Original article

Influence of shade on photosynthetic gas exchange of 7 tropical rain-forest species from Guadeloupe (French West Indies)

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Summary — Young seedlings from 7 tropical rain-forest species of Guadeloupe (French West Indies): *Dacryodes excelsa, Amanoa caribaea, Richeria grandis, Simaruba amara, Symphonia globulifera, Byrsonima coriacea* and *Podocarpus coriaceus* were grown for 1–2 yr in full sunlight or under 4 artificially shaded tunnels transmitting 6, 11, 19 and 54% daylight. Photosynthetic gas exchanges of attached leaves or branches were then studied in the laboratory. Net photosynthesis-light curves were analysed for an average of 4 seedlings per species and per light treatment. Maximum photosynthesis on a leaf-area basis of sungrown seedlings varied from 3.4 µmol CO_2 m^{-2} s^{-1} for *Dacryodes excelsa* to 7.9 µmol CO_2 m^{-2} s^{-1} for *Simaruba amara*. For all the species studied and when the measurements were expressed on a leaf-area basis, maximum photosynthesis of sun-grown seedlings was higher than for shade-grown seedlings. The opposite was observed for photosynthesis under limited light and for apparent quantum yield. We also observed a decrease in maximum photosynthesis and an increase in apparent quantum yield when specific leaf area increased, ie when the plants were more shaded. The range of variation in photosynthetic response between full sunlight and full shade made it possible to characterize the photosynthetic plasticity of the species. The results were compared with those obtained for other tropical rain-forest species. They are discussed in terms of photosynthetic and morphological plasticity, shade adaptation, and of the species' place in tropical rain-forest succession.

tropical rain forest / forest succession / shade tolerance / net photosynthesis / photosynthetic plasticity

Résumé — Influence de l'ombrage sur les échanges gazeux photosynthétiques de 7 espèces de la forêt tropicale humide de Guadeloupe (Petites Antilles). *De jeunes semis de 7 espèces de la forêt tropicale humide de Guadeloupe (Petites Antilles) :* Dacryodes excelsa, Amanoa caribaea, Richeria grandis, Simaruba amara, Symphonia globulifera, Byrsonima coriacea *et* Podocarpus coriaceus *ont été élevés pendant 1 à 2 ans en pleine lumière et sous 4 tunnels artificiellement ombragés laissant passer 6%, 11%, 19% et 54% de la pleine lumière. À la fin de cette période, on a étudié au laboratoire les échanges gazeux photosynthétiques de feuilles ou de rameaux rattachés aux jeunes plants. Des courbes photosynthèse nette – éclairement ont ainsi été réalisées en moyenne pour 4*

plants par espèce et par tunnel. La photosynthèse maximale des plants de pleine lumière varie de 3,4 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ pour Dacryodes excelsa à 7,9 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ pour Simaruba amara. Pour toutes les espèces étudiées et lorsque les mesures sont rapportées à l'unité de surface foliaire, la photosynthèse maximale des plants de pleine lumière est supérieure à celle des plants d'ombre, tandis que l'on observe l'inverse pour la photosynthèse en éclairement limitant et pour le rendement quantique apparent. On note parallèlement une diminution de la photosynthèse maximale et une augmentation du rendement quantique apparent lorsque la surface spécifique des feuilles augmente, c'est-à-dire quand les plants sont de plus en plus ombragés. L'amplitude des variations de photosynthèse entre la pleine lumière et le plus fort ombrage permet de caractériser la plasticité photosynthétique des espèces. Les résultats sont comparés à ceux obtenus avec d'autres espèces forestières de la zone tropicale humide. Ils sont enfin discutés en termes de plasticité morphologique et photosynthétique, d'adaptation à l'ombrage, et d'emplacement dans le cycle de succession des espèces dans les forêts tropicales humides.

forêt tropicale humide / succession forestière / tolérance à l'ombrage / photosynthèse nette / plasticité photosynthétique

INTRODUCTION

The morphological, anatomical, structural, ultrastructural, biochemical or photosynthetic response of herbaceous species and shrubs to different light conditions during growth is well known (eg, Boardman, 1977; Björkman, 1981; and Givnish, 1988). In general, the light-saturated rate of photosynthesis, the light compensation point, and the light saturation plateau are higher for sun-grown plants than for shade-grown plants. On the other hand, sun-grown plants have leaves with a lower specific area, and which contain smaller chloroplasts than shade-grown plants.

