CARBON BUDGETS OF *QUERCUS RUBRA* L. SEEDLINGS AT SELECTED STAGES OF GROWTH: INFLUENCE OF LIGHT[1/]

P. J. Hanson, J. G. Isebrands and R. E. Dickson[2/]

Abstract.--To determine potential growth responses of northern red oak (*Quercus rubra* L.) seedlings to various field light environments, carbon budgets of one-, two-, and three-flush seedlings were calculated. Leaf carbon dioxide exchange rate (CER), root respiration, and growth analysis provided inputs for the budgets. Daily CO_2 assimilation rates obtained from these budgets were lower than, but consistent with, actual red oak seedling growth rates. The budgets predicted that optimum daily CO_2 assimilation occurs under saturating irradiances in the absence of other stresses (e.g., drought), and that daily CO_2 assimilation is inadequate to match seedling respiration under the shade of a typical closed forest canopy. Calculated minimum incident photosynthetic photon flux densities required for sufficient CER to balance daily seedling respiration ranged from 30 to 150 µmol m^{-2} s^{-1}, depending on plant size.

Keywords: CO_2 exchange rate, respiration, roots

INTRODUCTION

The importance of light to the establishment and growth of oak forests has been studied since the early 1900's (Watt 1919; Korstain 1927; Shirley 1929ab). Watt (1919) stated that "for the oak the lightest possible shade of seed bearers is compatible with most successful natural regeneration." Korstain (1927) recommended the shelterwood silvicultural system for obtaining adequate oak regeneration. Since those early studies, numerous researchers have studied the influence of light on the growth of northern red oak seedlings (Kramer and Decker 1944; Musselman and Gatherum 1969; Phares 1971; Gottschalk 1985). However, despite the large amount of research completed, uncertainties remain about the quantity of light required to maintain "optimal" growth rates of red oak in the field.

The purpose of this paper was to calculate CO_2 exchange budgets for seedlings under several hypothetical yet realistic light regimes. Carbon budgets have been used successfully in past studies to verify observed growth rates from photosynthetic and respiratory information (Heichel 1971a; Proctor *et al.* 1976), and as tools for contrasting physiological characteristics of different plant species (Brunes *et al.* 1980). Carbon budgets were calculated (1) to determine the relation between a seedling's leaf carbon dioxide exchange rate (CER) and daily growth rates (mass) of seedlings grown under controlled environment conditions, (2) to project mean daily net carbon accumulation under a variety of hypothetical light regimes, and (3) to predict the minimum photosynthetic photon flux density (PPFD) required for seedling photosynthesis to balance total seedling respiration.

[1/]Paper presented at the Sixth Central Hardwood Forest Conference, Knoxville, TN, February 24-26, 1987.

[2/]The authors are: Research Associate - Oak Ridge National Laboratory, Environmental Sciences Division, Oak Ridge, TN 37831, and Plant Physiologists - North Central Forest Experiment Station, USDA Forest Service, Rhinelander, WI, respectively. This research was supported by the North Central Forest Experiment Station, USDA Forest Service, St. Paul, MN; the College of Forestry, University of Minnesota; and the University of Minnesota Agricultural Experiment Station under Project MN-42-36 of the McIntire-Stennis Cooperative Forestry Research Program. Published as paper No. 2105 of the Miscellaneous Journal Series of the Minnesota Agricultural Experiment Station. The manuscript was prepared at Oak Ridge National Laboratory (operated by Martin Marietta Energy Systems, Inc., under Contract No. DE-AC05-84OR21400 with the U.S. Department of Energy). Publication No. 2883, Environmental Sciences Division.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Northern red oak (Quercus rubra L.) seedlingswere grown from acorns in a controlled environment chamber under 16-h photoperiods, 26/20°C day/night temperatures, 70/90 percent relative humidity, and a PPFD of 300 to 400 µmol m^{-2} s^{-1}. Carbon dioxide concentrations in the growth chambers were not controlled and were typically around 450 cm^3 m^{-3}. Additional details of plant culture conditions and procedures for selecting plants for measurements were reported by Hanson et al. (1986).

Root Respiration Measurements

Whole root respiration was measured for three seedlings in the first-lag (1-Lag), second-lag (2-Lag), and third-lag (3-Lag) stages of development. The "Lag" stage of oak seedling development is defined as the time between the end of internode and leaf elongation of a flush and macroscopic expansion of the next flush's terminal bud (Hanson et al. 1986). Root respiration measurements complemented foliar gas exchange measurements and enabled the carbon budgets to be determined with fewer assumptions. Respiration was measured on detached root systems enclosed in a humidified cuvette with a volume of 7845 cm^3. Humidity in the cuvette was maintained near 100 percent by occasional mistings during the measurement, and temperature was 25 ± 2 C. A fan in the cuvette circulated air around the root system, and a pump forced chamber air through a sampling loop. Samples of the chamber atmosphere were collected in 10-ml syringes at 5- to 10-min intervals and analyzed for CO_2 on an infrared gas analyzer (Clegg and Sullivan 1978).

