LEAF CONDUCTANCE TO WATER VAPOR TRANSFER FROM LEAVES OF A BLACK WALNUT (*Juglans nigra* L.) SAPLING [1/]

Phillip M. Dougherty

University of Missouri
Columbia, Missouri

Thomas M. Hinckley

University of Missouri
Columbia, Missouri

and

James P. Lassoie

Cornell University
Ithaca, New York

- - - - - - - - - - - - - - - - ABSTRACT - - - - - - - - - - - - - - - - -

Data on leaf conductance and xylem pressure potential were collected from a field grown black walnut (*Juglans nigra* L.) sapling in two successive years. Moderate to severe droughts were observed during both summers. As soil moisture decreased, maximum leaf conductance, maximum xylem pressure potential, and the range observed in both conductance and xylem pressure potential decreased. Complete recovery in both were noted following heavy August rains and recovery in soil moisture. Under light sufficient conditions, leaf conductance in this sapling depended more upon an interaction between pre-sunrise xylem pressure potential and xylem pressure potential than on xylem pressure potential alone in contrast to what has been found in a wide variety of species.

- -

INTRODUCTION

The extent to which plants regulate foliar water loss appears to depend on the particular adaptive strategy utilized to compete for limited resources within a given environment. It is unlikely that any single adaptation, such as a modification in leaf or stomata morphology, would be sufficient to assure competitive success in an environment where water is limiting. In most environments, adaptations probably consist of a unique combination of numerous growth and development processes

[1/] Contribution of Missouri Agricultural Experiment Station. Journal Series Number 7575.

which lead to an integrated biological system where an observed physiological response is a function of a particular set of conditions rather than a single variable. Information about such systems could be acquired by simultaneously monitoring all plant processes and existing environmental conditions. However, because of the apparent complexity involved, this approach is impractical if not impossible. A more realistic approach is to measure only those variables which seem to control a particular process. The second approach was taken in this study in order to describe the interaction between soil moisture, xylem pressure potential, and leaf conductance to water vapor in a black walnut (*Juglans nigra* L.) sapling.

METHODS AND MATERIALS

This study was conducted at the University of Missouri's Forestry Research Site located on the Ashland Wildlife Area in Central Missouri. The area is characterized by a warm, humid continental climate with annual temperatures averaging 13°C while total precipitation averages 961 mm.

The soil on this study site is a Weldon silt loam and has been fully described by Metcalf (1975). It is 122 cm deep and consists of an A_1 and A_2 horizon composed of 10.3% and 11.0% sand, and 67.9% and 62.6% silt, respectively. The B_1 horizon (24-34 cm) is composed of 10.1% sand and 55% silt. The B_{21} horizon contains 52.5% clay and extends from 35 to 53 cm. Horizons below this dense clay horizon have decreasing clay contents. These clay horizons undergo seasonal wetting and drying cycles and thus may contribute to the plant water supply.

The study tree was a 5.0 m tall black walnut sapling located on an old field site surrounded by a 57-year-old second growth oak-hickory forest. Fully expanded sun leaves located in the upper half of the tree crown were sampled during this study.

The set of measurements selected to characterize plant responses and environmental conditions included: xylem pressure potential, leaf conductance, leaf temperature, wet and dry bulb temperatures, photosynthetically active radiation, total incoming solar radiation and soil moisture content. All of the above parameters, except soil moisture, were measured at hourly intervals from 0500 to 1800 hours for 5 days between June 6 and July 22, 1974, and for 9 days between June 13 and August 27, 1975.

At each sample interval, leaf resistance to water vapor loss (R_1) was estimated on four leaflets using a Lambda diffusion porometer described by Kanemasu *et al.* (1969). Operating procedures were those of Morrow and Slatyer (1971). Measurements were taken only on lower surfaces since black walnut leaves are hypostomatous. These resistance values were then converted to conductance ($1/R_1$) and averaged. Xylem pressure potential (P) was estimated for two rachii each hour using the

pressure chamber technique (Ritchie and Hinckley 1975). Since this technique necessitates destructive foliar sampling which would affect the root/shoot ratio, some progressive modification in the sapling's water status may have occurred during the study.

Leaf temperature was measured on the lower surface of each leaf sampled using a fine wire copper-constantan thermocouple (Gale et al. 1970). Wet and dry bulb air temperatures were measured using aspirated diodes located 3 m from the base of the study sapling at a height of 1.5 m above the ground. These values were used to calculate vapor pressure deficits.

