physiological variables in response to critical or threshold levels of the independent variables.

MATERIALS AND METHODS

Study Site

The study was conducted in a plantation located in Rapides Parish, Louisiana. The soil at the site is a well-drained Beauregard silt loam (fine-silty, siliceous, thermic, plinthaquic paleudult). In May 1981, 14-week-old containerized loblolly pine seedlings were planted at a 1.8 x 1.8-m spacing. Survival was 97 percent seven years after planting (Haywood 1994). Twelve plots (0.057 ha and 13 x 13 trees each plot) were established in the fall of 1988. Two levels of fertilization (fertilized and non-fertilized) and thinning (thinned and non-thinned) were randomly assigned to these plots in a 2 x 2 factorial design with three replications. Thinning was done by removing every other row of trees and every other tree in the remaining rows, leaving 721 trees ha“. Non-thinned plots had 2990 trees ha-‘. Fertilization was completed by broadcast application with diammonium phosphate (134 kg N ha-’ and 150 kg P ha-‘). Understory vegetation was minimized by herbicide application as needed. Post-treatment tree growth and stand yield during 1989-l 992 was reported by Haywood (1994). Thinning and fertilization were conducted again in March 1995. After re-treatments, thinned plots had 512 trees ha” (15.6 m^2 ha^{-1}) left, whereas non-thinned plots maintained the density of 2863 trees ha^{-1} (42 m^2 ha-‘). Urea (200 kg N ha-‘), monocalcium phosphate (50 kg P ha^{-1}) and potash (50 kg K ha-‘) were applied in fertilized plots. Steel towers and wooden walkways were built in two replications (eight plots) in 1991-1992 to access the upper and lower portion of the live crowns.

Physiological Measurements

Net photosynthesis (Pn), stomatal conductance to water vapor (gw), transpiration rate (E), and vapor pressure difference (VPD) from the intercellular space of needles to air were measured in situ on the branches within the upper and lower crown, with a LI-6200 photosynthesis system and a 250-ml leaf chamber (Li-Cor, Inc., Lincoln, NE). Photosynthetic photon flux density (PPFD) and air temperature (Ta) within the upper and lower crown were

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[2] Post-Doctoral Research Associate and Professor, School of Forestry, Wildlife and Fisheries, Louisiana State University Agricultural Center, Baton Rouge, LA 70603; and Project Leader, USDA Forest Service, Southern Research Station, Pineville, LA 71360, respectively.

recorded with a LI-190S quantum sensor and a thermocouple mounted on the leaf chamber. During each measurement, the middle section of two fascicles was enclosed in the leaf chamber and recorded for changes in CO, concentration in the leaf chamber in their natural orientation on the branch. The fascicles were then detached from the branch and their xylem pressure potentials (XPP) were measured with a pressure chamber (PMS Instrument Co., Corvallis, OR). Predawn XPP was taken between 0400 and 0500 h. Total needle volume and surface area per fascicle were determined by water displacement (Johnson 1984). We expressed Pn, gw, and E on a leaf surface area basis.

Two kinds of physiological and environmental data were collected for boundary-line analyses. They were: (1) monthly diurnal measurements in one replication and (2) semi-monthly measurements in two replications. Diurnal measurements were taken on dominant or codominant trees accessible from the walkways during June through November 1995. On each sampling day, three south-facing branches in the upper crown and other three in the lower crown were randomly chosen in each plot. Same set of the selected branches was used throughout the growing season. Previous- and current-year fascicles on terminal or nearby lateral shoots were measured separately seven times between 0800 and 1700 h at a 1.5-hour interval on partly or fully sunny days. A total of 84 measurements per plot were completed on each sampling day. Additional diurnal measurements were taken on a different set of branches during June and July 1998.

Twice each month during June through October 1995, gas exchange measurements were conducted between 0930 and 1130 h, on three south-facing branches in the upper and lower crown of dominant or codominant trees. Trees and branches were randomly selected at the start of each measurement. On one day, four plots of the first replication were measured and four plots of the second replication were taken on the next day. Similar measurements were performed between 0930 and 1130 h and between 1300 and 1500 h during April through December 1998. A total of 3326 observations were collected during 1995 and 1996.