Before measuring respiration, roots were detached from the shoot and gently washed to remove attached soil. Then the whole root system was transferred to a 1:1 dilution of aerated nutrient solution at 25 C (Hanson 1986). The root system was allowed to equilibrate for 1 h to minimize wound-induced respiration and then transferred from solution culture into the cuvette. This 1-h respiration measurement provided rates representative of high assimilate availability in the roots. After this initial measurement, the roots were returned to the solution bath for 8-h (timed from the detachment of the shoot) and remeasured (8-h measurement) to represent rates under low assimilate availability.

Calculating Carbon Budgets

Average seedlings at the 1-, 2-, and 3-Lag stages of development were defined as in Table 1, using information on seedling dry matter from Hanson (1986). Carbon dioxide exchange rate (CER) properties of median, attached leaves were defined using additional information from Hanson et al. (1987a). Median flush leaf CER was extrapolated to all other leaves of the same flush because at full leaf expansion CER differed little between leaves of a particular flush (Hanson et al. 1987b). Environmental variables for calculating carbon budgets are presented in Table 2. The two photoperiods represent the maximum and minimum normally experienced by field-grown oak seedlings in the Lake States (Fowells 1965; List 1966). Analogous CER data were not available for plants grown under short days, but we assumed they were similar. Representative PPFD values were taken from studies by Zavitkovski (1982), Allard (1947), and Shirley (1929a). We assumed that temperature was constant at 25 °C, CO_2 concentrations were ambient (320-340 cm^3 m^{-3}; Garrett et al. 1978), and nutrients were optimal.

Carbon budgets (i.e., mass of CO_2 assimilated per day) of the seedlings were determined for a single day using equations similar to those of Heichel (1971a) and Brunes et al. (1980). To convert net CO_2 uptake to dry matter accumulation, we multiplied net CO_2

Table 1.—Component dry mass and leaf area data for 1-, 2-, and 3-Lag stages of Quercus rubra L. seedlings used to define seedlings for calculating carbon budgets.1/

Variable	Stage of Growth2/ 1-Lag	2-Lag	3-Lag
1-flush:			
Leaf area3/	3.80	3.69	3.00
Leaf mass4/	1.179	1.839	1.660
Stem mass4/	0.216	0.945	2.222
2-flush:			
Leaf area	—	7.64	7.61
Leaf mass	—	2.874	4.258
Stem mass	—	0.611	2.169
3-flush:			
Leaf area	—	—	14.60
Leaf mass	—	—	6.622
Stem mass	—	—	1.862
Shoot mass	1.395	6.269	18.793
Root mass	0.438	1.747	7.024

1/ Obtained from measurements of at least 12 plants (Hanson 1986).
2/ Stages defined by the Quercus Morphological Index (Hanson et al. 1986).
3/ Projected leaf area is in dm^2.
4/ Dry mass is in grams.

Table 2.—Assumptions about environmental conditions in the Lake States (approx. 45 N. Lat) used to calculate *Quercus rubra* L. seedling carbon budgets. (Values in parentheses were used in calculations).

Variable	Duration or level
Photoperiod (in hours)	16 and 12[1/]
Incident PPFD (in $\mu mol\ m^{-2}\ s^{-1}$)	
Clear day	1850–1980 (1900)[2/]
Cloudy day	600–800 (700)[2/]
PPFD passing through canopy (as a percent of incident PPFD)	
Sunflecks	25 – 40[2/] 10 – 49[3/] (30)
Shade	Less than 1, (1)[2,3/]
Temperature (in degrees °C)	25[4/]
CO_2 concentration (in $cm^3\ m^{-3}$)	320–340[4/]
Mineral nutrients	Assumed optimum

1/ List (1966) and Fowells (1965); representing possible extremes.
2/ Zavitkovski (1982) for a *Populus* canopy.
3/ Allard (1947) for a hardwood canopy (e.g., *Acer*, *Quercus*).
4/ Hanson (1986) and Hanson *et al*. (1987a).

