Comparative Photosynthesis of Three Gap Phase Successional Tree Species*

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Summary. Photosynthesis was measured in situ on trees growing in an open, gap-like site and under a closed canopy. Photosynthetic responses also were monitored on trees grown in the laboratory under either a high or low light regime or on those trees transferred from a low to a high light regime. All three species studied, *Liriodendron tulipifera*, *Acer rubrum* and *Cornus florida*, were able to acclimate to a high light environment as evidenced by their higher photosynthetic rates. This acclimation was achieved by an increase in transfer conductance and was ultimately due to changes in leaf anatomy. Species avoided photo-bleaching primarily by changes in leaf orientation and canopy structure. Species-specific physiological responses to high light intensity may account for each species' known growth response following canopy opening.

Introduction

It has long been believed that the climax deciduous forest is not a static entity. Raup (1937) stated that the climatic climax will undergo localized changes frequently and regularly. This phenomenon was later recognized by other workers and called "gap phase" succession (Watt, 1947; Bray, 1956). More recently, Loucks (1970) has proposed that the forest ecosystem as a whole has evolved to withstand periodic perturbations, and that they are required to maintain community diversity and productivity. In order for this ecosystem to be resilient to minor and localized perturbations certain components of the vegetation need to be capable of either 1) invading an opening or 2) responding to openings occurring over them (Trimble and Tyron, 1966; Wales, 1972).

The three species under consideration here include *Liriodendron tulipifera* L., yellow poplar, which is a shade-intolerant tree that requires an opening to reach maturity and cannot survive as a suppressed understory tree (Fowells, 1965). *Acer rubrum* L., red maple, is a shade-intermediate tree (Fowells, 1965). It may grow as either a suppressed understory tree or, when released, may grow into the canopy. *Cornus florida* L., flowering dogwood, has been classified as a shade-tolerant tree (Fowells, 1965). It may exist as a suppressed understory tree but also plays an important role in gap closure (Wales, 1972).

The question we considered in this study is which physiological and morphological attributes allow these species to respond to gap openings. The ability of understory species to respond to canopy opening depends upon their ability to endure sudden exposure and to take advantage of increased water, nutrients and space (McGee and Hooper, 1970). Since these species do respond to canopy opening, it is possible that they possess these attributes. This study focused primarily upon their response to increased incident light as would be experienced within a forest gap. Measurements of gas exchange characteristics, light-harvesting capacities, and foliage morphology were made on saplings in situ under both a closed canopy and an open, gap-like environment. Measurements were made on laboratory-grown trees to determine how rapidly different physiological and morphological systems responded.

Material and Methods

Site Description

Both the closed canopy and open sites were located in the Coweeta Hydrologic Laboratory in the Nantahala Mountains of western North Carolina. The mean annual precipitation is 1,813 mm and the mean annual temperature is 13° C (Johnson and Swank, 1973). The closed canopy or control site (792 m mean elevation) had a NE aspect with an average 40.5° slope. The open or cut site (747 m mean elevation) at the base of a clearcut watershed had a SE aspect and an average slope of 9°. Clearing of this site occurred in the January prior to these experiments.

Air temperature, relative humidity and average wind speeds were monitored continuously at each site during the growing season using hygrothermographs and cup anemometers. Light intensity was measured several times during the summer using a Fritschen net radiometer modified to a 180° all-wave radiometer and a Lambda (PAR) quantum sensor (LI-190 SR Lambda Instruments Co., Inc., Lincoln, NB). Leaf temperatures were measured on several days at solar noon using a copper-constantan thermocouple.

Table 1. Growth chamber light regime

	Langleys (cal cm^{-2}) per 15 h day	Maximum langleys min^{-1}
High light regime		
all wave down	1,666.3	1.5
short wave down	1,443.4	1.2
Low light regime		
all wave down	102.5	0.2
short wave down	153.7	0.3
Field sites (short wave down)		
open canopy	675	0.75
closed canopy	54	0.06

Laboratory Measurements

Eight to twelve seedlings of each species were removed from the Coweeta Hydrologic Laboratory and grown in clay pots for one year. Plants were randomly divided into two populations, one of which was grown in full sunlight near the University of Georgia Department of Botany plant growth facilities in Athens. The other was grown under screening in a lathehouse (0.1 full sunlight) at the same location. Standard greenhouse watering and fertilizing schedules were followed for all trees. Following the onset of dormancy in the fall, trees were stratified in a cold room (4° C) for six weeks.

The trees were then placed in an Environmental Growth Chamber (EGC, Chagrin Falls, OH) modified for production of full sun light intensities with the addition of eight 400 w metal halide lamps. These lights were cycled on and off in three hour intervals during the 15 h day period. Diurnal temperatures were 20° C day, 15° C night. We measured light intensities using a Fritchsen net all-wave radiometer modified to 180° and a Kipp-Zonen Solarimeter (Table 1). Trees on the shelf of the chamber were exposed to high light intensities. The maximum light intensity values obtained were twice those of predicted full sunlight values at Coweeta of 750 langleys per 15 h day (Lloyd Swift, personal comm.). Low incident light intensities were produced on the floor of the same chamber by placing neutral density screening on the shelf.

We moved trees to different light regimes according to the following schedule. Trees grown under full sun were placed first on the shelf (high light) and those grown under the lathehouse were placed on the floor (low light). After one month, gas exchange measurements were made on the youngest fully-expanded leaves. Then, all of the low light grown trees were moved to the shelf (transferred). Due to space limitation half of the high light grown trees remained on the shelf (high-high). The other half were placed on the floor. An acclimation period of one month was allowed so that leaves formed under the new light regime could expand fully (Day and Monk, 1977). All measurements were made only on these leaves.

