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Dependence of Photosynthetic Rates on Leaf Density Thickness in Deciduous Woody Plants Grown in Sun and Shade

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ABSTRACT

Comparisons of photosynthetic rates were made on leaves of ten species of woody dicotyledons grown in the field under full sun or under a canopy which transmitted approximately 18% of full light. Photosynthesis and dark respiration were measured and compared on various bases: area, chlorophyll, fresh weight of lamina, density thickness (fresh weight per unit area), and protein.

Light-saturated photosynthesis per unit area or unit chlorophyll was about 1.5 times greater in the sun leaves than in the shade leaves and essentially equal per unit fresh weight or unit protein. Sun leaves were thicker but the enzymes per unit fresh weight remained constant as thickness varied. Chlorophyll per unit area remained about constant; chlorophyll per unit fresh weight varied inversely with changes in leaf thickness. Thus, density thickness variation is important in photosynthetic adaptation to sun and shade. This is also shown by the relationship between light-saturated photosynthesis per unit area and density thickness.

It is well known that the photosynthetic characteristics of a broad range of plants are influenced by the light climate in which they are grown (for review: 2, 3, 19). Sun leaves are generally described as requiring a higher light saturation photon flux density, and having a higher light-saturated photosynthetic rate and light compensation point than corresponding shade leaves. However, the basis (5) on which the photosynthetic rate is expressed will make a difference in this comparison, because if sun leaves are thicker than shade leaves (2, 3, 11, 12), the amount of enzyme capacity per unit area will vary from this cause alone. Inasmuch as it is customary to express photosynthetic rates per unit area, we felt that a comparison on various other bases would be informative. Furthermore, most studies have been done with herbaceous plants (20), whereas trees have a greater need for physiological adaptability to photosynthesize in the shade of their own canopy.

Some aspects of this study have been previously reported (12–14); here we report the photosynthetic rates of ten species of deciduous temperate trees grown in field plots under full sun or under partial shade simulating a natural canopy.

MATERIALS AND METHODS

Five specimens each of ten species of trees were planted in adjacent sun and shade plots as previously described (12–14). The shade was produced by a plastic shade screen transmitting 18% of PAR. Young, fully expanded leaves or leaflets (except for Kentucky coffeetree and red oak, which produce only one flush of leaves) were selected and the petioles severed under water early on the day of measurement. The petioles were maintained in water throughout. One leaf from each available tree (five from the only shade cottonwood alive in 1977) was sampled in 1976 and 1977. The actual number of replicates was: cottonwood, *Populus deltoides* Marsh (ten sun; ten shade); American plum, *Prunus americana* Marsh (eight sun; six shade); Kentucky coffeetree, *Gymnocladus dioicus* (L.) Koch (nine sun; ten shade); catalpa, *Catalpa speciosa* Warder (eight sun; five shade); redbud, *Cercis canadensis* L. (nine sun; six shade); green ash, *Fraxinus pennsylvanica lanceolata* (Borck) Sarg. (eight sun; ten shade); red oak, *Quercus rubra* L. (three sun; five shade); mulberry, *Morus alba* L. (ten sun; ten shade); silver maple, *Acer saccharinum* L. Sarg. (eight sun; ten shade); sugar maple, *Acer saccharum* Marsh (three sun; eight shade).

Photosynthesis was measured with a Beckman model 865 infrared gas analyzer (IRGA) in the differential mode (21), using optical water filters. The leaf was held in a thermostated (30°C) plastic cuvette (13), and illuminated from above through 4 cm of water with ten incandescent reflectorized 100-w bulbs. The air was humidified at 23°C and measured 26.5 ± 0.5°C (inlet) to 27 ± 0.5°C (outlet) in the cuvette. The light was varied by the use of screens, and measured at the leaf position using a sensor reading in μmol m^{-2} s^{-1} (Lambda Instruments, model LI-185 meter with LI-190-S sensor) of PAR (400–700 nm). Air used in the measurements was ambient air from the roof of a three-story building and had CO_2 of 324 ± 10 μl/l which was similar to values reported by others (23). Each leaf was brought to the laboratory as rapidly as possible; measurement of the light curve began with the lowest flux density and worked up, with dark respiration being measured after the highest flux density. Measurements were completed between 9 AM and 3 PM. Transpiration rates or stomatal resistances were not measured, but care was taken to use leaves in good condition; if photosynthetic rates declined markedly, the leaf was discarded.

