THE EFFECTS OF AN EXTREME DROUGHT ON TREE WATER STATUS AND NET ASSIMILATION RATES OF A TRANSPLANTED NORTHERN RED OAK UNDER GREENHOUSE CONDITIONS [1/]

James P. Lassoie

University of Missouri
Columbia, Missouri

and

Jim L. Chambers

University of Missouri
Columbia, Missouri

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Tree water status and net assimilation rates (NAR) were measured in a transplanted northern red oak (Quercus rubra L.) sapling under greenhouse conditions on sunny days before, during and immediately following an induced drought. Water status was characterized by measurements of foliar transpiration rate (TR), leaf conductance, branch diameter, and xylem pressure potential and these factors were interpreted in relation to selected environmental factors. During the peak of the drought, daily average NAR and TR were reduced 98 and 70%, respectively, compared to predrought averages. Hydraulic recovery following irrigation commenced immediately but physiological recovery was incomplete. The control of gas exchange throughout the study was primarily due to hydroactive stomatal closure.

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INTRODUCTION

Conditions conducive to the uptake of carbon dioxide, necessary in the photosynthetic process, may also favor the rapid loss of water through transpiration. Associated with the daily loss of water is the development of internal plant water deficits which can greatly influence stomatal opening, photosynthesis, respiration, protein synthesis and translocation, all of which ultimately affect growth and survival (Hsiao 1973). Therefore, the availability of water often determines the success or failure of many plants and affects the composition of most vegetative communities (Daubenmire 1968).

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Within the oak-hickory forest region, climax forest types are quite variable and are site specific depending primarily upon the availability of soil water (Bourdeau 1954). Northern red oak (Quercus rubra L.) is one of the most widely distributed and commercially important oaks throughout much of this region (Harlow and Harrar 1958, Core 1971). It is generally considered intermediate in shade tolerance and is typically found sharing dominance in climax stands on mesic sites (Fralish, Chambers, and Anderson 1971). Though a mesophytic species, northern red oak is usually deep rooted which is regarded as a drought resistant characteristic (Longman and Coutts 1974).

Severe and persistent summer droughts in mid-Missouri, though abnormal, occur periodically (e.g., 1972, 1975). Therefore, northern red oak must be capable of surviving periods of low soil moisture in association with high atmospheric demands. This study examines the effect of an extreme, artificially induced drought on the diurnal patterns of net assimilation and tree water status of a transplanted northern red oak sapling under greenhouse conditions. The short-term effects of such a drought on the relationships between selected physiological processes (net assimilation, transpiration, leaf conductance) and certain environmental factors (light, temperature, soil moisture) are also discussed.

METHODS

This study was conducted during May, 1975, in a greenhouse located at the University of Missouri, Columbia. The study tree was a transplanted northern red oak sapling approximately 2 m tall with stem diameter at breast height of 1.5 cm. The sapling was originally obtained from the School of Forestry, Fisheries and Wildlife research site at the Ashland Wildlife Area. In August, 1974, it was trenched following the summer drought period in order to stimulate and contain the growth of new roots. After a cold treatment in January, the tree and its large, intact soil mass (approximately 1.0 m in diameter and 0.5 m deep) were removed and transported to the greenhouse, and a 16-hour photoperiod was used to break bud dormancy. The sapling remained well watered until a major drought was induced by withholding water from May 4 to May 22.

Carbon dioxide differentials (i.e., ambient minus cuvette carbon dioxide concentrations) were assessed for three leaves (1.68 dm^2 total area) enclosed in a thermoelectrically cooled cuvette (Hinckley et al. 1974) using a Beckman 315B infrared gas analyzer. Transpiration rates were similarily determined using an EGG Cambridge 880 Dew Point Hygrometer and a switching system which enabled the measurement of ambient and cuvette dew points (Mooney et al. 1971). Leaf conductance (the reciprocal of leaf resistance) was calculated by dividing the vapor pressure gradient between the leaf and the air into the transpiration rate (Holmgren, Jarvis and Jarvis 1965). Inside the cuvette, leaf temperature was measured by cementing a fine-wire copper-contantan thermocouple to the underside of a leaf, and photosynthetically active radiation (400 to 700 nm) was measured using a Lambda quantum sensor (Biggs

et al. 1971). All factors were continuously recorded on a 24-channel Esterline Angus stripchart recorder.