Carbon Fixation

We measured carbon dioxide and water vapor exchange rates on field-grown saplings at both sites from April 20 to May 7
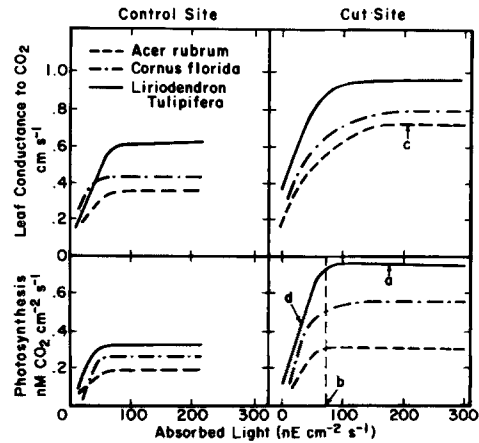

Fig. 1. Light response curves of photosynthesis and leaf conductance for each species at both sites during the summer measurement period. Each curve represents a visual mean of the responses of six trees at each site. Examples of the points taken for statistical analysis in Tables 3–6 are: *a*) maximum rate of photosynthesis, *b*) amount of absorbed light at saturation, *c*) leaf conductance at the point of maximum photosynthesis and *d*) the mean ratio of CO_2 fixed per quanta absorbed for all points on the linear portion of the light response curve

(spring) and from July 19 to August 10, 1977 (summer) on only the youngest, fully-expanded leaves. All trees appeared to be between four and seven years old. An open gas exchange system similar to that described by Mooney et al. (1971) was used on both field and laboratory-grown plants. Most of our sampling effort in the field was directed towards obtaining light response curves of photosynthesis although CO_2 and temperature response curves were obtained on a few individuals. We measured all three types of responses in the laboratory. The following points were taken from each individual light response curve similar to those presented in Fig. 1, and compared using a standard one-way ANOVA (Barr et al., 1976): a) maximum rate of photosynthesis (nM CO_2 s^{-1}) expressed on a leaf area (cm^{-2}) and dry weight (g DW^{-1}) basis, b) the amount of absorbed light (nE cm^{-2} s^{-1}) required for light saturation of photosynthesis, c) leaf and mesophyll conductances to CO_2 at the maximum photosynthetic rate (cm s^{-1}), d) a light efficiency term indicative of quantum yield and equal to the mean ratio of CO_2 fixed per quanta absorbed for all points on the linear portion of the light response curve. Mesophyll conductance was calculated as the reciprocal of mesophyll resistance using Gaastra's (1959) formulation. Intracellular conductances calculated as the slopes of the response curves of photosynthesis to changes in internal CO_2 concentration (Dunn, 1972) were also compared. Any differences in intracellular conductance values between sites would indicate changes in the carboxylation and/or transfer conductance across cell walls. Mesophyll conductance as calculated by Gaastra's (1959) formulation is greatly affected by stomatal conductance and hence would not yield an unbiased estimate of the sum of carboxylation and transfer conductances. However, mesophyll conductances rather than intracellular conductances had to be considered for *C. florida* since the very dry, CO_2-free air caused stomatal closure in this species. Finally, percent total leaf nitrogen was compared for each species between sites or growth chamber regimes. Nitrogen content of the field-grown tissue was determined using an autoanalyzer (Technicon)

Table 2. Environmental parameters monitored at each field site

	Control site	Cut site
Environmental parameter		
Light intensity	Less than full sun 3.4 nE cm^{-2}s^{-1}	Full sun 123.7 nE cm^{-2}s^{-1}
Air temperature	Smaller diurnal range Maximum 25.5° C Minimum 1.7° C	Greater diurnal range Maximum 31.7° C Minimum −4.4° C
Relative humidity	Greater diurnal range Maximum 100% Minimum 4%	Smaller diurnal range Maximum 100% Minimum 5%
Average wind velocity	Relatively calm Average 3.75 m s^{-1}	Relatively calm Average 3.97 m s^{-1}
Leaf temperature	Range at solar noon 17–20° C	Range at solar noon 20–25° C

Fig. 2. Temperature response curves of photosynthesis and leaf conductance for each species at both sites. Each curve represents a visual mean of the responses of two individual trees at each site in the summer measuring period

technique which included digestion of the leaf tissue using a modified micro-Kjeldahl procedure. We measured the nitrogen content of the laboratory tissue using a Coleman model 29 nitrogen analyzer (Coleman Instruments, Oak Brook, IL).

Light Harvesting Capacity

Several light harvesting characteristics of individual leaves compared between sites for each species included a) leaf absorptance, b) chlorophyll concentration (mg chlorophyll a + b cm^{-2}), c) photosynthetic unit (PSU) size (chlorophyll/P$_{700}$ ratio), d) photosynthetic unit (PSU) number (nM P$_{700}$ cm^{-2}), e) leaf angle and f) specific leaf weight (g DW cm^{-2}).