Boundary-line Analysis

Boundary-line analysis is a tool for determining and predicting a relationship between a dependent variable and an independent variable (Chambers and others 1985, Webb 1972). When Pn (dependent variable) is plotted against PPFD (independent variable), for example, a scatter diagram is produced (fig. 1). If data are sufficient to enclose a broad range of variation in the dependent variable response, the upper extreme of the data points (excluding outliers) can be drawn with a boundary line as in Figure 1. The boundary line represents the maximum response of Pn to a given level of PPFD, when all other important variables are optimum for Pn, or when a variable overriding PPFD reduces the level of the Pn response. Data points below the response line include: (1) measurement errors, (2) responses when the independent variable is non-optimum, and (3) variation caused by other overriding or interacting variables that limit the dependent variable response (Chambers and others 1985, Webb 1972).

Several two-variable scatter diagrams were constructed with the physiological and environmental data (a total of 3326 observations) collected in 1995 and 1996. In order to reduce potential overestimation of physiological responses due to possible measurement errors (Chambers and others 1985), and to assist in developing boundary lines, we chose the upper limit 5 percent of the data points for each dependent variable to draw a boundary-line curve for each diagram. Least-square regression was developed with SAS statistical software (SAS Institute, Inc. Cary, NC) and used to draw the resulting boundary line for each two-variable response. Each line represented an average response of the uppermost 5 percent of the dependent variable points. It was utilized to show the potential optimum response of the physiological variable to a single environmental or plant variable. Data points above the boundary-line curve were assumed to be outliers and measurement errors, whereas those below the curve were considered as non-optimum responses. This interpretation provides a slightly conservative estimate of the maximum dependent-variable response for the range of the independent variable shown, but represents the shape of the response patterns and should adequately reflect critical or threshold values of the independent variables.

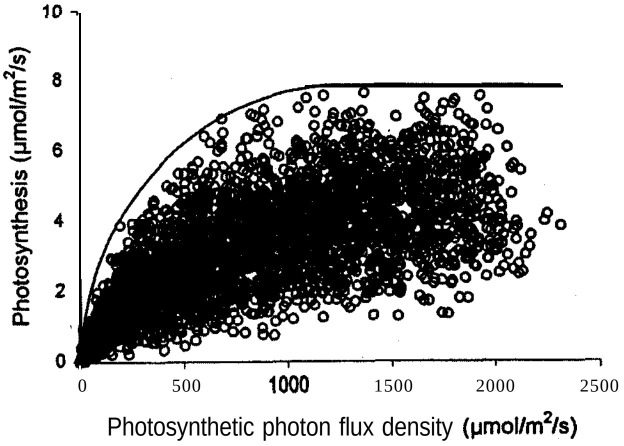

Figure 1—Scatter diagram of data and the boundary line drawn for needle net photosynthesis in response to photosynthetic photon flux density.

RESULTS AND DISCUSSION

Our data covered an extensive range of within-crown environmental conditions (table 1). Photosynthetic photon flux density varied from 2 to 2316 $\mu mol\ m^{-2}\ s^{-1}$, Ta was between 4 and 43 °C, and VPD changed from 0.14 to 5.0 KPa during the measurement periods. Because of frequent precipitation, needle predawn XPP fluctuated from -0.44 to 0.81 MPa, with the most negative values recorded in November 1995 and December 1996 (fig. 2A and 2B). These predawn values (higher than -1.0 MPa) showed that soil moisture supply was sufficient for gas exchange of foliage during the growing season (Gravatt and others 1997, Tang and others 1999a). The broad coverage of within-crown environmental variation assures the reliability of using the boundary-line technique for assessing gas exchange responses of field-grown trees (Chambers and others 1985, Dougherty and Hinckley 1981).

Large variation in the physiological variables was found in the field (table 1). We used a regression curve as the boundary line to closely represent the optimum response of

Table I-Statistical summary of the physiological and environmental variables measured in a 15- to 16-year-old loblolly pine plantation

Variable[a]	n	Mean	Minimum	Maximum	Standard deviation
PPFD (μmol m^{-2} s^{-1})	3326	867	2.0	2316	542
Ta (°C)	3326	28.8	4.0	43.0	6.8
VPD (KPa)	3326	1.78	.14	5.00	.91
Pn (μmol m^{-2} s^{-1})	3326	3.19	.00	8.12	1.51
gw (mmol m^{-2} s^{-1})	3326	88.4	4.51	247	38.7
E (mmol m^{-2} s^{-1})	3326	1.46	.04	5.42	.83
XPP (-MPa)	3326	1.31	.49	2.74	.35

[a] PPFD = within-crown photosynthetic photon flux density, Ta = within-crown air temperature, VPD = vapor pressure difference, Pn = net photosynthesis, gw = stomatal conductance, E = transpiration, and XPP = daytime xylem pressure potential.