Most of the responses described above are also applicable to trees, but the responses of trees may be modified because of their variable social status within a forest. For example, sun-shade responses within a tree may be different from sun-shade responses of seedlings of the same species (Leverenz and Jarvis, 1980). It is also important to investigate sun-shade adaptation at the genotype level.

The sun-shade responses can be expressed by different degrees of shade tolerance, and have long been used by foresters in the silvicultural management of forest stands. Baker's (1949) tables of tolerance for conifers and hardwood species of North America are an example.

Generally, shade-intolerant forest species are characterized by higher photosynthetic potentials than those of shade-tolerant species. However, what differentiates the species and makes it possible to classify them in relation to one another, is the possible capacity for intolerant species to tolerate more or less shade, and for tolerant species to survive in high light conditions.

When a species' forest behavior is empirically known, then it is usually possible to explain its photosynthetic capacities and its morphology in terms of shade tolerance (see, for example, Tsel'Niker, 1977; Bazzaz and Carlson, 1982; McMillen and McClendon, 1983, among others). However, when there is no empirical knowledge for a given species of its ecology or its silvicultural behavior, is it possible to deduce the degree of shade tolerance simply from its photosynthetic capacities and its reactions to experimental variations in light environment? This question is fundamental for a wide variety of forest species which

make up the tropical rain forest and about which we have almost no silvicultural knowledge.

In unmanaged tropical rain forests, the presence of a species in a particular place at a particular time is almost always conditioned by its response to light. Of course, it also depends on other factors, such as seed availability, dispersal and germination of these seeds, competition and allelopathy processes, or edaphic conditions. This is the way the species' succession cycle is developed from pioneer species, which require high quantities of light, which are generally shade intolerant, and which colonize open space, to species of stable adult stands, which are generally more shade tolerant when young (Whitmore, 1978; Rollet, 1983). The opening of these stable stands by natural wind-fallen wood or partial harvesting, creates gaps whose size (ie light conditions as well) partially determines which species will be able to establish themselves.

The problem of species succession and shade tolerance has been posed for the Guadeloupe tropical rain forest where we conducted silvicultural studies on 7 commercially interesting species. The objective was to favor natural regeneration of these species (Ducrey and Labbé, 1985). The study of the seedlings in relation to the intensity of regeneration fellings gave us preliminary information about light response of the species whose regeneration was induced by silvicultural treatment (Ducrey and Labbé, 1986). To improve this information, we cultivated seedlings from 7 forest species under semi-controlled light conditions under differently shaded tunnel greenhouses. In a previous article (Ducrey, 1992), we studied the morphological variations of the leaf system in relation to shade. In this paper, we shall examine the photosynthetic response of the seedlings of these 7 species cultivated under 5 different shade environments. We shall also try

to answer the following question. Can a species' shade tolerance be predicted by the photosynthetic response of seedlings of that species grown under a range of light environments?

PLANT MATERIAL AND STUDY METHOD

Species studied and seedling growth conditions

The seedlings used for the experiment were sampled from the tropical rain forest of Guadeloupe, French West Indies, in the Caribbean Islands. They come from the area called "Débauchée" (Ducrey, 1986) at an elevation of 250 m. Mean temperatures were 23°C for January and 26°C for July. Mean annual rainfall was more than 3 000 mm. There was a short dry season from January to April, where monthly rainfall was always greater than 100 mm.

The 7 species studied were evergreen dominant and co-dominant trees from middle and late successional cycle of the Guadeloupe's rain forest. Dacryodes excelsa Vahl, Amanoa caribaea Kr and Urb, and Podocarpus coriaceus LC Rich are late successional, shade-tolerant species. Simaruba amara Aubl and Richeria grandis Vahl are mid-successional, shade-intolerant species. Byrsonima coriacea is present in mid- and late succession, whereas Symphonia globulifera L, a wet soil specialist, is a late successional species. However the shade reaction of these 2 species is not well known.