Tree water status was assessed outside the cuvette by periodically measuring leaf conductance, xylem pressure potential, and fluctuations in branch diameter. Leaf conductances for water vapor loss were estimated using a diffusion porometer (Kanamasu, Thurtell and Tanner 1969) and procedural methods as described by Morrow and Slatyer (1971). Measurements of conductance were taken only on the lower surfaces since northern red oak leaves are hypostomatous (Phelps, Chambers and Hinckley 1976). Two measurements were taken at least every 30 minutes between about 0500 hours (i.e., predawn) and 1900 hours (i.e., dark) on various days before, at the peak, and after the drought period. During daylight periods, one measurement was made on a leaf in the direct sun while the other was on a leaf in the shade. In conjunction with each of these measurements, photosynthetically active radiation incident to the upper leaf surfaces was measured (Biggs et al. 1971), and lower surface leaf temperatures were assessed (Gale, Manes, and Poljakoff-Mayber 1970). Petiole xylem pressure potentials were estimated before sunrise and near midday on each study day for two leaves (one sun and one shade when applicable) using the pressure chamber technique (Ritchie and Hinckley 1975). Predawn measurements were considered indicative of soil moisture tensions while the midday values were considered primarily a function of atmospheric evaporative demand (Hinckley and Ritchie 1973). In addition, diurnal variation in diameter of a major branch was continuously monitored using a linear variable differential transducer and recorded on the stripchart recorder (Hinckley et al. 1974).

RESULTS AND DISCUSSION

The Effect of Drought on the Diurnal Patterns of Net Assimilation and Transpiration

Diurnal fluctuations in net assimilation rate (NAR), transpiration rate (TR), photosynthetically active radiation (PAR_c), and leaf temperature (TL_c) in the cuvette are shown for clear days before (May 5), at the peak (May 22), and immediately after (May 23) the induced drought period (Fig 1). Diurnal trends in leaf conductance (C), changes in branch diameter (ΔD), sun and shade TL and PAR measured outside the cuvette are also illustrated for these days (Fig 2). Overhead obstructions in the greenhouse often caused the temporary shading of the cuvette resulting in abrupt changes in PAR_c and variable TL_c (Fig 1). Leaf energy balances within the cuvette were modified by the fluctuating radiation inputs, the activity of the thermoelectric cooling plate, and vigorous air circulation resulting in lower leaf temperatures compared to those measured outside the cuvette. The assessment of TR, and hence leaf conductivities in the cuvette (C_c), was often complicated by the presence of condensation on the cooling plate during the morning. Therefore, TR and C_c may be underestimated in the morning but overestimated later in the day as condensed water evaporated back into the cuvette air stream.