The size and number of the PSU were determined by measuring chlorophyll concentration (Arnon, 1949) and the amount of P$_{700}$ per unit leaf area. P$_{700}$ content was determined using a method modified from Black and Mayne (1970). Broken, twice-washed chloroplasts were isolated in a solution containing 0.35 M NaCl, 10 mg/ml Bovine Serum Albumin, 1% PVP-40 in 0.1 M Tricine, pH 7.8. The final chloroplast solution was made up in a 1:10 diluted mixture of the above buffer. An aliquot of this solution containing from 15–50 μg of chlorophyll was added to a reaction mixture containing 70 μmole sucrose, 100 μmole Tricine NaOH buffer, pH 7.8, 0.06 μM DCMU, 10 μmole ascorbate, 10 μmole DPIP and 1% Triton X-100 made up to 2.1 ml total volume with double glass distilled water. The reversible change in absorbance at 697 nm following exposure to blue actinic light was monitored by a Kok system spectrophotometer. An extinction coefficient of 42 mM cm^{-1} was used (Marsho and Kok, 1971).

Leaf reflectance was determined using a Bausch and Lomb 505 spectrophotometer with a reflectance attachment sensitive to the range of PAR (400–700 nm). Transmissivity was calculated as a percentage of incident light (PAR) passing through the leaf and absorptivity was calculated by difference. Leaf anatomy was examined in free hand sections of fresh leaves. Mesophyll and palisade layer thickness was measured using a stage micrometer. Leaf angles were measured using a protractor and a plumb line.
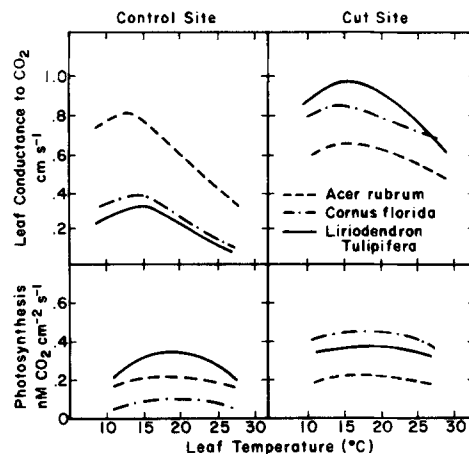
Results

1) Changes in Abiotic Parameters after Canopy Opening

The environmental parameter which exhibited the largest relative difference between the cut and control sites was incident light intensity measured 0.5 m above the ground on several days throughout the growing season (Table 2). Mean maximum quantum flux (PAR) measured at the control site was only 3% of that incident at the cut site. The maximum downward flux of energy at the control site (0.074 cal cm^{-2} min^{-1}) was 6.2% of that at the cut site (1.184 cal cm^{-2} min^{-1}). These parameters agree closely with those noted by other workers for gap versus closed canopy environments (Minckler et al., 1973; Goodfellow and Barkham, 1974). A greater diurnal range of air temperature, relative humidity and wind velocity was noted at the cut site. These data were collected continuously throughout the growing season.

2) Carbon Fixation

The broad, flat temperature response curves of photosynthesis (Fig. 2) indicate that each species is not very responsive to changes in leaf temperature normally experienced. The maximum rate of light-saturated photosynthesis was higher for trees at the cut site (Table 3). In laboratory-grown trees, maximum rates were measured on trees grown in the high light regime for only one month. Following transfer from the low light to the high light regime, no significant changes in photosynthesis were noted. However, after a prolonged period of growth in the high light regime, photosynthetic rates were lower than those measured after only one month of growth in the high light (Tables 4–6).

Leaf conductance and internal conductance were both higher in the cut site trees (Table 3). We measured a greater percentage difference in internal conductance than in leaf conductance between the two sites for each species. For example, in *L. tulipifera,*

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Table 3. Comparisons of responses of each species between the cut and control sites. Values are mean responses of six trees at each site during both the spring and summer. Values of intracellular conductance are the mean response of only two trees. Significance levels are $p < 0.05$ (**), $p < 0.10$ (*), $p > 0.10$ (−)

Response	L. tulipifera			A. rubrum			C. florida		
	Control	Cut	Sign.	Control	Cut	Sign.	Control	Cut	Sign.
Photosynthesis/area ($nM\ cm^{-2}s^{-1}$)	0.434	0.672	**	0.271	0.382	−	0.267	0.556	**
Photosynthesis/g dry wt.	22.49	19.45	−	11.19	12.24	−	11.16	16.59	**
Light required to saturate ($nE\ cm^{-2}s^{-1}$)	40	49	*	37	44	*	50	51	−
Leaf conductance ($cm\ s^{-1}$)	0.480	0.738	**	0.470	0.785	*	0.577	0.849	−
Mesophyll conductance ($cm\ s^{-1}$)	0.030	0.061	**	0.019	0.031	*	0.018	0.046	**
Intracellular conductance ($cm\ s^{-1}$)	0.071	0.117	**	0.055	0.103	**	0.074	0.093	−
Light use efficiency ($nM\ CO_2/nE$)	0.021	0.031	*	0.012	0.025	*	0.008	0.032	**
% Total nitrogen	1.53	1.50	−	1.16	1.16	−	1.15	1.31	−
Leaf absorptance (%)	77.2	76.6	−	79.5	68.9	*	75.9	73.0	−
mg chlorophyll a + b cm^{-2}	0.068	0.097	*	0.108	0.100	−	0.103	0.090	*
Leaf angle	−10.5	9.3	*	−1.6	−30.2	*	−8.4	−35.3	*
Specific leaf weight ($g\ cm^{-2}$)	0.032	0.036	*	0.040	0.035	−	0.023	0.034	**
PSU size (chlorophyll/P_{700})	585	358	−	699	349	−	496	504	−
PSU number ($mM\ P_{700}/cm^{-2}$)	0.123	0.166	*	0.060	0.081	−	0.167	0.220	−

Table 4. Comparisons of responses of *Liriodendron tulipifera* before and after transfer to the high-light regime. Significance levels are $p < 0.05$ (**), $p < 0.10$ (*), $p > 0.10$ (−). Missing values are indicated by XXX