The seedlings were generally aged 1 yr, harvested from the forest margin in January 1981, and transplanted to 9-l pots filled with soil from the upper horizon of the forest floor. The pots were placed under a forest canopy to ensure a better recovery. After 3 months, the pots were transferred to tunnel greenhouses, 15 m long and 6 m wide, covered with shade cloth transmitting the amount of light desired. The same procedure was applied to all species except P coriaceus whose seedlings were all placed in the same tunnel in March 1981 and then distributed to the different tunnels in January 1982, and A caribaea which was started 1 yr later in March 1982. The seedlings were regularly wa-

tered twice a week. No fertilizer was used during the experiment.

The seedlings were separated into 5 treatments: 4 treatments under plastic tunnels and 1 open air, full sunlight treatment. The 4 tunnel shelters were covered with reinforced transparent PVC to protect against rainfall. Three of them were shaded with different black neutral shade screens in order to obtain various shade conditions. Finally, global radiation measurements with Li–Cor, Li 200 pyranometers indicates 6.4% light under tunnel I, 11.4% light under tunnel II, 18.8% light under tunnel III, and 54.3% light under tunnel IV.

Table I shows climatic data under tunnel shelters. These were opened and oriented in the direction of prevailing winds. The temperature and humidity of the air under the tunnels were the same as those in the open-air treatment (meteorological data measured with a weather station), except for tunnel IV whose maximum temperatures were slightly higher than in the others. In fact, the shade under this tunnel was created using only a reinforced transparent plastic cover which caused a more significant warming effect. Because of only small climatic differences between experimental treatments and additional watering, we can consider that light is the major variable between the 5 treatments.

Measurements of net photosynthesis

Photosynthesis measurements took place from the end of October to the end of December 1982. The seedlings were kept under the experimental light conditions for close to 2 yr (except for A caribaea and P coriaceus which were kept for only 1 yr) and all the leaves measured were initiated and grown under the treatment conditions. These leaves could be considered as being completely acclimated to the experimental light conditions. Measurements were made on fully developed leaves. The mean size of the seedlings used in photosynthesis measurements is shown in table II.

The measurements of net photosynthesis were carried out in the laboratory on attached leaves or branches placed in a ventilated chamber, perpendicular to the light source. The measurement of carbon dioxide exchange was made in an open system using an infrared differ-

ential gas analyser of carbon dioxide (ADC model) which measured the difference in CO_2 concentration between the reference circuit and the measured circuit. The temperature was set between 25 and 27°C using a water cooling system where the measurement chamber was submerged in a tank containing cooled water. Relative humidity of the air was maintained between 70 and 90% by bubbling air into a water flask maintained at the temperature of the desired dew point.

Lighting was achieved using a mobile stand of tungsten-halogen quartz lamps with a unit power of 1 000 W. Photosynthetic active radiation was measured with a Li–Cor, LI 190 quantum sensor. Four light levels were used: 28 and 56 μmol m^{-2} s^{-1} for low light; 368 and 632 μmol m^{-2} s^{-1} for saturating light. A few measurements were also taken at 924 μmol m^{-2} s^{-1}, but the results were always less than or equal to those at 632 μmol m^{-2} s^{-1}. We thus considered that saturation was reached between 368 and 632 μmol m^{-2} s^{-1}, and we did not use the data for 924 μmol m^{-2} s^{-1}. Gas exchange measurements were made first in darkness to calculated dark respiration and then with increasing light levels.

The area and dry weight of the leaves studied were also calculated. This made it possible to calculate photosynthesis per unit of leaf area and per unit of leaf dry matter, and to determine the specific leaf area (ratio between leaf area and leaf dry weight) of the leaves studied (table III).

Dark respiration and photosynthesis in low light made it possible to determine the initial slope of the net photosynthesis-light curves which is called apparent quantum yield and which approximates to the quantum yield of the leaf (number of moles of CO_2 assimilated per mole of photons absorbed by the leaf) except that only incident photon flux density was measured.

Light-saturated net photosynthesis was then calculated as an average of photosynthesis values recorded at 368 and 632 μmol m^{-2} s^{-1}. In the same way, light-limited net photosynthesis is an average of photosynthesis values recorded at 28 and 56 μmol m^{-2} s^{-1}.

An average of 4 seedlings per tunnel and per species were used, representing a total of 147 plants and 147 net photosynthesis-light curves. The 4 variables defining the 147 net photosynthesis-light curves carried out for this study were analysed by an analysis of variance with 1 factor, Tunnel, for each species. Differences be-

Table I. Description of microclimatic conditions under experimental tunnel shelters.