assimilation by the following factor (Brunes *et al*. 1980):

$$\text{Net dry matter accumulated} = \text{Net } CO_2 \text{ assimilated} * \left(\frac{12}{0.45 * 44}\right)$$

where 12 and 44 are the molecular weights of carbon and carbon dioxide, respectively, and 0.45 is the mean proportion of total seedling dry matter as carbon (Hanson 1986). A calculated carbon budget for a 3-Lag red oak seedling under cloudy conditions in the open is presented in Table 3. Stem respiration rates were not measured, but were assumed equal to leaf respiration on a dry mass basis (Proctor *et al*. 1976). We assumed that stem respiration was constant throughout the day. Coe and McLaughlin (1980) and Han and Suzaki (1981) reported rates of oak stem or branch respiration similar to the leaf respiration rates (per unit mass) used here. Root respiration rates from the 1-h measurements were used to calculate root respiration during the day, and the mean of the 1-h and 8-h rates was used to calculate night period respiration to approximate known diurnal patterns (Huck *et al*. 1962). The photosynthetic photon flux densities of 1900 and 700, 570 and 210, and 19 and 7 $\mu mol\ m^{-2}\ s^{-1}$ represent open-field sunlight regimes on a clear and cloudy day, sunfleck light regimes on a clear and partially cloudy day, and forest shade light regimes on a clear and cloudy day, respectively. To simplify calculations of the carbon budgets we assumed that mutual shading of leaves did not occur (i.e., radiation was diffuse).

Table 3.—A carbon budget for an average three-flush *Quercus rubra* L. seedling growing in an open field on a day with thin clouds. (Photoperiod = 16 h, temperature = 25 C, incident PPFD = 700 $\mu mol\ m^{-2}\ s^{-1}$)

Plant material		CO_2 exchange rate (CER)		Integrated CER	
Variable	Quantity	Day	Night	Day	Night
Leaves	(dm^2)	($mg\ CO_2\ dm^{-2} h^{-1}$)[1/]		($mg\ CO_2$ day/night^{-1})	
1-flush	3.00	7.10	-1.06	341	-25
2-flush	7.61	7.68	-1.19	935	-72
3-flush	14.60	4.51	-0.52	1053	-61
Stems	(g)	($mg\ CO^2 g^{-1} h^{-1}$)			
1-flush	2.222	-1.92	-1.92	-68	-34
2-flush	2.169	-2.13	-2.13	-74	-37
3-flush	1.862	-1.15	-1.15	-34	-17
Roots	(g)	($mg\ CO^2\ g^{-1}\ h^{-1}$)			
	7.024	-1.80	-1.50	-202	-84
Day or night net CO_2 assimilation (g)				1.951	- 0.330
Daily net CO_2 assimilation (g)				1.621	

1/ From Hanson (1986).

RESULTS

Mean 1-h respiration rates of the root systems were always greater than rates measured 8 h after the shoot was detached (Table 4), but the results of an analysis of variance between the observation periods were only statistically significant for the 3-Lag growth stage. Respiration rates per gram of root decreased from 1-Lag plants through 3-Lag plants, but was statistically significant only for the 1-h observation time (analyses not shown).

Table 4.—Respiration rates per unit mass of the same detached, whole, root systems of plants in the 1-, 2-, or 3-Lag stage of shoot development.

Stage of growth[1/]	Time of measurement		
	1-h	8-h	Mean
	($mg\ CO_2\ g^{-1}\ h^{-1}$)		
1-Lag	5.5 ± 0.6[2/]	3.8 ± 0.6	4.7 ± 0.5
2-Lag	4.4 ± 1.1	2.9 ± 0.9	3.6 ± 1.0
3-Lag	1.8 ± 0.1	1.2 ± 0.2	1.5 ± 0.2

1/ Stages defined by the *Quercus* Morphological Index (Hanson *et al*., 1986).
2/ Mean ± SE of three root systems.

Growth rates of the oak seedlings calculated from gas exchange measurements were only 63 (1-Lag) and 65 (2-Lag) percent of measured growth rates (Table 5). Because seedlings were grown only through three flushes of shoot growth, observed mean growth rates corresponding to post 3-Lag growth were not available for the 3-Lag seedlings.

Table 5.—Comparison of observed and calculated mean growth rates of *Quercus rubra* L. seedlings at three stages of growth.[1/]

Stage of growth[2/]	Total leaf area	Mean growth rate: Observed	Calculated	CO_2 corrected[3/]
	(dm2)	(g day-1)		
1-Lag	3.80	0.30	0.19	0.29
2-Lag	11.30	0.55	0.36	0.56
3-Lag	25.20	—	0.81	—

1/ Calculations assume an incident PPFD of 400 µmol m^{-2} s^{-1} for all leaves of a seedling.
2/ Stages defined by the *Quercus* Morphological Index (Hanson *et al.* 1986).
3/ To obtain corrected mean growth rates, carbon budget photosynthetic rates were multiplied by the ratio of growth chamber to ambient CO_2 concentrations (450/330 = 1.36).