Following photosynthetic analysis, the leaf area was measured and discs (30, total area 9.96 cm^2) were punched from smooth, vein-free regions of the leaf. These were humidified and weighed for density thickness (mg cm^{-2}; 11). Fresh weight of the leaf lamina was calculated from the leaf area and density thickness. The punches were homogenized in 80% acetone and the Chl determined according to Arnon (1); the washed residue was air dried and subsequently extracted overnight with 20 ml of 1 N NaOH. The alkali-soluble extract was assayed for protein according to Lowry *et al.* (10), using a BSA standard.

Errors are expressed as SD. The differences between sun and shade samples of the same species were statistically significant at the 0.1 level (t test) except where noted. McMillen (13) reported photosynthetic rates per fresh weight with the use of whole leaf weight, instead of the leaf lamina weight calculated as above.

RESULTS

Two representative curves of gas exchange rates *versus* light flux density are shown in Figures 1 and 2. In Table I, the light-

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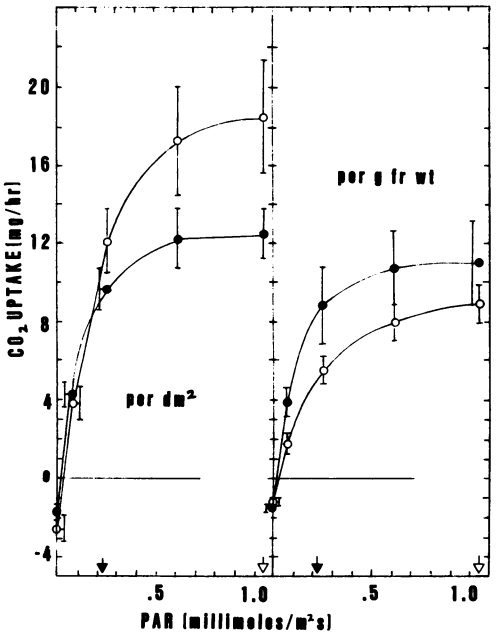

FIG. 1. Light response curves on an area and fresh weight basis for sun (○) and shade (●) leaves of Kentucky coffee tree. Each point is an average of one leaf per tree measured during two growing seasons. Arrows (▼, shade; ▽, sun) indicate 50% of maximum photon flux density in the field.

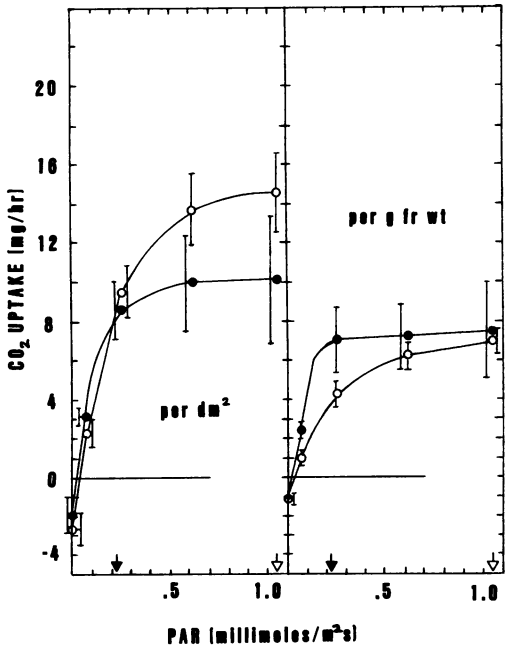

FIG. 2. Light response curves on an area and fresh weight basis for sun (○) and shade (●) leaves of silver maple. Each point is an average of one leaf per tree measured during two growing seasons. Arrows (▼, shade; ▽, sun) indicate 50% of maximum photon flux density in the field.

saturated photosynthetic rates (PSM^2) per unit area are represented, with the species ordered from high to low (sun leaves) in two groups. In group I, the sun leaves have a PSM from 1.3- to 1.8-fold greater (average 1.5) than the corresponding shade leaves. In group II, the ratio is much smaller, from 1.0 to 1.2. The differences between the two groups appear to be due to low rates for group II sun leaves, since the average and the range of absolute values for the shade leaves is almost the same for both groups. Further justification of this grouping is offered below.