Photosynthetically active radiation (PAR: 400-700 nm was measured with a Lambda quantum sensor parallel to the upper sample leaf surfaces (Biggs et al. 1971). Total incoming radiation was monitored above the forest canopy using a Kipp and Zonen solarimeter located on top of a 20 m tower.

Soil moisture content was estimated by the neutron probe method using a Nuclear Chicago P19 depth probe and model 2800 A scaler. Water content was estimated to a depth of 120 cm in a single access tube located 0.5 m from the base of the study tree. Measurements were taken every 15 cm and then converted to percent soil moisture on a volumetric basis.

RESULTS AND DISCUSSION

Diurnal Leaf Conductance Patterns

Diurnal patterns of leaf conductance (C) were recorded throughout prolonged drought periods during the summers of 1974 and 1975. The recovery of C following soil moisture recharge was also examined in 1975. Normally, soil moisture and plant water content are closely related since the amount of water in the soil represents the absolute maximum available for plant root uptake (Ritchie and Hinckley 1975). This dependency was illustrated by determining the relationship between the 0500 hour P value (base P or BP, bars) and the soil moisture content (SMC, %) in the top 30 cm of soil under both dehydrating and rehydrating conditions during the two summers. The best fit equation obtained for the relationship between BP and SMC using linear regression techniques was $\ln BP = 8.465 - 2.520 \ln SMC$ ($r^2 = 0.89$, $n = 15$). This close relationship of BP and SMC should be kept in mind during the following discussion of observed changes in C and P at various soil moisture contents.

Diurnal response patterns of leaf conductance on clear warm days before, during, and after the 1975 summer drought are shown (Figure 1). An impaired photoactive stomatal response and a reduction in the maximum observed C were noted under low versus high SMC conditions (0.035 versus 0.17 cm/s). On August 6, a day marked by very low soil moisture content

and BP, apparent stomatal closure was initiated by 0700 hours. The inability to recover sufficient turgor to reopen stomata resulted in extremely low conductances for the remainder of the day even though xylem pressure potentials were slightly higher than on days of higher SMC (Figure 1: August 6 versus June 21).