		Tunnel I			Tunnel II			Tunnel III			Tunnel IV			Full sunlight		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Warm month September 1981	Temperature (°C)	22.3	26.3	30.2	21.9	25.8	29.7	20.5	25.1	29.7	21.4	26.7	32.0	21.9	25.8	29.7
	Relative humidity (%)	66		93	72		99	70		99	68		97	67		94
Cool month January 1982	Temperature (°C)	19.1	22.6	26.1	20.1	23.6	27.1	19.3	23.3	27.2	18.8	23.2	27.6	19.7	23.3	26.8
	Relative humidity (%)	65		97	62		94	62		95	62		97	72		98
Mean May 81 to February 82	Temperature (°C)	21.8	25.1	28.4	22.0	25.3	28.6	21.0	24.8	28.5	21.4	26.0	30.6	21.8	25.1	28.4
	Relative humidity (%)	71		94	72		97	70		96	67		97	71		95
Relative light intensity (%)			6.4			11.4			18.8			54.3			100	

Table II. Mean height (in cm) of the seedlings used for studies of photosynthetic gas exchange. *

	Tunnel I	Tunnel II	Tunnel III	Tunnel IV	Full sunlight	Species average
Dacryodes excelsa	56	48	44	–	58	53[d]
Amanoa caribaea	52	65	65	57	50	58[d]
Richeria grandis	70	83	89	79	57	77[c]
Simaruba amara	71	72	51	45	44	56[d]
Symphonia globulifera	90	98	93	77	78	85[b]
Byrsonima coriacea	99	102	127	101	81	103[a]
Podocarpus coriaceus	62	68	57	55	42	57[d]
Tunnel average	70[ab]	77[a]	76[a]	68[b]	61[c]	

* Identical letters indicate values not significantly different at a 5% level (Duncan's test) for averages by species and by tunnel.

Table III. Specific leaf area (in $dm^2 \, g^{-1}$) of the leaves used for gas-exchange measurements. *

	Tunnel I	Tunnel II	Tunnel III	Tunnel IV	Full sunlight	Species average
Dacryodes excelsa	1.74[a]	1.49[a]	1.76[a]	–	1.04[b]	1.48[b]
Amanoa caribaea	1.69[a]	1.64[a]	1.47[b]	1.35[b]	0.99[c]	1.46[b]
Richeria grandis	2.52[a]	2.25[b]	1.93[c]	1.51[d]	1.11[c]	1.87[a]
Simaruba amara	1.87[a]	1.78[ab]	1.52[b]	1.06[c]	0.84[c]	1.38[bc]
Symphonia globulifera	1.86[a]	1.68[a]	1.88[a]	1.15[b]	1.36[b]	1.50[b]
Byrsonima coriacea	1.68[a]	1.66[a]	1.31[b]	0.93[c]	0.81[c]	1.30[c]
Podocarpus coriaceus	1.21[a]	1.07[ab]	0.97[b]	0.74[c]	0.79[c]	0.95[d]
Tunnel average	1.79[a]	1.65[b]	1.56[b]	1.11[c]	1.04[c]	

* For each species, identical letters indicate means between tunnels not significantly different at a 5% level (Duncan's test). The last column shows statistical differences between species, all tunnels combined.

tween tunnels were set out with a Duncan's test of multiple mean comparisons. Relationships between these 4 variables and relative light intensity were analysed by linear regression, species by species, on raw data.

RESULTS

The results shown in table IV represent data recorded per unit of leaf area; those in table V show data recorded per unit of dry matter. To facilitate the interpretation

of these results, we combine the net photosynthesis-light curves for each species in dense shade (tunnel I, 6% relative light intensity) and full sunlight (tunnel V, 100% RLI) in figure 1.

Light-saturated net photosynthesis

For plants grown in full sunlight, light-saturated photosynthesis recorded per unit of leaf area was the highest for *S amara*

Table IV. Mean values of gas-exchange parameters expressed on a leaf-area basis and derived from net photosynthesis-light curves *.