[2] Abbreviation: PSM, photosynthetic maximum.

Table I. *Maximum Photosynthetic Rate—Area Basis*

Species	Sun	Shade	Sun/Shade
	mg CO_2 dm^{-2} h^{-1}		*ratio*
Group I			
Mulberry	19.4 ± 3.6[a]	12.3 ± 1.0	1.58
Cottonwood	19.2 ± 2.1[a]	10.5 ± 2.9	1.83
Kentucky coffeetree	18.5 ± 3.5[a]	12.2 ± 1.8	1.52
Silver maple	14.6 ± 1.9	10.0 ± 2.7	1.46
Red oak	10.4 ± 1.0	7.9 ± 5.8[b]	1.32
Sugar maple	8.5 ± 2.1	6.7 ± 1.2	1.27
Mean	15.1	9.9	1.50
Group II			
Catalpa	12.5 ± 2.6	10.4 ± 1.5	1.20
Green ash	11.0 ± 2.9	9.8 ± 2.3[b]	1.12
Redbud	10.4 ± 3.8	9.8 ± 1.1[b]	1.06
Plum	7.6 ± 3.9	7.2 ± 3.7[b]	1.06
Mean	10.4	9.3	1.11

[a] These sun leaves may not have been fully light saturated; see Figure 1.

[b] Difference between sun and shade was nonsignificant (*t* test).

Table II. *Maximum Photosynthetic Rate—Fresh Weight Basis*

Species	Sun	Shade	Sun/Shade
	mg CO_2 g^{-1} fresh wt h^{-1}		*ratio*
Group I			
Mulberry	12.15 ± 2.8	13.44 ± 2.3[a]	0.90
Cottonwood	9.51 ± 1.2	7.15 ± 2.2	1.33
Kentucky coffeetree	10.95 ± 2.2	15.93 ± 4.4	0.69
Silver maple	9.71 ± 1.5	10.48 ± 3.3[a]	0.92
Red oak	8.15 ± 0.5	6.81 ± 3.1[a]	1.20
Sugar maple	6.42 ± 1.9	7.13 ± 1.1[a]	0.90
Mean	9.48	10.16	0.99
Group II			
Catalpa	5.77 ± 1.4	9.19 ± 2.3	0.63
Green ash	5.05 ± 1.8	12.19 ± 5.1	0.41
Redbud	7.40 ± 1.7	10.12 ± 2.2	0.73
Plum	4.75 ± 3.2	7.08 ± 3.7[a]	0.67
Mean	5.74	9.64	0.61

[a] Difference between sun and shade was nonsignificant (*t* test).

The PSM expressed on a fresh weight basis is given in Table II. In eight of ten species, the shade leaves had a higher rate of photosynthesis, but the differences were nonsignificant in half the species. Group I had an average value of the sun/shade ratio of about 1.0, in contrast to group II where it is 0.6. Again, it appears that the sun leaves of group II may be deficient.

In Table III is shown PSM per unit Chl. In group I, the sun/shade ratios fell closely around 1.5 (1.43–1.55), while in group II they averaged about 1.0 with more scatter (0.88–1.26). The overall ratio of Chl per unit area in sun and shade leaves was 1.08 (Table IV), and the species values ranged from 1.36 to 0.85 (six species having nonsignificant differences). Inasmuch as the Chl amounts for group II are similar to those for group I (although somewhat less), it appears that the photosynthetic rates of group II sun leaves are low, rather than the Chl values being high.