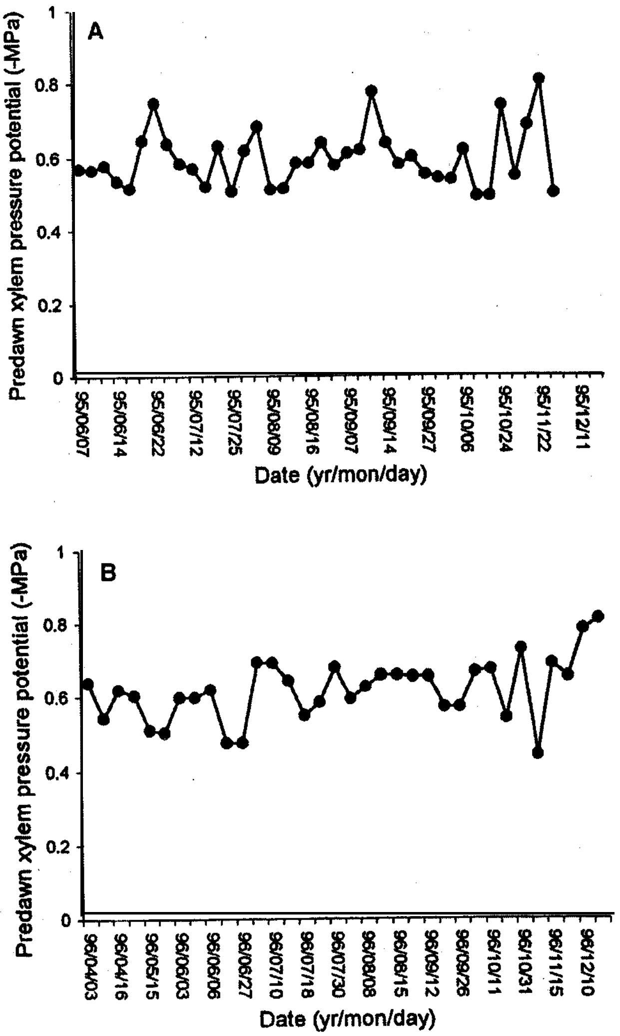

Figure 2—Seasonal pattern of predawn xylem pressure potential in (A) 1995 and (B) 1996.

each dependent physiological variable to an independent environmental or plant variable (fig. 3A-3D). The boundary-line Pn response to changing PPFD was in agreement with the findings by Teskey and others (1986) for loblolly pine, and Teskey and others (1994) for slash pine (*Pinus elliottii* Engelm. var. *elliottii*). Initially, Pn increased rapidly with rising PPFD, and it became light saturated as PPFD approached 1100 μmol m^{-2} s^{-1} .(fig. 3A). Maximum Pn was approximately 6.0 μmol m^{-2} s^{-1}, consistent with the light-saturated Pn point reported for this species (Fites and Teskey 1988). In addition, Pn rose quickly with small increases in Ta and reached the peak rates between 23 and 33 °C (fig. 3B). A similar relationship between Pn and Ta was observed by Teskey and others (1994) in 23-year-old slash pine trees. However, they did not have data to show how Pn of that species responded to Ta values above 35 °C. Field observations from the present study indicate that in loblolly pine, a rapid decline in Pn occurred as Ta exceeded 33 °C. It has been recognized that light availability is the most critical variable for Pn, although high Ta may limit the process (Leverenz and Hinckley 1990, Tang and others 1999a, Teskey and others 1994). Our boundary-line responses illustrate that Pn was significantly restricted by PPFDs lower than 1100 μmol m^{-2} s^{-1} (R^2 = 0.75) and by Tas outside a range from 23 to 33 °C (R^2 = 0.67). These results support the above conclusion.