	Tunnel I 6%	Tunnel II 11%	Tunnel III 19%	Tunnel IV 54%	Tunnel V 100%	Mean per species
Light-saturated photosynthesis (μmol m^{-2} s^{-1})						
D excelsa	2.4^a	2.7^a	1.9^a	–	3.4^a	2.7^c
A caribaea	3.5^c	4.7^a	4.3^{ab}	3.6^{bc}	4.2^{abc}	4.1^b
R grandis	3.8^c	4.1^c	4.2^{bc}	5.2^a	5.0^{ab}	4.5^b
S amara	4.2^b	6.2^{ab}	6.5^{ab}	5.9^{ab}	7.9^a	6.1^a
S globulifera	4.2^a	4.5^a	4.6^a	4.4^a	4.6^a	4.5^b
B coriacea	4.1^{bc}	3.5^c	5.1^{ab}	4.4^{abc}	5.5^a	4.5^b
P coriaceus	3.7^b	4.4^{ab}	4.4^{ab}	4.5^{ab}	5.1^a	4.4^b
Mean per tunnel	3.6^b	4.3^a	4.4^a	4.8^a	4.9^a	
Light-limited photosynthesis (μmol m^{-2} s^{-1})						
D excelsa	1.2^a	1.3^a	1.0^a	–	0.8^a	1.0^c
A caribaea	1.7^b	2.1^a	1.8^b	1.7^b	1.5^b	1.8^{ab}
R grandis	2.2^a	2.1^a	2.1^a	2.0^a	1.7^b	2.1^a
S amara	2.2^a	2.3^a	2.3^a	1.9^{ab}	1.7^b	2.1^a
S globulifera	2.2^a	2.0^a	1.7^a	1.7^a	1.8^a	1.8^a
B coriacea	2.1^{ab}	1.6^c	2.3^a	1.8^{bc}	1.6^c	1.9^a
P coriaceus	1.6^b	2.0^a	1.7^{ab}	1.0^c	1.2^c	1.5^b
Mean per tunnel	1.9^a	1.9^a	1.9^a	1.7^a	1.5^b	
Dark respiration (μmol m^{-2} s^{-1})						
D excelsa	0.13^a	0.04^a	0.13^a	–	0.15^a	0.11^{ab}
A caribaea	0.11^b	0.00^a	0.00^a	0.12^b	0.20^c	0.07^a
R grandis	0.06^a	0.15^{ab}	0.19^b	0.33^c	0.25^{bc}	0.22^{bc}
S amara	0.24^a	0.35^a	0.16^a	0.24^a	0.64^b	0.32^c
S globulifera	0.25^{ab}	0.04^a	0.12^{ab}	0.37^b	0.15^{ab}	0.13^{ab}
B coriacea	0.03^a	0.05^a	0.21^a	0.10^a	0.40^b	0.17^{ab}
P coriaceus	0.53^{ab}	0.22^a	0.40^{ab}	0.52^{ab}	0.58^b	0.45^d
Mean per tunnel	0.23^{bc}	0.12^a	0.14^{ab}	0.29^{cd}	0.37^d	
Apparent quantum yield (mmol mol^{-1})						
D excelsa	32^a	27^a	21^a	–	23^a	25^d
A caribaea	38^a	50^a	42^a	42^a	42^a	43^c
R grandis	54^{abc}	50^{bc}	57^{ab}	58^a	48^c	54^{ab}
S amara	59^{ab}	65^a	60^{ab}	52^b	56^{ab}	58^a
S globulifera	60^a	44^{ab}	40^{ab}	40^{ab}	30^b	43^c
B coriacea	52^{ab}	41^d	55^a	45^{cd}	49^{bc}	48^{bc}
P coriaceus	53^a	53^a	53^a	37^b	43^{ab}	48^{bc}
Mean per tunnel	49^a	49^a	47^a	47^a	42^b	

* For each parameter and each species, identical letters indicate means between tunnels not significantly different at a 5% level (Duncan's test). The last column shows statistical differences between species, all tunnels combined.

Table V. Mean values of gas-exchange parameters expressed on a leaf dry matter basis and derived from net photosynthesis-light curves *.