Overall, group I appears to have given a more uniform set of data. Furthermore since low photosynthetic rates could have a variety of trivial causes, we are inclined to pay more attention to

Table III. *Maximum Photosynthetic Rate—Chl Basis*

Species	Sun	Shade	Sun/Shade
	mg CO_2 mg^{-1} Chl h^{-1}		*ratio*
Group I			
Mulberry	4.62 ± 1.6	3.04 ± 1.7	1.52
Cottonwood	4.94 ± 2.5	3.25 ± 1.5	1.52
Kentucky coffeetree	3.62 ± 1.5	2.53 ± 0.8	1.43
Silver maple	4.28 ± 1.4	2.89 ± 0.8	1.48
Red oak	2.70 ± 1.3	1.74 ± 0.6[a]	1.55
Sugar maple	1.97 ± 0.4	1.30 ± 0.3	1.52
Mean	3.69	2.44	1.50
Group II			
Catalpa	4.19 ± 1.0	4.06 ± 0.9[a]	1.03
Green ash	2.14 ± 0.8	2.42 ± 0.4	0.88
Redbud	2.98 ± 1.6	2.37 ± 0.5[a]	1.26
Plum	2.13 ± 1.5	2.17 ± 1.0[a]	0.98
Mean	2.85	2.76	1.04

[a] Difference between sun and shade was nonsignificant (*t* test).

Table IV. *Chl—Area Basis*

Species	Sun	Shade	Sun/Shade
	μg cm^{-2}		*ratio*
Group I			
Mulberry	44 ± 10	41 ± 10[a]	1.07
Cottonwood	43 ± 10	35 ± 10	1.23
Kentucky coffeetree	54 ± 10	50 ± 20[a]	1.08
Silver maple	33 ± 10	36 ± 10[a]	0.92
Red oak	41 ± 20	43 ± 20[a]	0.95
Sugar maple	44 ± 10	52 ± 10	0.85
Mean	43	43	1.02
Group II			
Catalpa	32 ± 10	24 ± 10	1.33
Green ash	57 ± 10	42 ± 10	1.36
Redbud	40 ± 20	42 ± 10[a]	0.95
Plum	34 ± 10	33 ± 10[a]	1.03
Mean	41	35	1.17

[a] Difference between sun and shade was nonsignificant (*t* test).

Table V. *Maximum Photosynthetic Rate—Protein Basis*

Species	Sun	Shade	Sun/Shade
	mg CO_2 g^{-1} protein h^{-1}		*ratio*
Group I			
Mulberry	310 ± 200	500 ± 300	0.62
Cottonwood	190 ± 30	310 ± 200	0.61
Kentucky coffeetree	200 ± 100	280 ± 100	0.71
Silver maple	270 ± 40	310 ± 100[a]	0.87
Red oak	120 ± 30	100 ± 30[a]	1.20
Sugar maple	100 ± 30	110 ± 30[a]	0.90
Mean	198	268	0.82

[a] Difference between sun and shade was nonsignificant (*t* test).

group I.

We have taken fresh weight as a measure of the metabolic mass of the tissue, but since this may seem too crude, we have also measured total leaf protein (alkali-soluble, to include membrane proteins). PSM per unit protein for group I is shown in Table V. Expressed this way, the shade leaves appear more active than the sun leaves; the sun/shade ratios average 0.82. However, the measurement errors were larger than those in Tables I and II, reducing our ability to use this basis. On an absolute basis, the rates per unit fresh weight are roughly correlated with those per unit protein (Table II *versus* V). However, the protein measurements do not seem to provide a more useful basis than fresh weight.

Table VI. *Dark Respiration—Fresh Weight Basis*

Species	Sun	Shade	Sun/Shade
	mg CO_2 g^{-1} fresh wt h^{-1}		*ratio*
Group I			
Mulberry	2.05 ± 0.48	1.89 ± 0.42[a]	1.08
Cottonwood	1.97 ± 0.10	1.39 ± 0.60	1.42
Kentucky coffeetree	1.53 ± 0.48	2.15 ± 0.46	0.71
Silver maple	1.81 ± 0.64	1.64 ± 0.57[a]	1.10
Red oak	1.22 ± 0.31	1.25 ± 0.10[a]	0.98
Sugar maple	1.01 ± 0.19	1.07 ± 0.08[a]	0.94
Mean	1.60	1.56	1.04

[a] Difference between sun and shade was nonsignificant (*t* test).

Table VII. *Slope of Light-Limited Photosynthetic Curve—Area Basis*

The numbers represent the gross photosynthetic rate at 64 μmol photons m^{-2} s^{-1}, times 1000/64.