	Low	High	Sign.	Trans-ferred	High High	Sign.	High High	Low	Trans-ferred
Gas exchange parameter									
Photosynthesis/area ($nM\ cm^{-2}s^{-1}$)	0.224	0.310	−	0.219	0.301	**	−		−
Photosynthesis/(g dry wt.)	35.22	37.74	−	15.23	31.35	−	−		−
Photosynthesis/chlorophyll (mg a + b)	3.98	1.24	−	7.83	18.67	**	−		*
Light required to saturate ($nE\ cm^{-2}s^{-1}$)	38	66	*	47	67	**	−		−
Leaf conductance ($cm\ s^{-1}$)	0.079	0.079	−	0.064	0.106	−	−		−
Mesophyll conductance ($cm\ s^{-1}$)	0.027	0.048	*	0.034	0.038	−	−		−
Intracellular conductance ($cm\ s^{-1}$)	0.035	0.056	−	0.054	0.043	−	**		*
Dark respiration/area ($nM\ cm^{-2}s^{-1}$)	−0.012	−0.025	−	−0.08	−0.08	−	**		**
Light use efficiency ($nM\ CO_2/nE$)	0.01	0.007	−	0.009	0.011	−	−		−
% total nitrogen	XXX	XXX	XXX	2.84	2.58	−	XXX		XXX
Light harvesting parameter									
Leaf absorptance (%)	XXX	XXX	XXX	53.5	36.8	−	XXX		XXX
Chlorophyll a/b ratio	3.14	3.68	−	3.73	2.89	−	−		−
mg chloro. a + b cm^{-2}	0.061	0.025	**	0.028	0.018	*	−		**
Leaf angle	−9.3	18.3	**	25.0	19.2	−	−		−
Leaf density ($g\ cm^{-2}$)	0.006	0.009	*	0.011	0.011	−	−		**
PSU size (chlorophyll/P_{700})	304	163	−	246	210	−	−		−
PSU number ($mM\ P_{700}\ cm^{-2}$)	0.009	0.086	**	0.153	0.132	−	−		−

leaf conductance was an average of 15.7% higher at the cut site whereas internal conductance averaged 85.7% higher. The difference in photosynthetic rates between the two sites was 54.8% and hence was limited by internal conductance rather than leaf conductance.

In the laboratory, stomatal conductance was lower in trees in the high light regime than for trees in the low light regime (Figs. 3–5). Following transfer, stomatal conductance was lower than in the low light regime. Intracellular conductance was either unchanged or lower following transfer. After prolonged growth in the high light regime, intracellular conductance reached its highest values in two species.

Intracellular resistance (l/conductance) consists of two metabolic resistances in series, transfer resistance and carboxylation resistance (Dunn, 1972). Although neither can be measured directly by using gas exchange technology, changes in these components can be determined by measuring internal cell surface area or carboxylating enzyme activity.

Transfer resistance is commonly measured indirectly by measuring mesophyll cell surface area and expressing this as a ratio

Table 5. Comparisons of responses of *Acer rubrum* before and after transfer to the high-light regime. Significance levels are $p < 0.05$ (**), $p < 0.10$ (*), $p > 0.10$ (−). Missing values are indicated by XXX

	Low	High	Sign.	Transferred	High High	Sign.	High / High High	Low / Transferred
Gas Exchange Parameter								
Photosynthesis/area (nM cm^{-2}s^{-1})	0.309	0.231	*	0.280	0.143	−	**	−
Photosynthesis/ (g. dry wt.)	49.31	11.38	**	24.13	18.27	−	−	**
Photosynthesis/chlorophyll (mg a+b)	6.80	15.74	**	10.39	3.37	**	**	−
Light required to saturate (nE cm^{-2}s^{-1})	42	53	−	66	39	*	−	*
Leaf conductance (cm s^{-1})	0.185	0.052	**	0.092	0.055	−	−	−
Mesophyll conductance (cm s^{-1})	0.032	0.040	−	0.038	0.018	**	**	−
Intracellular conductance (cm s^{-1})	0.060	0.046	−	0.044	0.024	−	*	−
Dark respiration/area (nM cm^{-2}s^{-1})	−0.05	−0.037	−	−0.07	−0.05	−	−	−
Light use efficiency	0.009	0.008	−	0.010	0.008	−	−	−
% total nitrogen	XXX	XXX	XXX	2.23	2.16	−	XXX	XXX
Light Harvesting Parameter								
Leaf absorptance (%)	XXX	XXX	XXX	60.8	60.3	−	XXX	XXX
Chlorophyll a/b ratio	3.10	3.40	**	3.29	3.10	−	−	*
mg chloro. a+b cm^{-2}	0.046	0.020	**	0.027	0.043	**	**	**
Leaf angle	−9.7	−40.3	**	−26.1	−23.1	−	**	**
Leaf density (g cm^{-2})	0.006	0.015	**	0.012	0.011	−	*	**
PSU size (chlorophyll/P$_{700}$)	296	147	−	441	306	−	−	−
PSU number (mM P$_{700}$ cm^{-2})	0.174	0.106	−	0.066	0.065	−	−	−

Table 6. Comparisons of responses of *Cornus florida* before and after transfer to the high-light regime. Significance levels are $p < 0.05$ (**), $p < 0.10$ (*), $p > 0.10$ (−). Missing values are indicated by XXX