	Tunnel I 6%	Tunnel II 11%	Tunnel III 19%	Tunnel IV 54%	Tunnel V 100%	Mean per species
Light-saturated photosynthesis (nmol g^{-1} s^{-1})						
D excelsa	43[a]	40[a]	34[a]	–	35[a]	38[d]
A caribaea	59[bc]	77[a]	64[ab]	49[cd]	42[d]	59[bc]
R grandis	96[a]	91[ab]	82[ab]	79[b]	56[c]	81[a]
S amara	80[ab]	110[a]	98[a]	62[b]	65[b]	81[a]
S globulifera	77[a]	75[a]	83[a]	50[b]	61[ab]	67[b]
B coriacea	70[a]	58[ab]	66[a]	41[b]	44[b]	57[c]
P coriaceus	45[a]	47[a]	43[a]	33[b]	39[ab]	41[d]
Mean per tunnel	66[a]	71[a]	68[a]	53[b]	50[b]	
Light-limited photosynthesis (nmol g^{-1} s^{-1})						
D excelsa	20[a]	19[a]	18[a]	–	9[a]	16[d]
A caribaea	29[b]	35[a]	27[bc]	23[c]	15[d]	26[bc]
R grandis	56[a]	48[b]	41[c]	31[d]	19[e]	39[a]
S amara	40[a]	41[a]	36[a]	21[b]	14[b]	30[b]
S globulifera	42[a]	33[ab]	29[ab]	19[b]	23[b]	27[bc]
B coriacea	36[a]	27[a]	30[a]	17[b]	13[b]	25[c]
P coriaceus	20[ab]	21[a]	17[b]	8[c]	9[c]	15[d]
Mean per tunnel	34[a]	32[ab]	29[b]	19[c]	15[d]	
Dark respiration (nmol g^{-1} s^{-1})						
D excelsa	2.2[b]	0.6[a]	2.2[b]	–	1.5[ab]	1.6[a]
A caribaea	2.0[c]	0.0[a]	0.0[a]	1.5[b]	2.1[c]	1.0[a]
R grandis	1.6[a]	3.4[ab]	3.7[ab]	5.0[b]	2.8[ab]	3.5[b]
S amara	4.8[ab]	6.1[b]	2.5[a]	2.6[a]	5.3[ab]	4.1[b]
S globulifera	4.5[a]	0.7[a]	1.9[a]	4.3[a]	2.0[a]	1.9[a]
B coriacea	0.5[a]	1.0[ab]	2.7[bc]	0.9[a]	3.3[c]	1.7[a]
P coriaceus	6.6[b]	2.2[a]	3.9[ab]	3.8[ab]	4.6[ab]	4.2[b]
Mean per tunnel	3.6[b]	1.9[a]	2.0[a]	3.1[ab]	3.3[b]	

* For each parameter and each species, identical letters indicate means among tunnels not significantly different at a 5% level (Duncan's test). Last column shows statistical differences among species, all tunnels combined.

(7.9 μmol m^{-2} s^{-1}) and the lowest for D excelsa (3.4 μmol m^{-2} s^{-1}). Photosynthesis recorded per unit of dry matter was then 65 nmol g^{-1} s^{-1} for S amara and 35 nmol g^{-1} s^{-1} for D excelsa. The other species had intermediate values. Whether photosynthesis was recorded per leaf area or dry matter units, the species ranking was approximately the same. The small amount of change was due to small differences in specific leaf area between species, for plants grown in full sunlight.