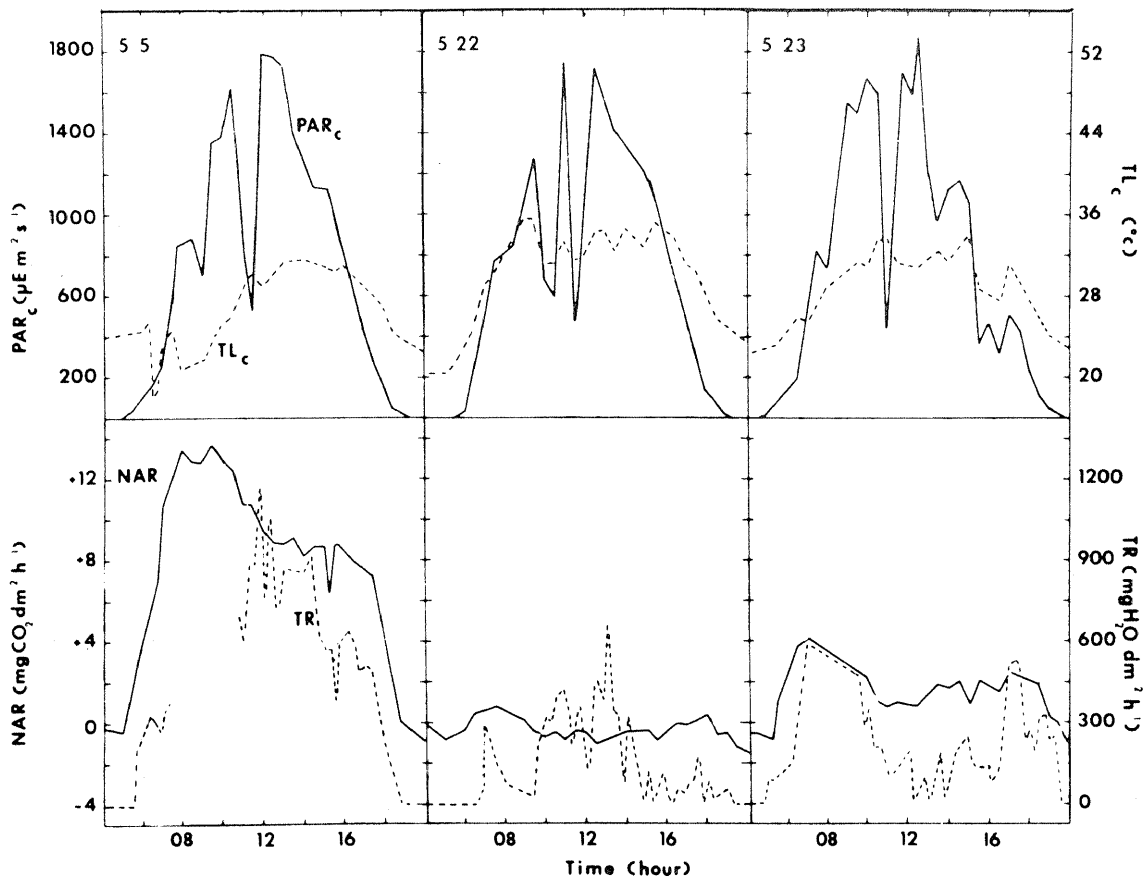

Figure 1. Diurnal fluctuations in photosynthetically active radiation (PAR_c) and leaf temperature (TL_c) inside the cuvette and net assimilation rate (NAR) and transpiration rate (TR) of a northern red oak sapling before (5-5), at the peak of (5-22) and after (5-23) an induced drought period. Missing TR data signifies a period when heavy condensation formed within the cuvette.

Predrought: Predawn (i.e., base) xylem pressure potentials (BP) during the predrought period were high (e.g., BP = -2.0 bars on May 5) indicating the nearly complete hydration of the sapling. During this period, stomata responded rapidly to changes in PAR_c (i.e., photoactively) especially in the morning and late afternoon. Rapid changes in stomatal aperture and hence C resulted in changes in NAR and TR (Fig 1 and 2). However, even under these well hydrated conditions, hydroactive stomatal closure during the day resulted in a marked midday depression in C (Fig 2). In response to this closure a gradual drop in NAR occurred after 0930 hours even though PAR_c was relatively high (Fig 1). This observed hydroactive stomatal closure was associated with a xylem pressure potential (P) of -13.6 bars and leaf temperatures (TL) above 35°C. Chambers

(unpublished data) has similarly observed hydroactive stomatal closure in saplings under comparable environmental conditions in the field when P approached about -14 bars. Such closure probably illustrates the loss of stomatal guard cell turgor via "peristomatal transpiration" (Hall and Kaufmann 1975). Under conditions of lower TL and lower vapor pressure gradients, P typically approached -16 to -18 bars before hydroactive stomatal closure was initiated in northern red oak saplings (Aslin 1975; Phelps et al. 1977).