We observed a threshold Pn response to both VPD and XPP (fig. 3C and 3D). Net photosynthetic rate remained at the highest level and showed little response to low VPD and high XPP (less negative). Threshold values of VPD and XPP for a Pn reduction were near 1.3 KPa and -1.3 MPa, respectively. Needle Pn decreased nearly 40 percent, as VPD increased to 3.5 KPa. A similar reduction occurred as XPP decreased to -2.3 MPa. Eventually, Pn approached zero as VPDs reached near 5.0 KPa and XPPs decreased below -3.0 MPa, respectively. These findings indicate that although PPFD was not limiting, either VPDs above 1.3 KPa or XPPs below -1.3 MPa reduced the maximum Pn level, implying that other variables may override or interact with the independent variable to control the Pn response. Teskey and others (1994) reported that in mature slash pine, Pn started to decline at a VPD of 1.5 KPa. A similar threshold

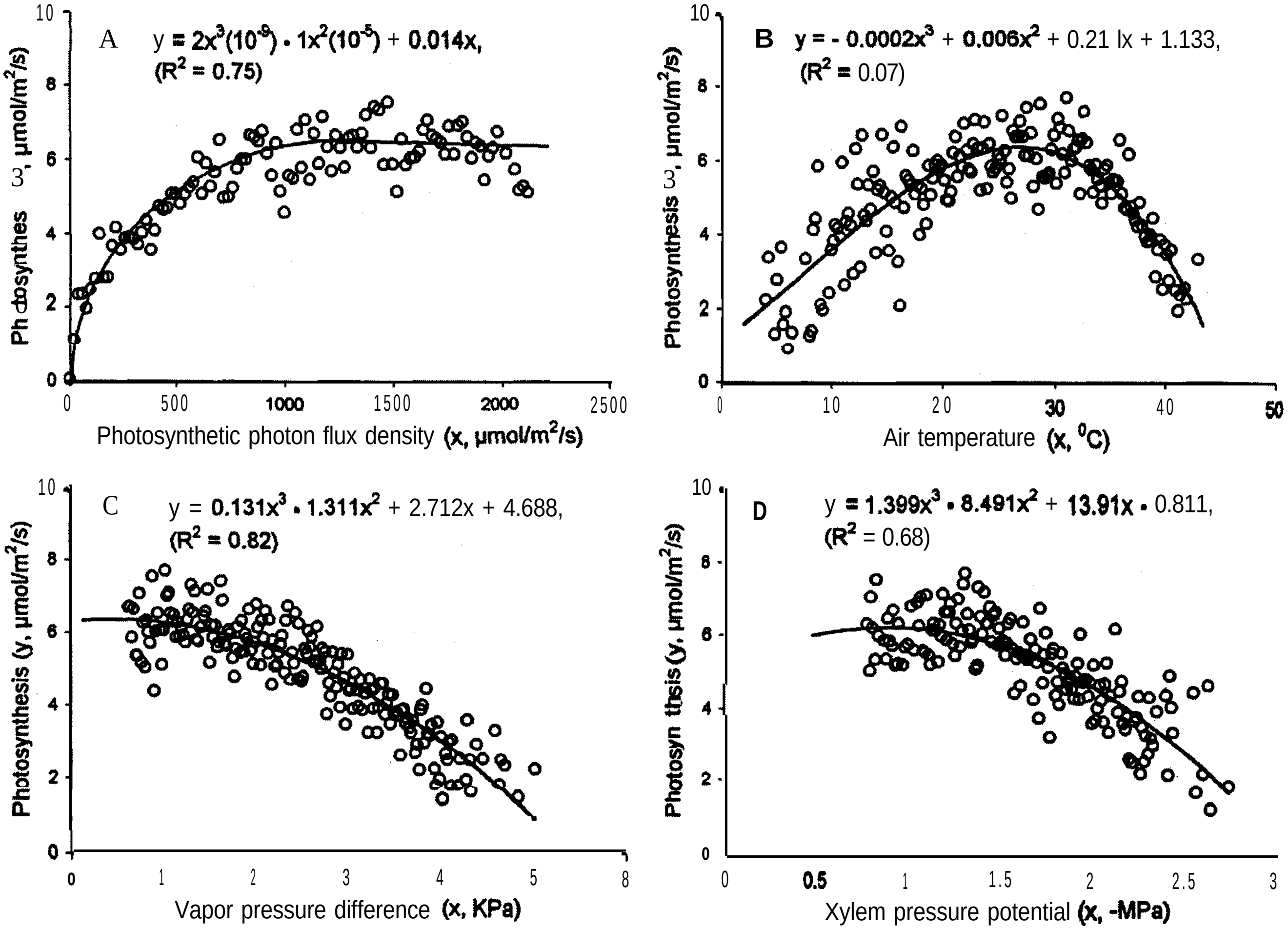

Figure 3-Boundary-line response of net photosynthesis to (A) photosynthetic photon flux density, (B) air temperature, (C) vapor pressure difference, and (D) daytime xylem pressure potential. Data represent the upper 5 percent of dependent variable responses to the entire range over the independent variable values.

Pn response to changing XPP was documented by Dang and others (1997) for jack pine (*Pinus* banksiana Lamb., -1.2 MPa), Sheriff and Whitehead (1984) for radiata pine (*Pinus radiata* D. Don, -1.8 MPa), and Jarvis (1980) for Scots pine (*Pinus sylvestris* L., -2.0 MPa). The threshold XPP for Pn from our study means that maximum carbon uptake of loblolly pine is more sensitive to water stress than that of radiata and Scots pine.