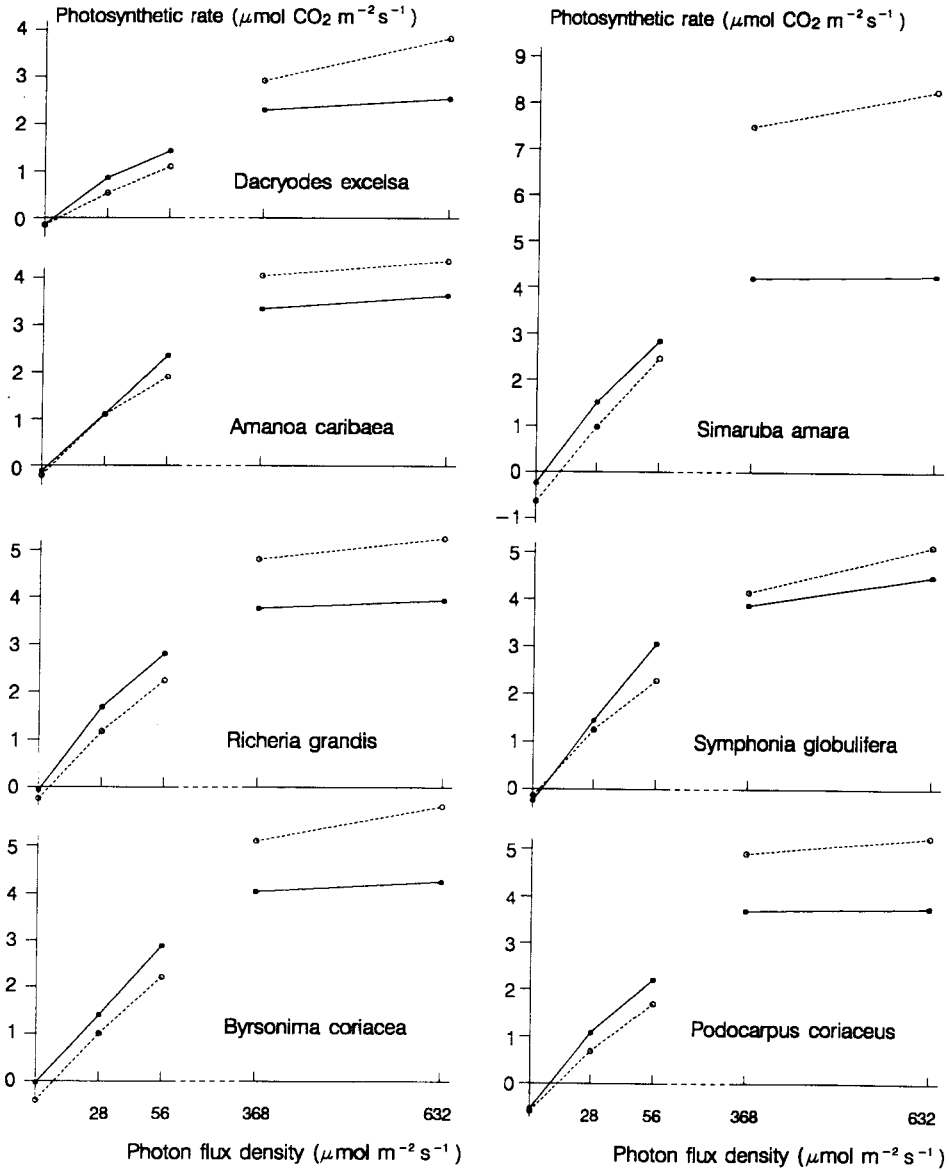For plants grown in shady conditions, light-saturated photosynthesis recorded

Fig 1. Net photosynthesis-light curves of the 7 species studied for densely shaded seedlings under tunnel I (6% RLI) (●—●), and sun-grown seedlings (100% RLI) (o---o).

per unit of leaf area showed a general trend, decreasing from light shade (tunnel IV, 54% RLI) to heavy shade (tunnel I, 6% RLI). Some species, like S amara, reacted more strongly than others to changes in light regime, as shown in figure 1. An opposite trend was found when photosynthesis was recorded in dry matter units. Photosynthesis is then higher for plants under heavy shade (tunnels I, II and III, 6–19% RLI) than for plants under light shade (tunnel IV, 54% RLI) or in full sunlight.

Light-limited net photosynthesis

For plants grown in full sunlight, light-limited photosynthesis on a leaf area basis was the highest for S globulifera (1.8 µmol m^{-2} s^{-1}) and the lowest for D excelsa (0.8 µmol m^{-2} s^{-1}). Photosynthesis recorded per unit of dry matter was then 23 nmol g^{-1} s^{-1} for S globulifera and 9 nmol g^{-1} s^{-1} for D excelsa and P coriaceus. The other species had intermediate values.

For plants grown under different shade treatments, light-limited photosynthesis on a leaf-area basis decreased from deep shade (tunnel I, 6% RLI) to light shade (tunnel IV, 54% RLI), the lowest values being encountered in full sunlight. At a species level, this trend was not always true because of high data variability. This trend appeared clearly for most of the species when photosynthesis was recorded per unit of dry matter.