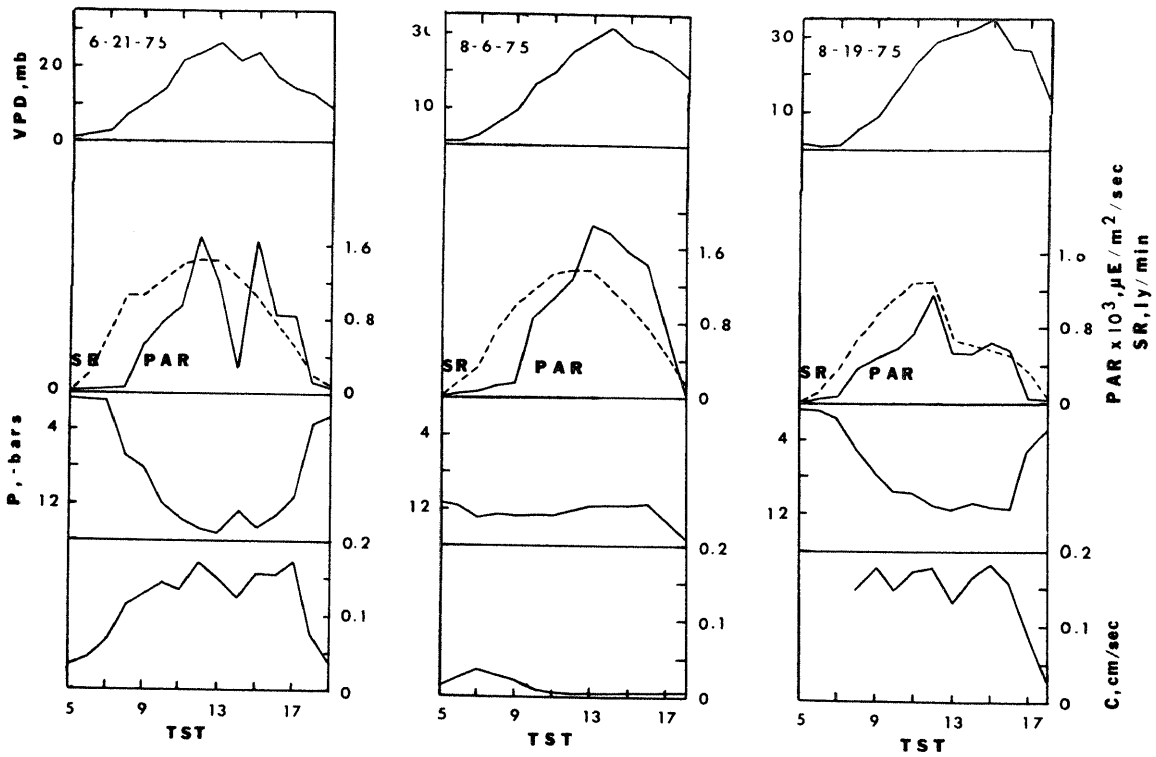


Figure 1. Diurnal trends of leaf conductance (C) and xylem pressure potential (P) for a field-grown black walnut sapling, photosynthetically active radiation (PAR), total incoming solar radiation (SR), and vapor pressure deficit (VPD) are presented for three days during the summer of 1975 (June 21, August 6 and 19). Soil moisture content (% by volume) was 29.7, 6.8 and 21.6% on these days, respectively. TST = true solar time.

The response pattern of C following recovery from a prolonged drought appeared similar to that observed under high soil moisture conditions which occurred earlier in the growing season (Figure 1: June 21 versus August 19). This suggested that the effects mediated by low soil moisture supply on leaf conductance were not permanent. Diurnal patterns in P were also considerably different under high versus low soil water

conditions (Figure 1: June 21 and August 6). The most salient differences between the moist and dry days were (1) the -11.2 bar difference in BP, (2) the apparent difference in photoactive stomatal opening, (3) the difference in the rates of change of P with time, (4) differences in midday values of P and (5) the difference in the extent of recovery of P at night.

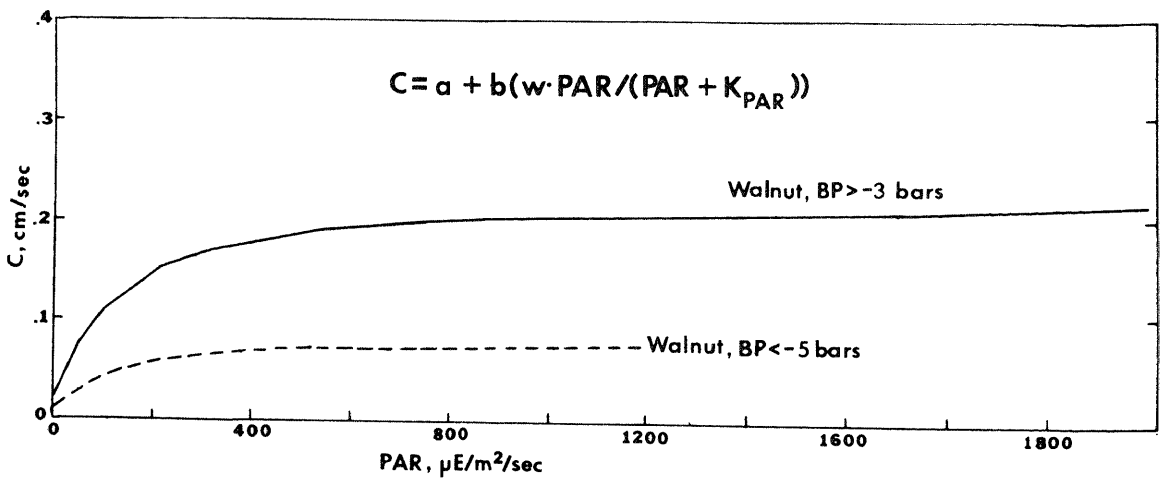
Classically, the reaction of plant processes such as photosynthesis and growth to plant water deficits depends upon both the absolute level and the duration of that deficit (Hsiao 1973). However, the data from black walnut suggested that the daily minimum deficit (i.e., maximum P or BP) was as critical in determining plant responses as the maximum deficit. There were approximately 450 bar-hours noted on the low soil moisture day (calculated by integrating above the P curve, with P from 1900 until 0500 hours assumed equal to BP) as compared to 260 bar-hours on the high soil moisture day. In addition, P never increased above -11.5 bars on August 6 while it was between -2.3 and -0.3 bars for at least eleven hours on June 21 (Figure 1: June 21 and August 6). Leaf conductance also averaged 0.148 cm/s on June 21 and 0.005 cm/s on August 6 during a period when photosynthetically active radiation exceeded 500 $\mu E/m^2/s$. Therefore, hydroactive stomatal closure would have restricted carbon dioxide uptake and limited photosynthesis on August 6 more than on either June 21 or August 19.