According to daily carbon budget predictions, maximum CO_2 assimilation for 1-, 2-, or 3-Lag seedlings occurred in the open-field environment on a clear day (Table 6). By comparison, the other hypothetical environments showed reduced daily rates of whole-seedling CO_2 assimilation. However, reductions did not approach net carbon loss until PPFD dropped below 500 µmol m^{-2} s^{-1} (e.g., sunflecks on a partially cloudy day -- Table 6). The projected daily net CO_2 assimilation in the shade of the hypothetical forest canopy was negative, which indicates unfavorable growing conditions at these light levels. Daily net CO_2 assimilation patterns predicted for 12-h photoperiods were similar to those predicted for the 16-h photoperiods, but had lower absolute rates of CO_2 assimilation.

Table 6.—Calculated daily net CO_2 assimilation at three stages of *Quercus rubra* L. seedling growth for several selected day lengths and environments.[1/]

Growth stage[3/]	Day length	Environment[2/]: Open, Clear	Open, Cloudy	Sunfleck, Clear	Sunfleck, Cloudy	Shade, Clear	Shade, Cloudy
	(h)	($g\ CO_2\ d^{-1}$)					
1-Lag	16	0.34	0.33	0.33	0.26	-0.09	-0.14
	12	0.21	0.21	0.21	0.15	-0.11	-0.15
2-Lag	16	0.91	0.75	0.69	0.29	-0.39	-0.46
	12	0.56	0.44	0.39	0.10	-0.41	-0.46
3-Lag	16	1.71	1.62	1.55	0.76	-0.77	-0.93
	12	1.03	0.97	0.91	0.32	-0.83	-0.95

1/ Temperature and CO_2 assumed constant.
2/ PPFD levels of 1900 and 700, 570 and 210, and 19 and 7 µmol m^{-2} s^{-1} corresponded to the open field on a clear and cloudy day, to sunflecks on a clear and partially cloudy day, and to forest shade on a clear and cloudy day, respectively.
3/ Stages defined by the *Quercus* Morphological Index (Hanson *et al.*, 1986).

Minimum incident PPFDs required for seedling CO_2 fixation to balance total daily seedling respiration were calculated for each growth stage (Table 7). Seedling respiration increased with plant size through the 3-Lag growth stage. A 2-Lag seedling was predicted to need a continuous PPFD of only 30 to 40 µmol m^{-2} s^{-1} throughout the day for CO_2 fixation to equal its respiration. However, 2- and 3-Lag seedlings typically needed more than 100 µmol m^{-2} s^{-1} throughout the day.

Table 7.—Calculated minimum incident PPFD level required to equal total daily seedling respiration.[1/]

Growth stage[2/]	Day length	Daily respiration	Minimum PPFD
	(h)	(mg CO_2 day^{-1})	(µmol m^{-2} s^{-1})[3/]
1-Lag	16	-106	30
	12	-121	40
2-Lag	16	-339	100
	12	-375	150
3-Lag	16	-708	90
	12	-780	130

1/ All leaves were assumed to receive the same light regime.
2/ Stages defined by the *Quercus* Morphological Index (Hanson *et al.* 1986).
3/ All values rounded to the nearest 10 µmol m^{-2} s^{-1}.

DISCUSSION

Root Respiration

Root respiration rates observed here are comparable to past measurements (Osman 1971; Billings *et al.* 1977; Szaniawski 1981). High root respiration rates of the young oak root systems (Table 4) probably reflect a greater proportion of root tissue exhibiting growth respiration rather than maintenance respiration (Amthor 1984). The lack of a significant difference in respiration rates between growth stages observed at the 8-h measurements probably indicates that most reserves available for growth had been used up and respiration rates decreased towards maintenance values. Previous studies have also reported changing respiration rates in relation to time of day and nonstructural carbohydrate concentrations in the tissue (Huck *et al.* 1962; Heichel 1971b; Osman 1971; Szaniawski 1981).

It is difficult to obtain measurements of root system respiration that are representative of *in situ* rates and attributable solely to root tissue. Root respiration rates reported here may include components of microbial and wound-induced respiration in addition to root tissue respiration. Furthermore, oxygen

concentrations during measurement (i.e., the same as in ambient air) were probably higher than in typical soil atmospheres and may have yielded higher respiration rates than expected from undisturbed root systems. Thus, the root respiration rates probably overestimate actual in situ rates. Conversely, the 8-h root respiration rates may have been underestimated. If the roots had remained attached to the shoot before the 8-h measurements (pre-photoperiod), additional translocated carbon from the shoot might have supported greater respiration even though transport to the roots decreases during the dark period (Geiger et al. 1985).