Species	Sun	Shade	Sun/Shade
	(mg CO_2 $dm^{-2}h^{-1}$) 1000/64		*ratio*
Group I			
Mulberry	92 ± 20	88 ± 10[a]	1.05
Cottonwood	102 ± 10	80 ± 20	1.28
Kentucky coffeetree	100 ± 20	94 ± 10[a]	1.06
Silver maple	78 ± 10	79 ± 20[a]	0.99
Red oak	69 ± 3	55 ± 10	1.25
Sugar maple	53 ± 4	49 ± 15[a]	1.08
Mean	82	74	1.12

[a] Difference between sun and shade was nonsignificant (*t* test).

Taking group I on either an area or Chl basis, the photosynthetic rates (light-saturated) of sun leaves are about 1.5 times higher than shade leaves. But on a fresh weight or protein basis, the rates of shade leaves are the same as (fresh weight) or greater than (protein) those of sun leaves. Since fresh weight per unit area can be taken as a measure of leaf thickness (density thickness), this means that the sun leaves are thicker than shade leaves, but have the same enzyme concentration.

A check on these ideas lies in the respiratory rates (Table VI). The rate per unit fresh weight is about the same in sun and shade leaves, with variation between species of 2-fold as in photosynthetic rate. Taking the ratios of dark respiration to net photosynthesis shows that the former averages 0.16 times the latter, with little difference between sun and shade leaves, and a range of from about 0.14 to 0.20 between species. Thus, it is not just the photosynthetic capacity that remains in constant concentration, but the respiratory capacity as well. The Chl per unit fresh weight (not shown, but calculable from Tables I and II) was in all cases greater in shade leaves, the sun/shade ratio averaging 0.60. Thus, PMS and Chl vary independently.

One would expect that the Chl content would control not the maximum photosynthetic rate but the light-limited photosynthetic rate. Inasmuch as the Chl content per unit area varies but little (Table IV), one would therefore expect the initial slopes of the light curves per unit area to vary little between sun and shade leaves. This is so (Figs. 1 and 2; Table VII). Comparison with the ratios in Table IV shows that much of the variation seen is explained by variation in Chl content (see also 13). The higher light compensation points of the sun leaves in these species is seen to be due almost entirely to the difference in leaf thickness in the presence of a constant Chl content per unit area, the higher respiratory rate of the thicker leaves displacing the curves downward (Figs. 1 and 2). The mean compensation points of sun and

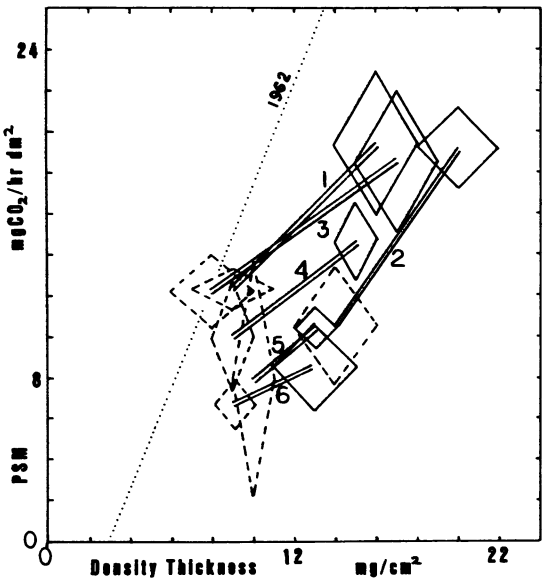

FIG. 3. Effect of leaf thickness on photosynthetic rate. The maximum photosynthetic rate—area basis is plotted *versus* the density-thickness, measured as the fresh weight per unit area of leaf punches from the leaf lamina. The corners of the diamonds represent the mean values ± 1 SD (from Table I and Ref. 12). The diamonds drawn with solid lines are the sun specimens, those drawn with dashed lines are the shade specimens. The double lines connect means of sun and shade specimens of each species: 1 (mulberry), 2 (cottonwood), 3 (Kentucky coffee tree), 4 (silver maple), 5 (red oak), 6 (sugar maple). The dotted line is the upper limiting value of the array shown previously (11), with the lower intercept being an approximate value for the thickness of the epidermis.

shade leaves of group I were 33 and 21 μmol m^{-2} s^{-1}, respectively; for all ten species, they were 29 and 21, respectively (13).