Boundary-line responses of gw to independent environmental and plant variables corresponded to the Pn response (fig. 4A-4D). The correspondence between gw and Pn responses was expected, because the physiological variables are closely correlated (R^2 = 0.70) (Teskey and others 1988). Initially, gw rose sharply with increasing PPFD and Ta (fig. 4A and 4B). As PPFD reached approximately 550 µmol m^{-2} s^{-1}, stomata appeared to become light saturated and gw attained a maximum level of 180 mmol m^{-2} s^{-1}. Stomatal conductance decreased quickly after Ta exceeded 33 °C. Additionally, no response of gw was found at low VPD and high XPP levels. However, gw showed a threshold response to a VPD of 1.3 KPa and a XPP of -1.3 Mpa (fig. 4C and 4D), suggesting that plant water stress may develop to reduce the level of the gw response. Stomata were partly closed as gw declined about 50 percent at a VPD of 3.5 KPa. Stomatal conductance also decreased about 50 percent as XPP approached near -2.3 MPa. This provides an explanation for a 40-percent reduction in Pn at that time. Complete stomatal closure occurred when VPD increased to 5.0 KPa and XPP decreased to -3.0 MPa. Teskey and others (1986) studied the effects of daytime XPP on Pn and gw in loblolly pine seedlings. They found that the most negative XPP causing a decrease in gw was about -1 .0 MPa, and complete stomatal closure took place at -2.0 MPa. Critical XPP values for a gw decline and full stomatal closure from our large trees are 0.3 MPa and 1 .0 MPa, respectively, lower than those of seedlings. This apparently shows distinct physiological differences between seedlings and trees of the same species, and demonstrates that seedling physiological performance may not accurately represent tree physiological responses to environmental variation.

Strong correlations were found between E and Ta and VPD (R^2 = 0.90 and 0.83, respectively). Initial increases in Ta enhanced E significantly (fig. 5A). Maximum E was about 3.5 mmol m^{-2} s^{-1} at a Ta near 40 °C. When gw was high at low VPD (fig. 4C), E remained low (fig. 5B), reflecting a low