Carbon Budget Analysis

Carbon budget estimates of net CO_2 assimilation calculated for hypothetical light regimes may provide reasonable growth projections (Ledig 1969). However, because carbon budgets in this paper are based on CER-PPFD relations of leaves grown under higher than ambient field CO_2 concentrations (i.e., 450 versus 340 cm^3 m^{-3}), we must consider the importance of the difference in CO_2 concentrations. Nelson and Ehlers (1984) measured photosynthetic capacities of Populus leaves grown in growth rooms and field environments and found lower CER levels at light saturation in growth room plants. Oberbauer et al. (1985) found different chlorophyll concentrations in leaves of two tropical tree species grown in different CO_2 environments. These experiments suggest that leaves of the red oak seedlings studied by Hanson et al. (1987a) are not strictly analogous to field grown leaves. However, red oak CER-PPFD properties (Hanson et al. 1987a) corresponded well with those for oak seedlings grown in the shade (Jurik et al. 1985; Loach 1967; McMillen and McClendon 1983). Therefore, we consider it acceptable to use CER characteristics for oak from Hanson et al. (1987a) to calculate carbon budgets.

The discrepancy between observed and calculated mean growth rates can also be explained (Table 5). Ambient CO_2 concentrations used in the laboratory cuvette for characterizing leaf CER-PPFD relations (320-340 cm^3 m^{-3}) were only 73 percent of CO_2 concentrations in the growth chamber (450 cm^3 m^{-3}). This percentage was similar to the 63 percent difference between calculated and observed dry matter accumulation rates. Calculated mean growth rates agreed closely with observed rates when corrections for the differences in CO_2 concentrations were considered (Table 5).

According to the carbon budgets calculated in this study, maximum net CO_2 assimilation of red oak seedlings would occur in full sunlight and would not drop appreciably until PPFD decreased to less than 50 percent of full sunlight (Table 6). Until recently, it was assumed that PPFDs between 30 and 50 percent of full sun were optimum for oak seedling growth (Kramer and Decker 1944; Musselman and Gatherum 1969). However, Gottschalk (1985) documented maximum height and diameter growth at all fluxes above 20 percent of maximum incident PPFD and concluded that water stress and/or excessive temperatures were responsible for lower growth at higher PPFDs in past studies. The assimilation of greater amounts of CO_2 under 16 as opposed to 12 h photoperiods (Table 6) is expected and has been documented (Immel et al. 1978).

Can a lack of light, by itself, be responsible for observed oak seedling mortality in the field? The carbon budget analysis suggests that it can. If a seedling is growing in the shade of a full forest canopy, or under dense understory vegetation, the budget predicts that it would not receive sufficient light to fix enough CO_2 to offset maintenance respiration (Table 6). Calculated minimum light requirements indicate that small seedlings with less respiration can survive with less light (Table 7). This conclusion does not consider the potential ameliorating effects of stored reserves in the acorn (Hanson 1986 and Hanson et al. 1987a). Larger seedlings with greater dry matter would require higher PPFD for increased photosynthesis to balance their whole-seedling maintenance respiration. A decrease in the leaf area ratios (total leaf area/plant dry mass) from 2 at the 1-Lag stage to 1 at the 3-Lag stage (Table 1) suggests why the carbon budget analysis predicts greater minimum PPFD levels for 2- and 3-Lag seedlings -- as plants get larger the leaf area available for photosynthesis per unit of plant dry matter decreases.

Larger plants have greater maintenance respiration requirements than smaller plants (McCree 1983). This physiological principle suggests that silvicultural practices designed to promote oak seedling regeneration must gradually remove forest canopies if sufficient light is to reach seedlings to compensate for maintenance respiration. Silvicultural systems employing this principle have been devised through empirical research based on available oak seedling characteristics (Korstain 1927; Fischer 1979; Sander 1979; Johnson 1984). Our ability to project the need for such a system from the simple carbon balance used in this study indicates that fundamental physiological and ecological properties of our important tree species can be used for practical purposes.

Throughout this paper all environmental variables except light were assumed to be optimum or to approximate ambient conditions. However, factors other than light affect oak seedling establishment and growth (Merritt 1979). Lassoie and Chambers (1976) showed that water stress could decrease red oak seedling photosynthesis by up to 90 percent. Reich and Amundson (1985) found that photosynthesis of

concentrations during measurement (i.e., the same as in ambient air) were probably higher than in typical soil atmospheres and may have yielded higher respiration rates than expected from undisturbed root systems. Thus, the root respiration rates probably overestimate actual in situ rates. Conversely, the 8-h root respiration rates may have been underestimated. If the roots had remained attached to the shoot before the 8-h measurements (pre-photoperiod), additional translocated carbon from the shoot might have supported greater respiration even though transport to the roots decreases during the dark period (Geiger et al. 1985).