Relationship of Leaf Conductance to Photosynthetically Active Radiation at Various Soil Moisture Contents

The lack of complete photoactive opening of stomata on days of low (Figure 1: August 6) versus high soil moisture (Figure 1: June 21 and August 19) suggested a need for further analysis of the C-PAR relationship. Data collected during both 1974 and 1975 were segregated on the basis of BP and were limited to early morning observations, a period when vapor pressure deficit is at a minimum and P is near a maximum. Two separate ranges of BP were delineated: (1) when BP was greater than -3.0 bars and (2) when BP was less than -5.0 bars. An equation, using the method of least squares and expressing C in the form of a Michaelis-Menton equation, was developed for each data set within the above two BP ranges (Figure 2).

Maximum leaf conductance was 2.2 times greater on days when BP was $\geq$ -3.0 bars than on days when BP was $\leq$ -5.0 bars. A comparison of the average rate of change of leaf conductance as PAR ranged from 19 to 250 $\mu E/m^2/s$, indicated a 2.6 to 2.9 times greater stomatal response per unit change in PAR when soil moisture was high than when soil moisture was low. Ninety percent of maximum C was observed (0.07 cm/s) when PAR was 400 $\mu E/m^2/s$ on days when SMC was low. In contrast, on moist days, an irradiance of about 1200 $\mu E/m^2/s$ was required to produce 90% of the maximum conductance observed (0.21 cm/s). This suggested a possible extended response of the stomata to PAR under conditions of high soil moisture. In addition, stomata might have been responding to increasing leaf

temperatures (Jarvis 1976). The reduced stomatal response to light as BP decreased might also be a result of decreased photosynthesis and leaf energy supplies. For example, guard cell membrane integrity and the maintenance of potassium influx and proton efflux pumps depends upon energy sources derived from photophosphorylation (Hsiao 1973). A guard cell osmotic adjustment as noted by Turner (1974) in field-grown crop species may have also occurred.



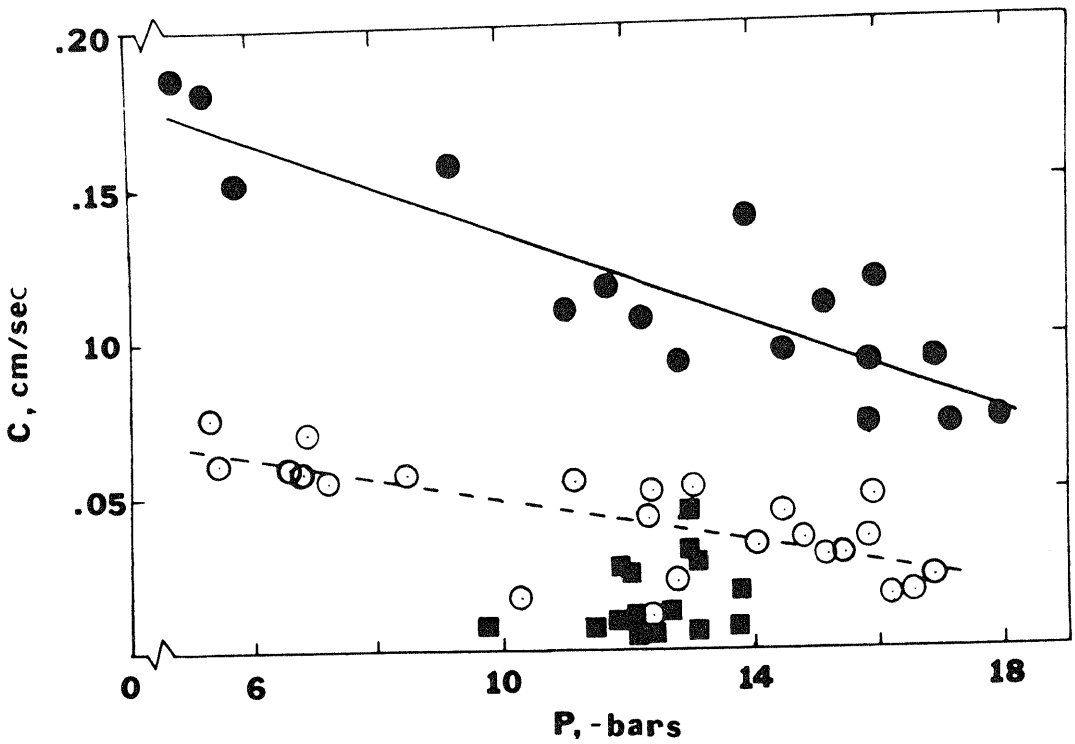
BP (Bars)	W (cm/sec)	K_{PAR} (μE/M²/sec)	DF	A	B	R^2	F
>-3	0.230	120	65	.0186	.901	.85	350.3
<-5	0.075	110	16	.0093	.989	.86	95.3