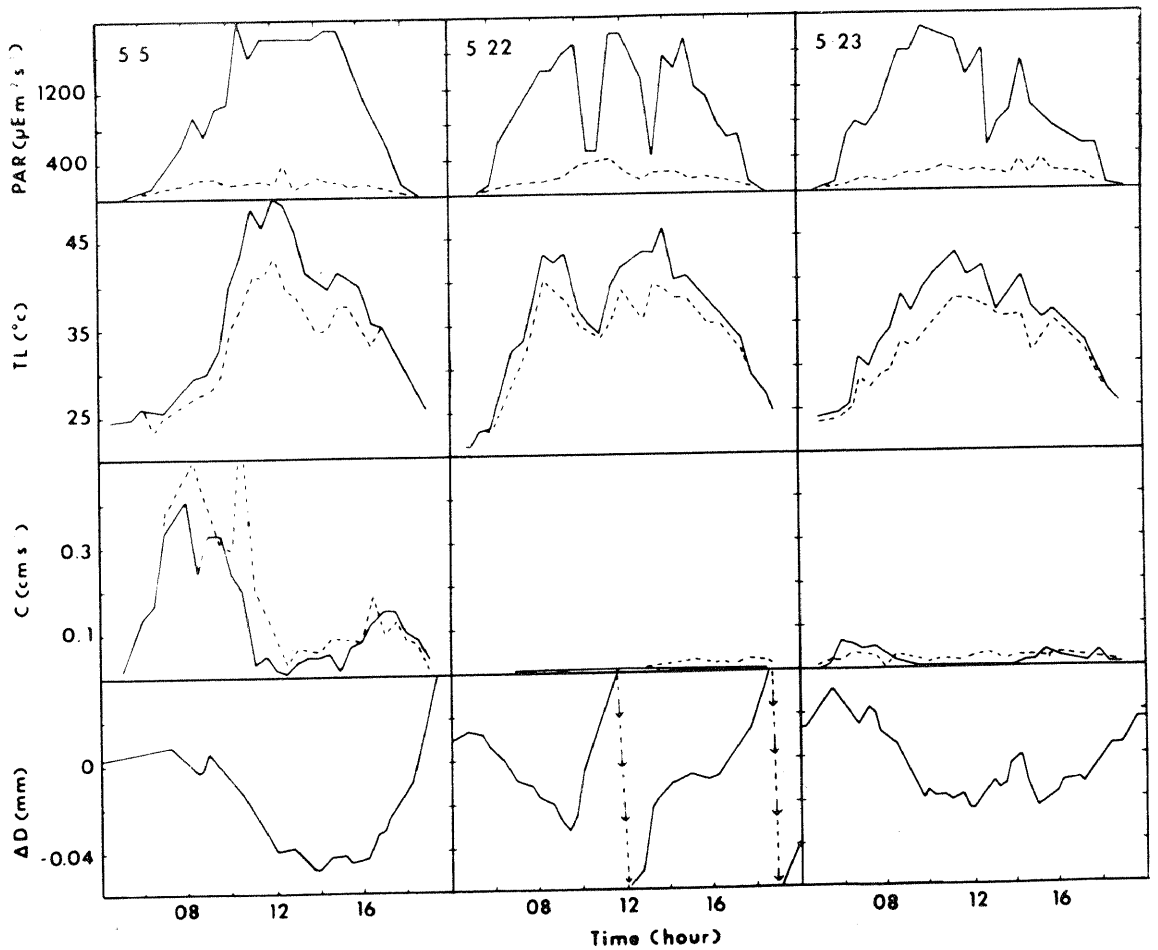

Figure 2. Diurnal fluctuations of photosynthetically active radiation (PAR), leaf temperature (TL) and leaf conductance (C) for foliage outside the cuvette currently in the sun(——) or shade (----) and change in branch diameter (ΔD) for a northern red oak sapling before (5-5), at the peak of (5-22), and after (5-23) an induced drought period.

Hydroactive stomatal closure was not implied by TR measurements, possibly due to the aforementioned condensation problems rather than actual water loss (Fig 1). However, since cuvette-leaf energy balance was modified by the presence of the cuvette resulting in lower leaf temperatures than observed outside the cuvette, pronounced hydroactive stomatal closure within the cuvette may not have occurred. Outside the cuvette, higher conductivities in shaded leaves were generally associated with lower temperatures as compared to leaves measured in the direct sun, thus illustrating the effect of vapor pressure gradient on the stomatal mechanism (Fig 2). Furthermore, the lack of a significant secondary peak in NAR during the afternoon also suggested the absence of appreciable hydroactive stomatal closure within the cuvette (Fig 1).

Changes in branch diameter (ΔD) were the inverse of changes in TL and hence vapor pressure gradient (Fig 2). Similar ΔD in a white oak sapling (*Quercus alba* L.) have been shown to correlate well with changes in P when ΔD lagged P by two hours (Hinckley *et al*. 1974). Thus, during the period of the day (May 5) marked by hydroactive stomatal responses (i.e., about 0800 to 1500 hours), major fluctuations in branch diameter were also observed which suggested critical changes in internal water deficits (Fig 2).

Peak Drought: The peak drought period was characterized by dry soil conditions. Base xylem pressure potentials observed during this period were very low (*e.g.*, BP = -19.7 and -23.1 bars on May 21 and 22, respectively). Noticeable heat injury (i.e., necrotic spots) on some leaves exposed to direct sunlight was evident on May 22. Such damage was not observed on leaves in the cuvette due to the alteration of leaf energy budgets within the cuvette as discussed previously. The sapling was irrigated on May 22 at 0915 hours in order to prevent further injury. Xylem pressure potentials at that time had reached -33.2 bars.

Environmental trends and gas exchange rates were observed to be generally similar on May 21 and 22 (Table 1) suggesting that irrigation had a minimal effect on immediate physiological responses of the sapling. Thus, May 22 was used to characterize the peak drought period (Fig 1). However, certain differences were noted. A temporary cloudy period during the morning of May 21 caused the daily average PAR_c to be lower than on May 5 (Table 1). Leaf temperatures on May 21, however, were above 36°C most of the day (between 1100 and 1700 hours) and exceeded 48°C at 1300 hours. Associated with the high TL_c was a very low average NAR (Table 1) possibly due to enhanced respiration (Bauer 1972) and/or severe hydroactive stomatal closure. Heat stress near 48°C has been observed to completely eliminate positive NAR and produce foliar necrotic injuries in mountain maple (*Acer pseudoplatanus* L.) (Bauer 1972).