Carbon Budget Analysis

Carbon budget estimates of net CO_2 assimilation calculated for hypothetical light regimes may provide reasonable growth projections (Ledig 1969). However, because carbon budgets in this paper are based on CER-PPFD relations of leaves grown under higher than ambient field CO_2 concentrations (i.e., 450 versus 340 cm^3 m^{-3}), we must consider the importance of the difference in CO_2 concentrations. Nelson and Ehlers (1984) measured photosynthetic capacities of Populus leaves grown in growth rooms and field environments and found lower CER levels at light saturation in growth room plants. Oberbauer et al. (1985) found different chlorophyll concentrations in leaves of two tropical tree species grown in different CO_2 environments. These experiments suggest that leaves of the red oak seedlings studied by Hanson et al. (1987a) are not strictly analogous to field grown leaves. However, red oak CER-PPFD properties (Hanson et al. 1987a) corresponded well with those for oak seedlings grown in the shade (Jurik et al. 1985; Loach 1967; McMillen and McClendon 1983). Therefore, we consider it acceptable to use CER characteristics for oak from Hanson et al. (1987a) to calculate carbon budgets.

The discrepancy between observed and calculated mean growth rates can also be explained (Table 5). Ambient CO_2 concentrations used in the laboratory cuvette for characterizing leaf CER-PPFD relations (320-340 cm^3 m^{-3}) were only 73 percent of CO_2 concentrations in the growth chamber (450 cm^3 m^{-3}). This percentage was similar to the 63 percent difference between calculated and observed dry matter accumulation rates. Calculated mean growth rates agreed closely with observed rates when corrections for the differences in CO_2 concentrations were considered (Table 5).

According to the carbon budgets calculated in this study, maximum net CO_2 assimilation of red oak seedlings would occur in full sunlight and would not drop appreciably until PPFD decreased to less than 50 percent of full sunlight (Table 6). Until recently, it was assumed that PPFDs between 30 and 50 percent of full sun were optimum for oak seedling growth (Kramer and Decker 1944; Musselman and Gatherum 1969). However, Gottschalk (1985) documented maximum height and diameter growth at all fluxes above 20 percent of maximum incident PPFD and concluded that water stress and/or excessive temperatures were responsible for lower growth at higher PPFDs in past studies. The assimilation of greater amounts of CO_2 under 16 as opposed to 12 h photoperiods (Table 6) is expected and has been documented (Immel et al. 1978).

Can a lack of light, by itself, be responsible for observed oak seedling mortality in the field? The carbon budget analysis suggests that it can. If a seedling is growing in the shade of a full forest canopy, or under dense understory vegetation, the budget predicts that it would not receive sufficient light to fix enough CO_2 to offset maintenance respiration (Table 6). Calculated minimum light requirements indicate that small seedlings with less respiration can survive with less light (Table 7). This conclusion does not consider the potential ameliorating effects of stored reserves in the acorn (Hanson 1986 and Hanson et al. 1987a). Larger seedlings with greater dry matter would require higher PPFD for increased photosynthesis to balance their whole-seedling maintenance respiration. A decrease in the leaf area ratios (total leaf area/plant dry mass) from 2 at the 1-Lag stage to 1 at the 3-Lag stage (Table 1) suggests why the carbon budget analysis predicts greater minimum PPFD levels for 2- and 3-Lag seedlings -- as plants get larger the leaf area available for photosynthesis per unit of plant dry matter decreases.

Larger plants have greater maintenance respiration requirements than smaller plants (McCree 1983). This physiological principle suggests that silvicultural practices designed to promote oak seedling regeneration must gradually remove forest canopies if sufficient light is to reach seedlings to compensate for maintenance respiration. Silvicultural systems employing this principle have been devised through empirical research based on available oak seedling characteristics (Korstain 1927; Fischer 1979; Sander 1979; Johnson 1984). Our ability to project the need for such a system from the simple carbon balance used in this study indicates that fundamental physiological and ecological properties of our important tree species can be used for practical purposes.

Throughout this paper all environmental variables except light were assumed to be optimum or to approximate ambient conditions. However, factors other than light affect oak seedling establishment and growth (Merritt 1979). Lassoie and Chambers (1976) showed that water stress could decrease red oak seedling photosynthesis by up to 90 percent. Reich and Amundson (1985) found that photosynthesis of