Figure 2. The relationship between black walnut leaf conductance (C) and photosynthetically active radiation (PAR) within two ranges of base xylem pressure potential (BP). The formula and statistics for each line are also shown and are: W = maximum conductance, K_{PAR} = PAR at which conductance is 50% of maximum, DF = degrees of freedom, A = intercept, B = slope, R^2 = coefficient of determination, F = F-test statistic.

Relationship of Leaf Conductance to Decreasing Xylem Pressure Potential

Ultimately changes in leaf conductance are related to changes in guard cell turgor pressure (Turner 1974, Jarvis 1976). These changes in turgor may either be triggered by light (photoactive response) or by reduced epidermal and/or leaf water content (hydroactive response). Limiting observations to those made when PAR was greater than 600 $\mu E/m^2/s$ and when P was decreasing, created a data set in which photoactive stomatal responses were minimized and where P was influencing C more than the reverse.

A plot of conductivity versus P under the limiting conditions described above is shown for July 6 and 22, 1974 and for August 6, 1975 in figure 3. Base xylem pressure potentials were -1.2, -5.2 and -11.5 bars on these days, respectively. Unique relationships between C and P were obtained depending on the particular BP value. On July 6 when BP was high, C decreased linearly in response to decreasing P. Conductances on this day ranged from a high of 0.185 cm/s when P was less than -6 bars to a low 0.073 cm/s when P was -18 bars. However, on July 22 when BP was -5.2 bars, C ranged from 0.076 cm/s when P was less than -6 bars to 0.015 cm/s when P was -17 bars. On August 6 when BP was low, only a narrow range in P was observed (-9.7 to -13.8 bars) and C varied only between 0.045 and 0.003 cm/s. As BP decreased, the range of observed leaf conductances decreased and frequently minimum or midday P actually increased.



	Day	BP, -bars	R^2
●	7-6-74	1.2	.79
○	7-22-74	5.2	.56
■	8-6-75	11.5	.07

Figure 3. The relationship of leaf conductance (C) to decreasing xylem pressure potential (P) for a black walnut sapling on three days (July 6 and 22, 1974 and August 6, 1975) when base xylem pressure potentials were -1.2, -5.2 and -11.5 bars respectively and photosynthetically active radiation was greater than 600 $\mu E/m^2/s$.

Data from these three days suggested a strong interaction between BP and P as they affected leaf conductances. This was further confirmed when all P and C measurements from all days (n=138) were pooled and analyzed using a simple regression technique and the aforementioned criteria. The interaction between BP (an estimate of soil moisture content) and P explained 58% of the variation in C while P alone accounted for only 13% of the observed variation. A significant relationship between BP and maximum daily C has been observed in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by Running (1976). In contrast to these findings, others have reported a highly significant relationship between C and P (Tobiessen and Kana 1974, Hinckley *et al.* 1975).

In summarizing the relationship between leaf conductance and decreasing P at high light levels, it appeared that: (1) no single unique functional relationship existed between C and P, (2) a linear relationship was found between C and P for each day and hence for each BP level, (3) as BP decreased both the variation in observed P and C decreased, and (4) as BP decreased the maximum observed leaf conductance decreased.