Table 1. Daytime (PAR_c >0) means and ranges of net assimilation rate (NAR, mg $CO_2/dm^2/hr$), leaf conductance outside (C, cm/s) the cuvette, photosynthetically active radiation inside (PAR_c, $\mu E/m^2/hr$) and outside (PAR), the cuvette and leaf temperature inside (TL_c, degrees C) and outside (TL) the cuvette for a northern red oak sapling during an induced drought cycle.

	PREDROUGHT			PEAK DROUGHT						POST DROUGHT		
	(May 5)			(May 21)			(May 22)			(May 23)		
Variable	Mean	Low	High	Mean	Low	High	Mean	Low	High	Mean	Low	High
NAR	7.50	-0.26	13.72	-0.67	-2.83	1.69	-0.18	-1.18	0.84	1.93	-0.80	4.09
C	0.145	0.015	0.500	---	---	---	0.007	0.001	0.036	0.024	0.002	0.067
PAR_c	637	12	1835	370	20	1627	712	20	1745	661	12	1875
PAR	437	4	2000	---	---	---	485	7	1800	456	4	2200
TL_c	26.5	18.0	32.0	31.4	18.0	49.6	30.5	20.3	36.0	28.8	22.7	34.3
TL	31.8	22.5	50.5	---	---	---	33.2	21.0	46.0	31.3	23.4	43.0

The most striking feature during the peak of the drought was the absence of a photoactive stomatal response resulting in low leaf conductivities throughout most of the daylight period (Fig 2). Similar results have been reported for field grown northern red oak saplings (Phelps et al. 1976) and a black walnut (Juglans nigra L.) sapling under drought conditions (Dougherty, Lassoie and Hinckley 1976). This closure, combined with probable increases in respiration rates, caused negative NAR (i.e., net respiration) during May 22 (Fig 1) and resulted in the reduction of NAR to about 2% of the predrought average (Table 1). Similar effects of severe drought have been reported elsewhere (Bauer 1972, Hari and Luukkanen 1973). Transpiration rates were also reduced about 70% from predrought levels, and significant water loss occurred only after irrigation (Fig 1). Gas exchange measurements implied slight stomatal recovery during the afternoon (Fig 1) while outside the cuvette noticeable increases in C occurred only in shaded leaves (Fig 2).

Irrigation of the sapling immediately reversed the progression of daily branch shrinkage which had been initiated near sunrise (Fig 2). Thus, the recovery in P seemed to commence quickly with the addition of water (Hinckley 1973) and within 2.5 hours following irrigation, P had recovered 14.5 bars to -18.7 bars. Except for a temporary plateau associated with slight stomatal opening during the afternoon, the recovery in branch size was continuous with the twig diameter increasing over 0.2 mm between 0930 and 2000 hours (Fig 2). This large and rapid increase was probably indicative of the rehydration of various branch tissues which had been progressively depleted of water during the drought period. Similar fluctuations in a large, field-grown white oak stem have been closely correlated with changes in BP (Hinckley and Bruckerhoff 1975). In this study, BP the day following irrigation indicated a recovery of over 20 bars compared to the morning of May 22.

Post Drought: Following irrigation (May 23, Fig 1 and 2), there seemed to be a residual drought effect on the photoactive response of the stomata which limited gas exchange rates even though internal water deficits had nearly recovered (BP = -2.7 bars). In spite of similar environmental conditions, average daily NAR was reduced by about 75% as compared to the predrought level (Table 1). Persistent stomatal closure following rehydration after a severe drought has also been reported elsewhere (Brix 1962, Hinckley 1973, Hsaio 1973). Photoactive stomatal responses in the cuvette seemed to be reestablished but a midday depression in both NAR and TR suggested an early and rather complete hydroactive closure as compared to the predrought period (Fig 1). Similar stomatal responses were noted outside the cuvette; however, the magnitude of early morning opening, midday closure, and late afternoon recovery of the stomata was less pronounced (Fig 2). Cummulative daily ΔD on May 5 and 23 were similar, suggesting the development of comparable internal water deficits during both mornings. Therefore, the marked hydroactive response noted on May 23 indicated an altered sensitivity of stomata to internal water deficits following recovery from a severe drought. Such altered sensitivity of stomata has also been observed in black locust

Robinia pseudoacacia L.) after irrigation (Hinckley 1973). The rehydration and increase in size of the branch during the afternoon progressed at a much slower rate compared to the predrought period even though environmental conditions were relatively similar (Fig 2, Table 1). Both the low average leaf conductance (Table 1) and the reduced rate of branch diameter recovery suggested water deficit aftereffects on the stomatal mechanism and possibly on the ability of the root system to absorb water. Decreases in the absorptive ability of roots following a severe drought have been reported by Brix (1962) and Boyer (1971).