DISCUSSION

The adaptive response of group I is summarized in Figure 3, where the PMS per unit area (Table I) is plotted *versus* density thickness. The species specific differences in anatomy or cytology dictate the lack of exact correspondence between the species, but within the errors (shown by the diamonds), the slopes of the lines connecting the sun and shade treatments of single species are identical (or nearly so; see Table II). There are also evident differences between species in the extent of adaptability to the light climate of growth but these are not related to shade tolerance (12), since cottonwood (the most intolerant species) shows the largest response (Tables I, II, VI), and rates in the shade are similar to species much more shade tolerant.

The responses of group II are quite different, since the PMS per unit area was nearly the same in sun and shade specimens (Table I), leading to horizontal lines when plotted as in Figure 3 (not shown). Since the responses of group II in density thickness and in Chl content were similar to those of group I, we feel that the measured photosynthetic rates of the sun leaves of group II are in error.

A graph similar to Figure 3 was published previously (11) using data of Willstätter and Stoll (both CO_2- and light-saturated), where an upper limit ('roof') of active concentration was identified. That upper limit was higher than most values found here, due no doubt to the CO_2 concentration difference. Although the original roof was drawn (11) through an estimated value for the epidermal thickness, our current data do not permit us to distinguish this as distinct from an extrapolation through the origin.

Comparison with other work on the sun/shade response is hampered by lack of studies which measured density thickness. However, two studies have been found in which tissue volumes were measured from cross-sections, and so can be related to this work if an assumption is made for density (*i.e.* 1 g cm^{-3}). Chabot and Chabot (4), with the woodland herb *Fragaria vesca*, using a variety of light and temperature treatments, got data which fall at the lower end of the data displayed in Figure 3. Their epidermal thicknesses were between 2.4 and 3.5 mg cm^{-2}, but the total density thickness of the highest light treatment was only 11.5. The highest photosynthetic rate in the light treatment series was obtained with a medium flux density: 6 mg CO_2 $(h\ dm^2)^{-1}$ with density thickness of 6.7. It seems that they used a shade-adapted ecotype, since Willstätter and Stoll (11) reported the same species with a much greater photosynthetic rate and leaf thickness. Patterson *et al.* (17) used cotton in a comparison between field-grown and phytotron-grown plants in which the former received the larger daily light flux. Their epidermal thicknesses and rates fell beyond the display in Figure 3 (but in the range shown in Ref. 11). Both of these cases appear to fit the trend shown in Figure 3.

Other authors have measured other features of leaf anatomy (2, 3, 5, 6, 15, 16, 18, 24). In most of these cases, the thinner leaves (however measured) had either the same or larger photosynthetic rates as the thicker ones, when expressed on a thickness basis.

Our view is that density thickness is both an appropriate parameter and an easy one to measure, in the description of deciduous laminate leaves. The dry weight per unit area (specific leaf weight) is not a volume measure and may vary capriciously with stored carbohydrate. Total leaf thickness (and leaf volume calculated there from) suffers from the inclusion of air; while this is essential, it is energetically free and should not be adaptationally limited or limiting. Likewise, the internal leaf surface varies with the leaf thickness (15), and since all the chloroplasts are adjacent to intercellular spaces, the mesophyll volume, protein content, or (most easily) density thickness should essentially measure the same thing. Furthermore, it is likely that the true 'mesophyll resistance' in the pathway of CO_2 (*i.e.* from the substomatal cavity to the chloroplast) is negligible (7).

Optimization models of leaves and canopies are of much interest (7–9, 22). Variation in leaf thickness has not explicitly been taken into account in these, but the efficiency of leaves should be related to their thickness, if the water loss is a function of leaf surface and photosynthetic rate is a function of thickness.

Some authors have attributed the difference between sun and shade leaves to particular compositional factors such as the amount of ribulose-1,5-bisP carboxylase/oxygenase. Correspondence has been found in some cases and not in others (2, 3, 16), but in the model proposed by Hall (7, 9) the limiting rates of carboxylation and NADP reduction are equivalent. We believe, then, that the relationship found here between leaf density thickness and PMS is the one most likely to be found in species which must adapt to a wide range of light climates, such as forest trees.

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