	Low	High	Sign.	Transferred	High High	Sign.	High / High High	Low / Transferred
Gas Exchange Parameter								
Photosynthesis/area (nM cm^{-2}s^{-1})	0.129	0.257	**	0.121	0.181	−	*	−
Photosynthesis/ (g. dry wt.)	18.12	24.85	*	11.93	17.83	−	−	−
Photosynthesis/chlorophyll (mg a+b)	3.10	30.41	**	4.40	7.46	*	*	−
Light required to saturate (nE cm^{-2}s^{-1})	27	41	*	36	50	−	−	−
Leaf conductance (cm s^{-1})	0.137	0.080	*	0.049	0.095	**	−	**
Mesophyll conductance (cm s^{-1})	0.012	0.036	**	0.014	0.019	−	**	−
Intracellular conductance (cm s^{-1})	XXX	XXX	XXX	XXX	XXX	XXX	XXX	XXX
Dark respiration/area (nM cm^{-2}s^{-1})	−0.016	0.03	−	−0.066	−0.05	−	−	**
Light use efficiency	0.005	0.007	*	0.002	0.006	−	−	−
% total nitrogen	XXX	XXX	XXX	2.07	1.21	**	XXX	XXX
Light Harvesting Parameter								
Leaf absorptance (%)	XXX	XXX	XXX	50.3	58.6	−	XXX	XXX
Chlorophyll a/b ratio	3.00	3.12	−	3.15	3.07	−	−	−
mg chloro. a+b cm^{-2}	0.042	0.011	**	0.028	0.026	−	**	**
Leaf angle	−5.7	−40.7	**	−43.0	−26.1	*	−	**
Leaf density (g cm^{-2})	0.007	0.010	**	0.010	0.012	−	−	**
PSU size (chlorophyll/P$_{700}$)	502	329	−	438	338	−	−	−
PSU number (mM P$_{700}$ cm^{-2})	0.117	0.068	−	0.099	0.077	−	−	−

to leaf surface area, A^{mes}/A (Nobel et al., 1975). Lacking this, specific leaf weight and mesophyll thickness offer another method, with greater specific leaf weight corresponding with a greater internal surface area.

Specific leaf weight was greater in trees growing at the cut site, except for *A. rubrum*. The mesophyll layer was thicker in all three species growing at the control site. Average values and their standard deviations are 0.14 ± 0.08 mm for *L. tulipifera*, 0.07 ± 0.01 mm for *A. rubrum* and 0.07 ± 0.02 mm for *C. florida*. At the cut site, the average mesophyll thickness for the three
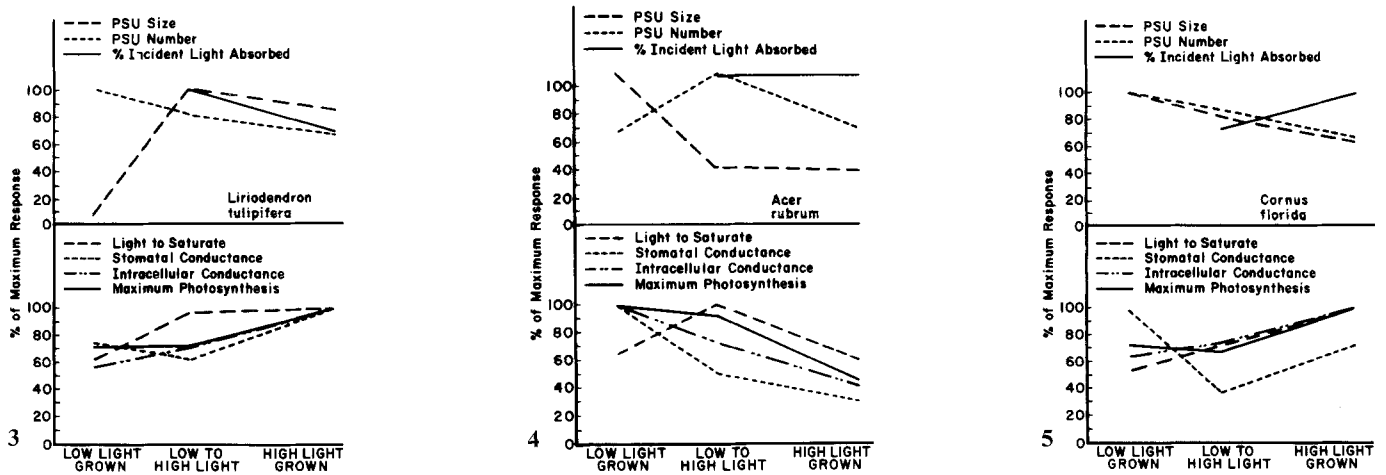
Fig. 3. Comparisons of the relative responses of gas exchange and light harvesting systems of *Liriondendron tulipfera* growing under three light regimes. The arrangement of the light regimes on the x-axis represents a gradient of increasing exposure to high light

Fig. 4. Comparisons of the relative responses of gas exchange and light harvesting systems of *Acer rubrum* growing under three light regimes. The arrangement of the light regimes on the x-axis represents a gradient of increasing exposure to high light

Fig. 5. Comparisons of the relative responses of gas exchange and light harvesting systems of *Cornus florida* growing under three light regimes. The arrangement of the light regimes on the x-axis represents a gradient of increasing exposure to high light

species respectively are 0.07 ± 0.02 mm, 0.05 ± 0.01 mm and 0.09 ± 0.02 mm. Although the absolute value of mesophyll thickness is greater at the cut site for *C. florida*, the mesophyll layer constituted a greater percentage of the thickness of the leaf at the control site (66% vs. 59% at the cut site). Thus differences in leaf anatomy were similar to those described by Nobel et al. (1975) with thicker mesophyll layers corresponding to lower specific leaf weight. Both traits are indicative of a lower transfer conductance in the control site trees.