The Effect of Drought on the Relationship Between Physiological Processes and Controlling Environmental Factors

The preceeding section illustrated the limiting effects of an extreme drought on diurnal gas exchange patterns. These limitations were closely related to apparent alterations in stomatal responses. In order to further understand these limitations, the changing relationships between either leaf conductance or net assimilation rate and certain environmental factors associated with the severe drought were investigated. Obviously, NAR and C are controlled by a complex combination of interrelated environmental factors (Hsiao 1973). Thus, when either is plotted as a function of any one independent variable, scatter diagrams will result. However, the upper limit of such diagrams indicate the response to a particular independent variable while values below this limit illustrate the influence of other controlling variables (Jarvis 1976). Therefore, such scatter diagrams can be used to interpret the combined physiological response of a plant to several environmental factors.

Under predrought conditions, NAR increased with increasing PAR_c levels and maximum rates (about 13.3 mg $CO_2/dm^2/hr$) occurred at light intensities of about 800 $\mu E/m^2/s$ (Fig 3A). Data collected, but not presented, at PAR_c levels above 800 $\mu E/m^2/s$ indicated that this was very near the light saturation point. This light saturation level seemed high compared to values reported for northern red oak by others (Kramer and Decker 1944, Aslin 1975). However, over 85% of the maximum observed NAR occurred near 400 $\mu E/m2/s$ which was more comparable to the findings of others and supported northern red oak's intermediate tolerance to shade (Longman and Coutts 1974). At saturating light intensities, reduced net assimilation rates reflected the influence of other limiting factors which caused hydroactive stomatal closure (Jarvis 1976).

At the peak of the drought period, light saturation of NAR was noted near 145 $\mu E/m^2/s$ and maximum rates were about 1.0 mg $CO_2/dm^2/hr$ which was considerably less than was observed earlier (Fig 3A). Such a reduction in both maximum NAR and the light level associated with this rate commonly occurs in response to high internal water deficits generated during drought periods (Hsiao 1973). The PAR_c compensation point (i.e., NAR = 0) was not affected by the development of high water deficits in contrast to observations for black locust (Hinckley 1973). Furthermore, the compensation point was relatively low (about 30 $\mu E/m^2/s$) indicating an intermediate shade tolerant species (Longman and Coutts 1974).