northern red oak exposed to an ozone dose of 30 ppm h^{-1} was decreased by almost 20 percent. Linit et al. (1986) reported that oak seedlings, growing in the oak-hickory forests of the Missouri Ozarks, typically lost an average of 22 percent of their leaf area to insect predation. These three examples demonstrate some of the problems red oak seedlings routinely experience in the field. Our carbon budget projected a net loss of carbon from the plant under shade conditions alone. If stress conditions coincided with growth under typical forest shade conditions, a very likely situation, further stress-induced reductions in photosynthesis would almost certainly lead to seedling mortality. However, the potential for seedling survival and growth under a canopy is probably greater than this discussion suggests. Sunflecks are common under forest canopies (Shirley 1929ab; Allard 1947; Zavitkovski 1982) and can potentially supply sufficiently high PPFD levels for significant photosynthesis to occur (Table 6). The number of hours of sunfleck exposure required for CO_2 uptake to balance respiration demands were calculated for 1-, 2- and 3-Lag seedlings under a 16-h photoperiod (data not shown). These calculations revealed that seedling exposures to sunflecks lasting 4 to 5 h on a clear day (570 µmol m^{-2} s^{-1}) or 5 to 9 h on a partially cloudy day (210 µmol m^{-2} s^{-1}) would be needed to satisfy daily seedling respiration. Sunflecks having even higher PPFD levels would allow significant growth to occur.

The carbon budget results presented here are only approximate. However, because conclusions drawn from the analysis support existing ecological observations, this approach should be helpful for planning future applied research. By using available knowledge of plant physiology and ecology in conjunction with forest tree improvement programs, practical solutions to silvicultural problems should be forthcoming.

LITERATURE CITED

Allard, H. A.
1947. Light intensity studies in Canaan Valley, West Virginia. Castanea 12:63-74.

Amthor, J. S.
1984. The role of maintenance respiration in plant growth. Plant Cell Environ. 7:561-569.

Billings, W. D., K. M. Peterson, G. R. Shaver, and A. W. Trent.
1977. Root growth, respiration and carbon dioxide evolution in an arctic tundra soil. Arct. Alp. Res. 9:129-137.

Brunes, L., G. Oquist, and L. Eliasson.
1980. On the reasons for the different photosynthetic rates of seedlings of Pinus silvestris and Betula verrucosa. Plant Physiol. 66:940-944.

Clegg, M. D., and C. Y. Sullivan.
1978. A sensitive technique for the rapid measurement of carbon dioxide concentrations. Plant Physiol. 62:924-926.

Coe, J. M., and S. B. McLaughlin.
1980. Winter season corticular photosynthesis in Cornus florida, Acer rubrum, Quercus alba, and Liriodendron tulipifera. For. Sci. 26:561-566.

Fischer, B. C.
1979. Managing light in the selection method. In: Proc., Regenerating oaks in upland hardwood forests, H. A. Holt and B. C. Fischer (eds.), Purdue Univ., West Lafayette, Indiana, Feb. 22-23, pp. 43-53.

Fowells, H. A.
1965. Silvics of forest trees of the United States. USDA Forest Service, Agric. Handbook 271, pp. 588-592.

Garrett, H. E., G. S. Cox, and J. E. Roberts.
1978. Spatial and temporal variations in carbon dioxide concentrations in an oak-hickory forest ravine. For. Sci. 24:180-190.

Geiger, D. R., L. M. Jablonski, and B. J. Ploeger.
1985. Significance of carbon allocation to starch in growth of Beta vulgaris L. In: Regulation of carbon partitioning in photosynthetic tissue, R. L. Heath and J. Preiss (eds.), pp. 289-308.

Gottschalk, K. W.
1985. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. I. Height, diameter, and root/shoot ratio. In: Proc., Fifth Central Hardwood Forest Conf., Urbana, Illinois., April 15-17, pp. 189-195.

Han, S. and T. Suzaki.
1981. Studies on the production and consumption of assimilates by trees (IX) bark photosynthesis and dark respiration of young green stems and branches of Fagus crenata and Quercus acutissima. J. Jap. For. Soc. 63:242-244.

Hanson, P. J.
1986. Studies of Quercus rubra L. seedling dry matter accumulation, morphological development, and carbon dioxide exchange under controlled conditions. Ph.D. Thesis University of Minnesota, St. Paul, Minnesota, 169 p.

Hanson, P. J., R. E. Dickson, J. G. Isebrands, T. R. Crow, and R. K. Dixon.
1986. A morphological index of Quercus seedling ontogeny for use in studies of physiology and growth. Tree Physiol. 2:273-281.

Hanson, P. J., J. G. Isebrands, R. E. Dickson, and R. K. Dixon.
1987a. Ontogenetic patterns of CO_2 exchange of Quercus rubra L. leaves during three flushes of shoot growth. I. Median flush leaves. For. Sci. (in review).

Hanson, P. J., J. G. Isebrands, R. E. Dickson, and R. K. Dixon.
1987b. Ontogenetic patterns of CO_2 exchange of Quercus rubra L. leaves during three flushes of shoot growth. II. Insertion gradients of leaf photosynthesis. For. Sci. (in review).

Heichel, G. H.
1971a. Confirming measurements of respiration and photosynthesis with dry matter accumulation. Photosynthetica 5:93-98.