Similarly in the laboratory, specific leaf weights are greater in the high light grown trees and increase significantly following transfer from the low to the high light regime (Tables 4–6). Mesophyll thickness was not measured on these trees. However, we believe that as in the field grown trees, a higher specific leaf weight results from lower mesophyll thickness and is indicative of greater transfer conductance in the high light grown trees.

The other component of internal resistance is carboxylation resistance. The most direct means of determining this is to measure carboxylating enzyme activity. This was not done in this study. However, since this enzyme constitutes the bulk of leaf protein (Larcher, 1975), we felt that two indirect measures of leaf protein content would indicate the relative change in carboxylation resistance. We measured percent total nitrogen of the leaves and dark respiration rates. Higher dark respiration rates in fully-expanded leaves result from higher maintenance costs usually associated with greater amounts of leaf protein (Beevers, 1970).

There was no difference in the total nitrogen contents of leaves growing at either field site (Table 3). Trees at the cut site had mean respiration rates which were lower than those of control site trees. *L. tulipifera* had rates of 0.01 nM CO_2 cm^{-2}s^{-1} at the cut site and 0.05 nM at the control site. The respiration rates of *A. rubrum* were 0.01 nM and 0.07 nM, respectively, while those of *C. florida* were 0.03 nM and 0.05 nM, respectively. Too few points were taken to examine these data statistically.

Due to equipment failure no determination of total nitrogen was made on laboratory grown trees prior to transfer. After transfer, there was no difference in the total nitrogen contents between transferred and high light grown trees (Tables 4–6). Total nitrogen contents of trees that had to be moved to the low light regime were not greatly different from those of their high light grown counterparts with *L. tulipifera* in the low light regime having 2.43% and *A. rubrum* and *C. florida* having 2.03% and 2.12%, respectively. Respiration rates were not significantly different between the original growth regimes. Following transfer to or prolonged growth in the high light regime, respiration rates increased for all species. We feel that this represents a damage response rather than an acclimation response. Thus, both indicators of carboxylation resistance are unchanged following exposure to high light. Changes in internal resistance appear to be primarily due to changes in transfer resistance.

Multiple regressions performed on the data using the maximum light-saturated photosynthetic rate as the dependent variable nearly all include some measure of internal conductance as a significant independent variable (Table 7). In over half of the equations, this variable is also the most important single variable in the model, accounting for at least 92.4% of the variance.

3) Light Harvesting Capacity

We examined the light harvesting system on several levels. The first level was leaf orientation, absorptance and a general, qualitative view of canopy structure. Canopy structure was open and conical in *L. tulipifera* growing at both field sites. However, both *A. rubrum* and *C. florida* maintained monolayer canopies at the control site and denser, multilayer canopies at the cut site (Horn, 1976). No changes in canopy structure could be discerned during the short-term laboratory experiments.

Leaf angles differed significantly between field growth sites for both *A. rubrum* and *C. florida*. Leaf orientation was nearly horizontal at the control site whereas it was 30–35° below horizontal at the cut site (Table 3). Leaf angles of *L. tulipifera* were

Table 7. Multiple regressions using the maximum photosynthetic rate as the dependent variable. Data from spring and summer field measurements are pooled. The independent variable giving the best one variable regression is underlined

Species	Site or growth regime	Regression equation[a]
L. tulipifera	Control	PMAX = 0.152 COND. + 13.01 MESCON + 0.001 NELS − 0.103 R^2 = 0.99 p = 0.0025
	Cut	PMAX = 0.072 COND. + 10.58 MESCON − 0.006, R^2 = 0.99 p < 0.0001
A. rubrum	Control	PMAX = 11.9 MESCON + 0.039, R^2 = 0.96 p < 0.001
	Cut	PMAX = 13.29 MESCON − 6.80 GDWCM + 0.124, R^2 = 0.99 p = 0.0103
C. florida	Control	PMAX = −0.004 NELS + 0.562, R^2 = 0.99 p = 0.0110
	Cut	PMAX = 10.50 MESCON + 0.069, R^2 = 0.99 p = 0.0283
L. tulipifera	Low light	PMAX = 1.37 COND + 4.90 MESCON − 0.018, R^2 = 0.99 p = 0.0086
	High light	PMAX = 1.849 COND + 3.70 MESCON − 0.0123, R^2 = 0.99 p = 0.0415
	Transferred	None possible due to missing values
	High High light	PMAX = 5.695 ICON + 4.97, R^2 = 0.97 p = 0.1117
A. rubrum	Low light	PMAX = 5.722 MESCON + 27.30 GDWCM − 0.52, R^2 = 0.98 p = 0.0027
	High light	PMAX = 2.466 COND + 2.540 MESCON + 0.001, R^2 = 0.99 p < 0.0001
	Transferred	PMAX = −1.87 COND + 15.80 ICON − 0.06 TN + 0.008, R^2 = 0.99 p = 0.1021
	High High light	PMAX = 1.86 COND − 17.39 GDWCM + 0.34, R^2 = 0.99 p = 0.0133
C. florida	Low light	PMAX = 0.077 COND + 10.45 MESCON − 0.001, R^2 = 0.99 p < 0.0001
	High light	PMAX = 1.275 COND + 4.552 MESCON − 0.01, R^2 = 0.98 p = 0.0022
	Transferred	PMAX = 0.005 NELS − 0.094, R^2 = 0.99 p = 0.0203
	High High light	PMAX = 1.318 COND − 0.13 TN + 0.32, R^2 = 0.98 p = 0.1379