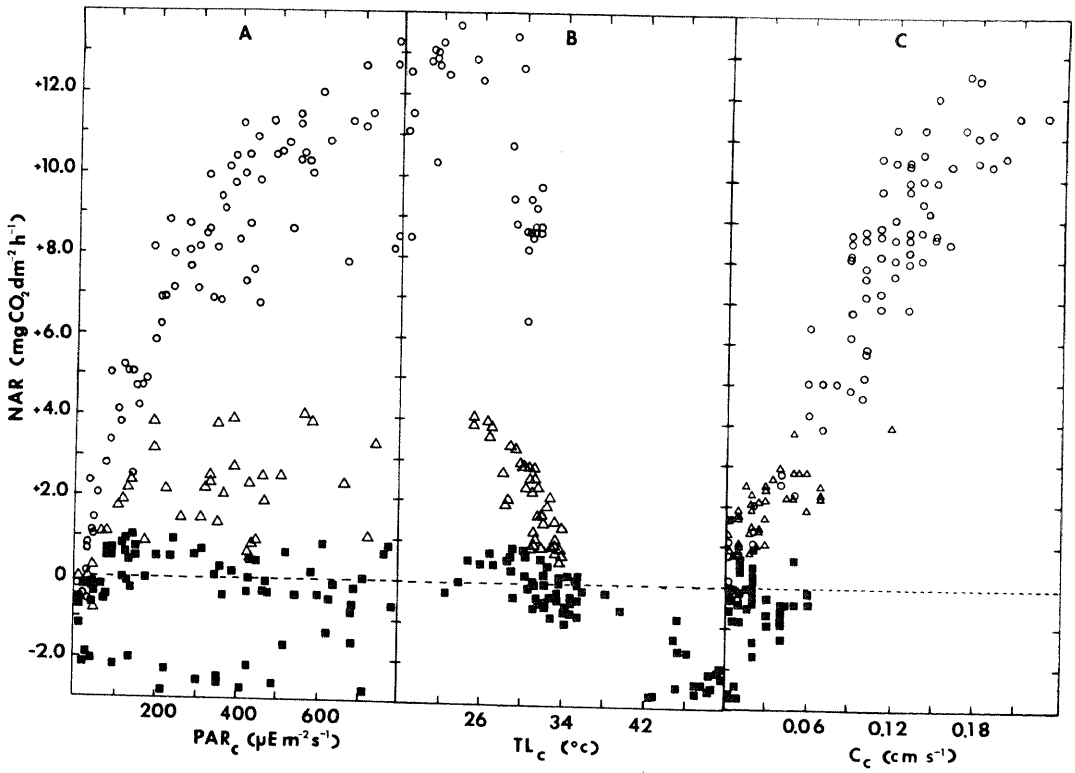

Figure 3. Scatter diagrams (Jarvis 1976) illustrating the relationship between net assimilation rate (NAR) of a northern red oak sapling and either (A) photosynthetically active radiation ($PAR_c > 0$), (B) leaf temperature (TL_c at $PAR_c > 90\%$ of light saturated level shown in A) or (C) leaf conductance (C_c, $PAR_c > 0$) within the cuvette for days before (May 2 and 5, ○) at the peak of (May 21 and 22, ■), and after (May 23, △) an induced period.

A portion of the light saturation curve for NAR (Fig 3A) would also be affected by the influence of PAR_c on the stomatal mechanism (Fig 4A) (Meidner and Willmer 1975). In field studies of northern red oak saplings, completely opened stomata (C = 0.15 to 0.50 cm/s) have been observed at PAR levels above 120 $\mu E/m^2/s$ (Aslin 1975). During the predrought period in this study, the stomatal response to increasing light was similar to that of saplings growing in the field (Fig 4A).

The primary effect of the water deficits on gas exchange rates during the peak of the drought period seemed directly attributable to hydroactive stomatal closure thereby masking the light response (Fig 4A).

During this period, maximum C (0.035 cm/s) was reached at about 100 $\mu E/m^2/s$ with higher light levels being associated with decreasing conductivities. Thus, daily average conductances were very low during the drought (Table 1), and carbon dioxide uptake was probably always limited by the stomatal mechanism.

Increasing leaf temperatures and probably increasing tree water deficits were associated with decreasing leaf conductivities (Fig 4B). Therefore, the relationship between NAR and TL_c (Fig 3B) was complicated by the interaction of temperature with various biochemical reactions (Hari and Luukkanen 1974) as well as with the development of internal deficits (Wuenscher and Kozlowski 1971). Maximum net assimilation rates appeared to occur at leaf temperatures between about 22 and 30°C which were comparable to the temperature optimum range noted under field conditions (Aslin 1975). Net assimilation rates at the same TL_c were less during and after the drought period than before, thus reflecting hydroactive stomatal closure and aftereffects of high internal water deficits on stomatal activity, respectively. During the drought, high net respiration rates were associated with leaf temperatures in excess of 42°C (Fig 3B) (Bauer 1972). Increases in vapor pressure gradients between the leaf and atmosphere, being related to increasing internal water deficits, also limited C (Fig 4C). However, direct interactions between vapor pressure gradients and guard cell hydration may have also been involved (Schulze et al. 1974, Hall and Kaufmann 1975). Calculated leaf conductances (C_c) were found to react similarly to changes in PAR_c, TL_c and vapor pressure gradients within the cuvette as noted for conductances measured outside the cuvette.