The poor relationship (R^2 = .13) observed herein between C and P might be caused by (1) the inability of petiole P to reflect guard cell water status (Paul Jarvis, Univ. Edinburgh, personal communication), (2) the possibility of guard cell osmotic adjustment, and/or (3) a decrease in xylem osmotic potential (John Boyer, Univ. of Illinois, personal communication). A decrease in xylem osmotic potential would cause P to overestimate leaf water potential (Ritchie and Hinckley 1975). If guard cell osmotic adjustment did occur then it was in the direction opposite to that noted by Turner (1974).

CONCLUSIONS

Leaf conductance to water vapor diffusion from leaves of this black walnut sapling appeared to be extremely sensitive to changes in soil moisture content as estimated by changes in BP. With decreases in BP, relationships between photoactive opening of stomata, and between P and C were altered. The apparent stomatal sensitivity of this black walnut sapling to decreasing BP would suggest that photosynthesis would be severely curtailed during periods of moderate water deficit as compared to other trees such as white oak (*Quercus alba* L.) in which open stomata have been observed at P values as low as -23 bars (Hinckley *et al.*, 1975). As a possible corollary, black walnut would probably use less soil moisture than white oak even under moderate drought conditions.

LITERATURE CITED

Biggs, W. M., A. R. Edison, J. D. Eastin, K. W. Brown, J. W. Maranville and M. D. Clegg. 1971. Photosynthesis light sensor and meter. Ecology 52:125-131.

Gale, J., A. Manes, and Alexandra Poljakoff-Mayber. 1970. A rapidly equilibrating thermocouple contact thermometer for measurement of leaf surface temperatures. Ecology 51:521-525.

Hinckley, T. M., M. O. Schroeder, J. E. Roberts, and D. N. Bruckerhoff. 1975. Effects of several environmental variables and xylem pressure potential on leaf surface resistance in white oak. For. Sci. 22:201-211.

Hsiao, Theodore C. 1973. Plant responses to water stress. Ann. Rev. of Plant Physiol. 24:519-570.

Jarvis, P. G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Phil. Trans. R. Soc. Lond. B. 273:593-610.

Kanemasu, E. T., G. W. Thurtell, and C. B. Tanner. 1969. Design, calibration and field use of a stomatal diffusion porometer. Plant Physiol. 44:881-885.

Metcalf, C. L. 1975. Diurnal and seasonal patterns of water stress in black oak and eastern redcedar. Unpublished M.S. Thesis, Univ. of Missouri, Columbia. 198 p.

Morrow, Patrice A. and R. O. Slatyer. 1971. Leaf resistance measurements with diffusion porometers: precautions in calibration and use. Agric. Metero. 8:223-233.

Ritchie, Gary A. and Thomas M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. Adv. in Ecol. Res. 9: 165-254.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. of Forest Res. 6:104-112.

Tobiessen, Peter and Tobb M. Kana. 1974. Drought-stress avoidance in three pioneer tree species. Ecology 55:667-670.

Turner, Neil C. 1974. Stomatal behavior and water status of maize, sorghum, and tobacco under field conditions. Plant Physiol. 53: 360-365.

ACKNOWLEDGMENTS

Thanks to Dave DeYoe, Dan Thompson and Wally Wilhelm for technical assistance.

- -

ABOUT THE AUTHORS

Phillip M. Dougherty received a B.S. degree in wildlife science from Texas A&M University in 1968 and a M.S. degree in forestry from the Texas A&M University School of Forestry in 1973. He is currently a candidate for a Ph.D. degree in eco-physiology from the School of Forestry, Fisheries and Wildlife at the University of Missouri-Columbia.

Thomas M. Hinckley was awarded his B.A. in biology in 1966 from Carleton College, Northfield, Minnesota and his Ph.D. in forest ecophysiology in 1971 from the University of Washington, Seattle. Since July 1971, he has been on the faculty of the School of Forestry, Fisheries and Wildlife at the University of Missouri-Columbia.

James P. Lassoie received his B.S. and Ph.D. in forestry in 1968 and 1975, respectively, from the University of Washington, Seattle. He has been a Research Technician at the Weyerhaeuser Forestry Research Center in Centralia, Washington and a postdoctoral fellow at the University of Missouri-Columbia. Currently, he is on the faculty of the Department of Natural Resources at Cornell University, Ithaca, New York.

For reprints write: Phillip M. Dougherty
School of Forestry, Fisheries and Wildlife
1-31 Agriculture Building
University of Missouri
Columbia, Missouri 65201