Heichel, G. H.
1971b. Response of respiration of tobacco leaves in light and darkness and the CO_2 compensation concentration to prior illumination and oxygen. Plant Physiol. 48:178-182.

Huck, M. G., R. H. Hageman, and J. B. Hanson.
1962. Diurnal variation in root respiration. Plant Physiol. 37:371-375.

Immel, M. J., R. L. Ramsey, and S. B. Carpenter.
1978. Comparative growth responses of northern red oak and chestnut oak seedlings to varying photoperiods. For. Sci. 24:554-560.

Johnson, P. S.
1984. Responses of planted northern red oak to three overstory treatments. Can. J. For. Res. 14:536-542.

Jurik, W., G. M. Briggs, and D. M. Gates.
1985. Carbon dynamics of northern hardwood forests: gas exchange characteristics. TR019, U.S. Dept. of Energy, Washington, D.C.

Korstain, C. F.
1927. Factors controlling germination and early survival in oaks. Yale Univ. School For. Bull. 19, 115 p.

Kramer, P. J., and P. J. Decker.
1944. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Plant Physiol. 19:350-358.

Lassoie, J. P., and J. L. Chambers.
1976. The effects of an extreme drought on tree water status and net assimilation rates of a transplanted northern red oak under greenhouse conditions. In: Proc., Central Hardwood Forest Conf. I, Carbondale, Illinois, Oct. 17-19, pp. 269-282.

Ledig, F. T.
1969. A growth model for tree seedlings based on the rate of photosynthesis and the distribution of photosynthate. Photosynthetica 3:263-275.

Linit, M. J., P. S. Johnson, R. A. McKinney, and W. H. Kearby.
1986. Insects and leaf area losses of planted northern red oak seedlings in an Ozark forest. For. Sci. 32:11-20.

List, R. J.
1966. Smithsonian Meteorological Tables, 6th Edition. Smithson. Misc. Collect. 114:506-510.

Loach, K.
1967. Shade tolerance in tree seedlings I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66:607-621.

McCree, K. J.
1983. Carbon balance as a function of plant size in sorghum plants. Crop Sci. 23:1173-1177.

McMillen, G. C., and J. H. McClendon.
1983. Dependence of photosynthetic rates on leaf density thickness in deciduous woody plants grown in sun and shade. Plant Physiol. 72:674-678.

Merritt, C.
1979. An overview of oak regeneration problems. In: Proc., regenerating oaks in upland hardwood forests, H. A. Holt and B. C. Fischer (eds.), Feb. 22-23, pp. 1-10.

Musselman, R. C., and G. E. Gatherum.
1969. Effects of light and moisture on red oak seedlings. Iowa State J. Sci. 43:273-283.

Nelson, N. D., and P. Ehlers.
1984. Comparative carbon dioxide exchange for two Populus clones grown in growth room, greenhouse, and field environments. Can. J. For. Res. 14:924-932.

Oberbauer, S. F., B. R. Strain, and N. Fetcher.
1985. Effects of CO_2-enrichment on seedling physiology and growth of two tropical tree species. Physiol. Plant. 65:352-356.

Osman, A. M.
1971. Root respiration of wheat plants as influenced by age, temperature, and irradiation of shoots. Photosynthetica 5:107-112.

Phares, R. E.
1971. Growth of red oak (Quercus rubra L.) seedlings in relation to light and nutrients. Ecology 52:669-672.

Proctor, J. T. A., R. L. Watson, and J.J. Landsberg.
1976. The carbon budget of a young apple tree. J. Am. Soc. Hortic. Sci. 101:579-582.

Reich, P. B., and R. G. Amundson.
1985. Ambient levels of ozone reduce net photosynthesis in tree and crop species. Science 230:566-570.

Sander, I. L.
1979. Regenerating oaks with the shelterwood system. In: Proc., Regenerating oaks in upland hardwood forests, H. A. Holt and B. C. Fisher (eds.), Purdue Univ., West Lafayette, Indiana, February 22-23, pp. 54-60.

Shirley, H. L.
1929a. The influence of light intensity and light quality upon the growth of plants. Am. J. Bot. 16:354-390.

Shirley, H. L.
1929b. Light requirements and silvicultural practice. J. For. 27:535-538.

Szaniawski, R. K.
1981. Growth and maintenance respiration of shoot and roots in Scots pine seedlings. Z. Pflanzenphysiol. Bd. 101:391-398.

Watt, A. S.
1919. On the causes of failure of natural regeneration in British oakwoods. J. Ecol. 7:173-203.

Zavitkovski, J.
1982. Characterization of light climate under canopies of intensively-cultured hybrid poplar plantations. Agric. Meteorol. 25:245-255.