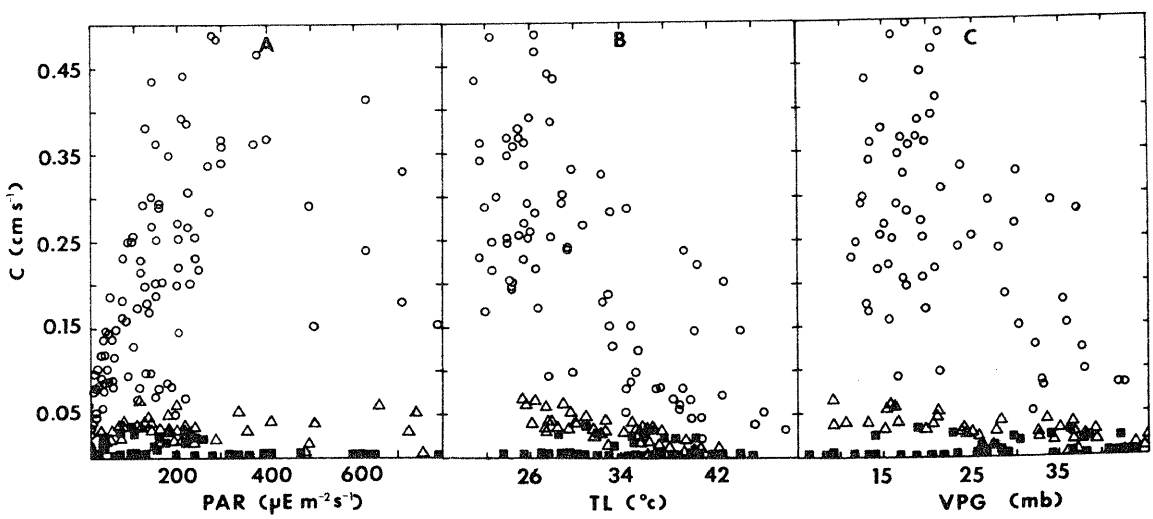

Figure 4. Scatter diagrams (Jarvis 1976) illustrating the relationships between leaf conductance (C) outside the cuvette and either (A) photosynthetically active radiation (PAR > 0), (B) leaf temperature (TL, at PAR > 80 $\mu E/m^2/s$) or (C) vapor pressure gradient (VPG, at PAR > 80 $\mu E/m^2/s$) on days before (May 2 and 5, ○), at the peak of (May 22, ■), and after (May 23, △) an induced drought period.

Following irrigation (May 23), partial recovery in the response between NAR and PAR_c was observed (Fig 3A). However, compared to the predrought period, this recovery was incomplete with maximum NAR (about 4.0 mg $CO_2/dm^2/hr$) occurring at about 400 $\mu E/m^2/s$. This limited recovery in carbon dioxide uptake seemed primarily due to the incomplete photoactive response of the stomata following irrigation (Fig 4A). Decreased photoactivity of stomata has commonly been noted during normal leaf senescence (Turner 1974) and following periods of high internal water deficit (Hinckley 1973), both of which may be related to increased abscisic acid levels (Meidner and Willmer 1975).

CONCLUSIONS

The physiological response of a transplanted northern red oak sapling to high internal water deficits developed during drought was similar to field grown individuals, and thus transplanting shock was assumed to be minimal. Considering the relatively large soil mass removed and the time involved this seemed understandable.

Northern red oak exhibited a low net assimilation compensation point for light and maintained relatively high rates of carbon dioxide fixation over a wide range of light intensities. Throughout the study, stomatal control of gas exchange rates was observed. Before the drought, stomata photoactively opened but then closed during midday due to reduced guard cell turgor associated with high leaf temperatures and steep vapor pressure gradients. Thus, hydroactive stomatal control of water loss could commonly occur even during hot periods marked by relatively high soil moisture levels. During periods of extreme drought, high internal water deficits promoted stomatal closure which completely suppressed the photoactive response resulting in net respiration rates and negligible water losses. Immediately following the drought, hydraulic recovery was complete. However, stomata seemed to exhibit an increased sensitivity to the daily development of internal water deficits resulting in marked hydroactive stomatal closure and reduced gas exchange rates during much of the day. Such major stomatal control of gas exchange and the residual drought effect might be an adaptive defense in an environment marked by fluctuating periods of soil water availability. Though ecologically significant, the exact mechanism involved in promoting persistent stomatal closure following hydraulic recovery from an extreme drought is not yet fully understood (Hsiao 1973). The northern red oak examined seemed capable of surviving an extreme drought period through its control of stomatal water loss. However, being a shade tolerant intermediate, high radiation during periods of reduced transpiration resulted in foliar heat injuries which would reduce the total tree assimilatory capacities (Bauer 1972).

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ABOUT THE AUTHORS

James P. Lassoie received a B.S.F. in forest sciences in 1968 and a Ph.D. in forest eco-physiology in 1975 from the College of Forest Resources, University of Washington, Seattle. From November 1974 to September 1976, he was a postdoctoral fellow in the School of Forestry, Fisheries and Wildlife, University of Missouri, Columbia, Missouri. He is currently an assistant professor in the Department of Natural Resources, New York State College of Agriculture and Life Sciences, Cornell University, Ithaca, New York.

Jim L. Chambers attended the University of Nebraska for two years in a pre-forestry curriculum, received a B.S. in forestry from Southern Illinois University in 1970, a M.S. in forest ecology from Southern Illinois University in 1972, and a Ph.D. in forest eco-physiology from the University of Missouri in 1976. He is currently an assistant professor of forest eco-physiology at the School of Forestry and Wildlife Management, Louisiana State University, Baton Rouge.

For reprints write: Dr. James P. Lassoie
Department of Natural Resources
Cornell University
Ithaca, New York 14850