[a] Independent variables

COND = Leaf conductance (cm s^{-1}); MESCON = Mesophyll conductance (cm s^{-1}); GDWCM = Specific leaf weight (g DW cm^{-2}); NELS = Light required to saturate (nE cm^{-2}s^{-1}); ICON = Intracellular conductance (cm s^{-1}); TN = % total nitrogen

essentially horizontal at both sites. These values were similar to those measured by Jackson (1970) in apple orchards (11–35° below horizontal). Leaf angles were determined with respect to their affect on amelioration of light from directly overhead. There were two reasons for this. First, sunfleck frequency and intensity at the control site were greatest when the sun was directly overhead. The brightest flecks were found to be approximately one fourth full sun. This is also the point by which most of the trees at this site have become light saturated. Hence, it appeared that photosynthesis occurring as a result of these sunflecks was of greater importance than that occurring in the diffuse light otherwise encountered. Second, the gap-like physiognomy of the cut site stand resulted in these trees being shaded by surrounding trees prior to midmorning and after midafternoon.

In the laboratory, leaf angles of both *A. rubrum* and *C. florida* were initially quite steep for plants in the high light regime (Tables 5–6). Plants in the low light regime had a horizontal leaf display. Following prolonged growth in the high light leaf angles became less steep. In the laboratory, *L. tulipifera* did undergo changes in leaf angle with the high light grown and transferred trees displaying their leaves at angles significantly above horizontal.

Changes in canopy structure and leaf orientation affect the amount of light incident upon the leaf. Changes in the amount of leaf reflectivity and transmissivity then affect the amount of light that is actually absorbed by the leaf. We determined leaf absorptance of the field grown plants and found that only *A. rubrum* absorbed significantly less light at the cut site. Hence,

any amelioration of light intensity at the chloroplast level of the other two species was a result solely of differences in leaf orientation or canopy shape. This differs from plants found in more xeric environments where most of the attenuation of the light impinging on the chloroplast is a result of the high reflectivity of the leaf surface (Ehleringer et al., 1976).

In the laboratory, absorptance was not determined during the first series of experiment due to equipment failure. We noted similar trends in these plants as in the field-grown plants (Tables 4–6). In the high light grown trees that had to be moved to the low light, absorptance values were 53.5% for *L. tulipifera*, 63.4% for *A. rubrum* and 62.5% for *C. florida*. These were essentially the same as for the high-light grown trees. No difference was noted between high light grown and transferred trees. Absorptivity was relatively low in these trees and is indicative of the very high light levels and xeric environment to which they were exposed.

The next level at which we examined the light harvesting capacity was cellular and subcellular level. We determined the number and size of photosynthetic units (PSU). The results we obtained were quite variable. Although no significant differences were found, trends in response could be ascertained (Figs. 3–5). As plants were grown in environments with more light, PSU size diminished in both field-grown and laboratory-grown trees. In the field, PSU number was greater in the cut site trees (Table 3). Both of these changes in the light harvesting apparatus are among those predicted for high light acclimation (Björkman, 1973) since they indicate the development of a greater electron transport capacity. However, as was noted by Armond and Mooney (1978),

there was no correlation between photosynthetic rates and PSU size. These workers suggested that some inactivation of reaction centers may have occurred during extraction thus yielding spurious estimates of both PSU size and number. The extreme amount of variability noted in this study would indicate that inactivation did occur. Thus, most of the acclimation response to high intensity light appears to be changes in leaf orientation and, over a longer time period, canopy structure.

Discussion

Many species of forest trees have been classified with respect to their tolerance of shaded conditions (Fowells, 1965). This situation is analogous to classifying these trees as sun or shade plants as has been done for many herbaceous species. Any classification of this sort is based upon a species' adaptability to a particular light intensity. As stated in Boardman's (1977) review, this adaptability is inherited and results from "...genetic adaptation to the light environment prevailing in the native habitat."

These tree species do not exist in an environment with a predictable, unique light intensity. Therefore, they must be preadapted to effectively utilize both high and low intensity light. This is a common adaptation within the canopy of large trees (Fuchs et al., 1977; Dinger et al., 1972; Larcher, 1969; Aubuchon et al., 1978). In suppressed understory trees, a shade adapted strategy must be utilized by the entire plant, much as in herbaceous species. Upon canopy opening, the entire plant will need to respond whereas the herbaceous shade plant may be incapable of acclimating. Therefore, which are the most responsive factors in these species' photophysiology that allow them to take advantage of canopy opening? McGee and Hooper (1970) stated that to take advantage of canopy opening, a species must be able to endure sudden exposure and be able to utilize increased water, space and nutrients. The increased utilization of water, space and nutrients involves longer-term responses than we considered here. The tree's response to sudden exposure must involve not only surviving but using the increased amounts of light available.

All three species responded to increased light intensity by increasing photosynthesis. The mechanism of this increase was not typical of sun-shade responses. The maximum light saturated photosynthetic rate most closely correlated with some measure of internal conductance. Changes in this conductance value were most attributable to changes in transfer conductance rather than carboxylation conductance. We feel this is the case since no changes were noted in total nitrogen content or dark respiration rates and since large differences were noted in specific leaf weight and leaf anatomy. This is contrary to the striking correlation several workers have found between the percent total nitrogen content of leaves and their photosynthetic rates (Mooney and Gulmon, 1979; Wilson, 1975).