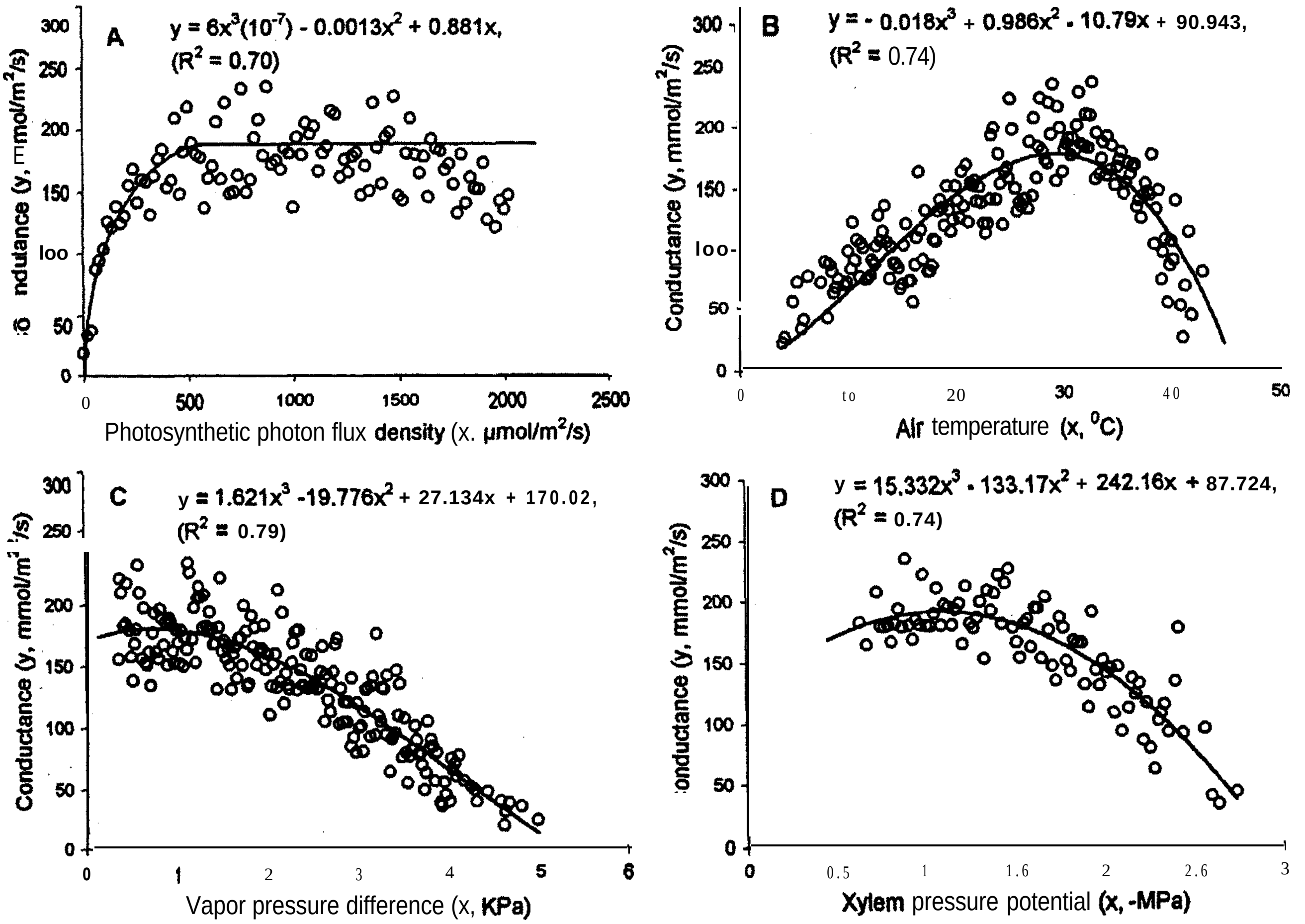

Figure 4—Boundary-line response of stomatal conductance to (A) photosynthetic photon flux density, (B) air temperature, @vapor pressure difference, and (D) daytine xylem pressure potential. Data represent the upper 5 percent of dependent variable responses to the entire range over the independent variable values.

evaporative demand. As VPD increased, E increased correspondingly. However, E began to decline with VPDs exceeding 3.5 KPa, because gw decreased nearly 50 percent and stomata became partially closed at that time. Our boundary-line responses of E and gw agreed with the results reported by Cregg and others (1990) who examined the water relations of a lo-year-old loblolly pine plantation in southeastern Oklahoma.

Microclimate variables in forest stands control the growth of trees through their effects on tree physiological processes (Teskey and others 1987). These variables will be influenced by global climate change. One of the predicted climate change scenarios is global warming (Hansen and others 1988). Current general circulation models of the global climate have projected that seasonal Ta and VPD will rise 2-4 °C and 0.2 KPa, respectively, in the southern United States (Cooter 1998). Predictions suggest that there will be more days with Ta above 33 °C and VPD above 3.5 KPa in the summer (Cooter 1998). Our boundary-line response equations indicate that increases in Ta and VPD may impact the gas exchange performance of southern pine forests. If current irradiance and precipitation remain unchanged, and if foliage of southern pine trees cannot acclimate to elevated Ta and VPD, the maximum gw, Pn and E will be decreased significantly with global climate change. Extremely high Ta (higher than 40 °C) and VPD (greater than 3.5 KPa) during the summer will cause leaf stomatal closure. Consequently, Pn and E will be reduced substantially.

Annual precipitation is predicted to decrease and the frequency and severity of drought are predicted to increase with global warming (Hansen and others 1988). During a drought, soil moisture supply and water potential of trees decrease, causing water stress that reduces leaf expansion, root growth, and aboveground productivity (Albaugh and others 1998, Linder and others 1987, Sword and others 1998, Teskey and others 1987). Boundary-line relationships between XPP and Pn and gw (R^2 = 0.88 and 0.74, respectively) found in our study predict that drought will restrict foliage gas exchange considerably by the effect of low XPPs (lower than -2.3 MPa) on gw and Pn. Other studies have suggested that low XPPs will impact plant carbon fixation directly by reducing the maximum catalytic capacity of Rubisco (Wong and others 1985). High VPDs associated with a drought may also limit gw, Pn. and E significantly.

In summary, boundary-line analysis is an effective technique for examining physiological responses of large trees under field conditions. When PPFD, Ta, and VPD were optimum, loblolly pine achieved a maximum Pn of 6.0 $\mu mol\ m^{-2}\ s^{-1}$, gw

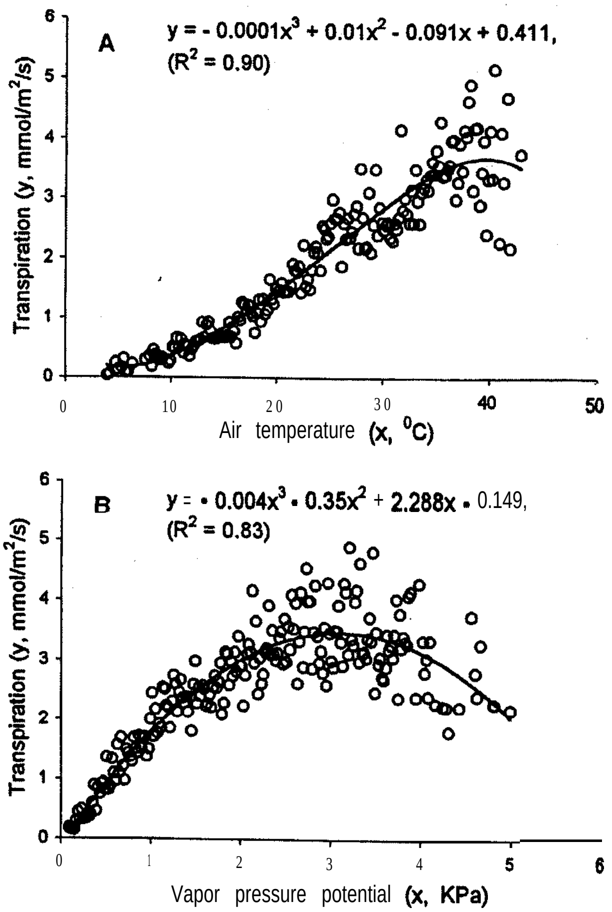

Figure 5—Boundary-line response of transpiration to (A) air temperature and (B) vapor pressure difference. Data represent the upper 5 percent of dependent variable responses to the entire range over the independent variable values.

of 180 mmol m^{-2} s^{-1}, and E of 3.5 mmol m^{-2} s^{-1}. Threshold values of the independent environmental variables and corresponding physiological responses may be useful in modeling the negative impacts of global climate change on carbon gain and tree growth in southern pine ecosystems. Our boundary-line responses demonstrate that elevated Ta and VPD will lead to significant decreases in photosynthetic production, stomatal activity, and water relations of trees. Further research must be conducted to determine the ameliorative role of cultural treatments in managing the detrimental effects of increasing Ta and VPD, and decreasing XPP on the responsive physiology, tree growth, and stand productivity of southern pine forests.

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