Since the anatomical changes noted in these species appear to be limiting rates of maximum photosynthesis via changes in transfer conductance, a discussion of whether this represents a response to water stress or only a response to increasing light intensity is in order. Anatomical differences between sun and shade leaves have been noted in many species. The thick palisade layer, more densely packed mesophyll cells, thick cuticle, etc. of sun leaves are also xerophytic traits (Sinnott, 1960). The anatomical differences noted in this study certainly may be xerophytic adaptations as well. If these plants were responding primarily to increasing water stress, one would expect stomatal conductance to be limiting to photosynthesis more frequently than was noted. Stoma-

tal conductance appeared to be limiting only in the laboratory study. In the field, cut site trees actually had higher stomatal conductances. Other responses that occurred along with changes in leaf anatomy included changes in PSU size, chlorophyll content and the amount of light required to saturate photosynthesis. None of these changes are particularly adaptive in water stress situations. Leaf size was generally larger in shade (or low-light) grown leaves than in sun (or high-light) grown leaves. Relative size differences in sun and shade leaves of a desert broadleaf, *Hyptis emoryi*, are independent of water availability and depend directly upon total daily illuminance (Smith and Nobel, 1977). Thus, it was felt that the adaptive responses observed in the field were due primarily to changes in the light regime. However, further work would be needed on water relations of these trees in order to determine the amount of effect caused by water stress, particularly in the laboratory-grown trees.

Plants in the laboratory were grown in a nonlimiting nutrient environment. However, no difference was noted in percent total nitrogen content of leaves grown in either high or low-light regimes. This would indicate that there is no difference in carboxylating enzyme concentration in trees in either regime, although nothing is known directly about enzyme activity. However, this response is also confounded by water stress since protein synthesis is inhibited in water stressed leaves.

The biochemical conductances to CO_2 movement are quite sensitive to the nutritional and water status of the plant and may undergo rapid changes as the status of the plant changes (Hsiao, 1973; Brandle et al., 1977). In a forest gap where water and nutrient supplies would actually increase (Minckler et al., 1973), then both biophysical (transfer) and biochemical (carboxylation) components of conductance should increase. In a nutrient-limited environment like the field site, and a xeric environment like the growth chamber, acclimation would occur via changes in biophysical conductance.

Since changes in leaf anatomy were responsible for acclimation to high light, only newly expanding leaves would be capable of responding. Since one month is required for full leaf expansion in these species (Day and Monk, 1977), the time required for at least partial acclimation would be one month. Further changes in canopy structure would occur over a longer period. Since gaps of all sizes will form, trees may be exposed to high light for only a short time in a smaller gap. Adjacent canopy trees could close the gap by epicormic branching before the understory could grow into the canopy. Perhaps this long period of time required for full acclimation via changes in canopy structure, etc. represents a "bet-hedging" mechanism on the part of the two slower growing species, *A. rubrum* and *C. florida*.

Changes in the light harvesting system would be most intimately involved in the tree's ability to endure sudden exposure. Shade-adapted herbaceous species undergo photobleaching and loss of reaction centers upon exposure to bright light (Boardman, 1977). Similarly, in these trees, bleaching was noted in the shade adapted leaves. However, the new leaves formed under the high light regime were normal in appearance and more vertically oriented. Within one growing season, branching patterns change to produce a multi-layed canopy. Although no conclusive statements concerning PSU size and number can be made, it appears that the changes in canopy structure, leaf orientation and absorptance reduce the amount of light reaching the chloroplast sufficiently to obviate the necessity of large changes in PSU size or number. Other workers have defined changes in leaf angle primarily as a function of leaf age (Ledent, 1978), relative position within the canopy (Monsi and Murata, 1970) or reduction in heat load and improved

water use efficiency (Mooney et al., 1977). This latter function could be a possibility in our system as well since leaf temperatures were similar at both field sites.

Differences between the responses of each species may be responsible for the known species-specific growth responses following canopy opening. The leaf physiology of *L. tulipifera* at both field sites was commensurate with effective utilization of either high or low intensity light. There was no difference in canopy shape or leaf orientation between field sites. Responses seen in the laboratory may be due to the xeric nature of the high-light regime.

This lack of morphological response may be the reason that *L. tulipifera* cannot survive as an understory species. Typically, very little net annual production (39.9%) is allocated to leaves compared to 46.6% for *A. rubrum* and 65% for *C. florida* (Day and Monk, 1977). Considering that *L. tulipifera* is usually an inbreeder with little new genetic input (Carpenter and Guard, 1950), this allocation pattern promoting bole formation, as well as the canopy structure, leaf angle and absorptance could all be under rigorous genetic control, i.e., they may be fixed.

Therefore, in a shaded environment, there would be low rates of photosynthesis occurring in only a few leaves. If this situation were prolonged, a suboptimal carbon balance could result. The open, conical canopy structure exposing horizontally held leaves to full ambient light intensities appears to preadapt this species to a high-light environment. This appears to be a major reason for the excellent proliferation of this species in forest openings (McGee and Hooper, 1970).

C. florida and *A. rubrum* are both quite plastic in comparison, adjusting both physiologically and morphologically. Both species have multilayer canopy structures in the open site versus monolayer canopy structures at the control site (Horn, 1976). Substantial differences in leaf angle and absorptivity were noted for both species. The least amount of change in PSU size and number was noted in *C. florida*. This may account for its attenuated upward growth because of photobleaching of exposed leaves. This phenomenon was frequently noted in the laboratory. By contrast, *A. rubrum* appears to be excellently adapted for growth either in the understory or within a gap.

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