Apparent quantum yield

For plants grown in full sunlight, apparent quantum yield was the highest for S amara (58 mmol mol^{-1}) and R grandis (54 mmol mol^{-1}) and the lowest for D excelsa (23 mmol mol^{-1}). These values were slightly lower for plants grown in full sunlight than for plants grown in shady conditions. All species considered together, apparent quantum yield was slightly, but statistically greater for shaded plants (47–49 mmol mol^{-1}) than for sun-grown plants (42 mmol mol^{-1}).
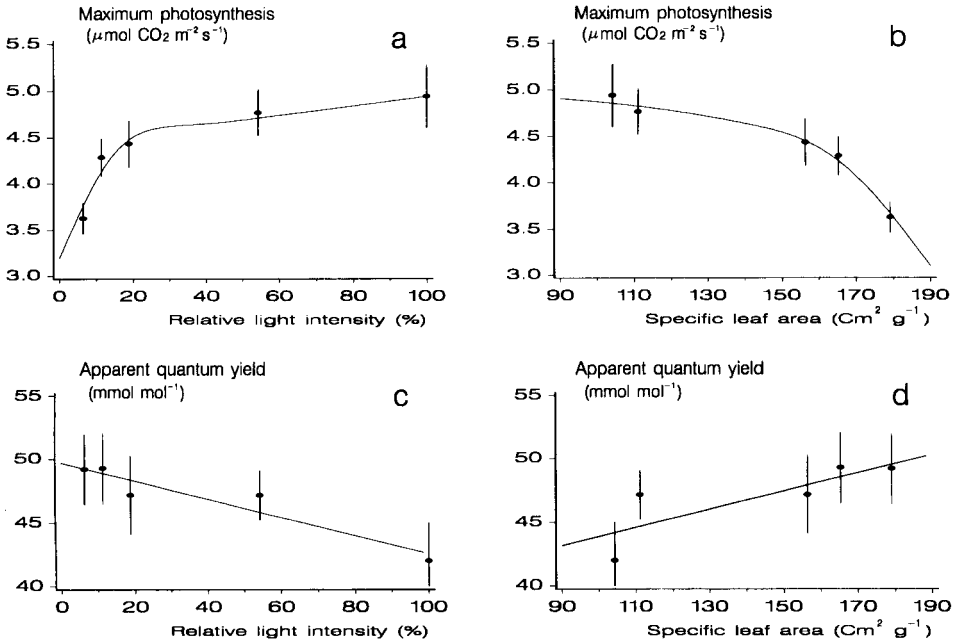
Dark respiration

Leaf dark respiration was very low for A caribaea and very high for P coriaceus, R grandis and S amara, whether it was expressed on dry-weight or leaf-area basis. Compared with apparent quantum yield, these data seem to indicate that species with a high apparent quantum yield also had a high dark respiration and vice versa. Only P coriaceus seems to be an exception and had a high dark respiration along with a low apparent quantum yield. All species considered together, respiration was lowest in tunnels II and III, and highest in strong shade and full sunlight.

Influence of growth conditions and leaf characteristics

It was interesting to relate the results obtained in the different tunnels to light conditions and specific leaf area. Figure 2 shows that when all the species are considered together, maximum photosynthesis per leaf area unit increased with relative light intensity during growth, at first rapidly until the relative light intensity was near 20% (tunnel III), then much more slowly (fig 2a). On the other hand, it decreased regularly when specific leaf area increased (fig 2b), ie with increasing shade.

Apparent quantum yield decreased with relative light intensity (fig 2c) and increased with specific leaf area (fig 2d). Its variation was the reverse of that found for

Fig 2. Global relationships, all species combined, between maximum net photosynthesis (top) and apparent quantum yield (bottom), and specific leaf area (right) and relative light intensity (RLI) (left) hand (means per tunnel ± standard error).

maximum net photosynthesis. This phenomenon has frequently been observed when comparing shade and sun phenotypes.

Linear regressions to explain specific leaf area, light-saturated photosynthesis, light-limited photosynthesis and apparent quantum yield as a function of relative light intensity, were calculated for each species (table VI). Most of the regressions were statistically significant at a 5% level, except for apparent quantum yield. The "a" coefficient in the regression equation expresses, for a given trait, the species plasticity in reaction to light conditions during growth.

According to specific leaf area, species may be ranked from the most plastic to the least plastic species: R grandis, S amara, B coriacea, D excelsa, A caribaea, S globulifera and P coriaceus. According to light-saturated photosynthesis, S amara was found to be the most plastic species. It was followed, in decreasing order, by R grandis, B coriacea and P coriaceus. D excelsa and A caribaea both had "a" coefficients not significantly different from zero, whereas S globulifera reacted negatively to increasing relative light intensity. For each species, light-limited photosynthesis and apparent quantum yield decreased with increasing light intensity.

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Table VI. Linear regression between specific leaf area, light-saturated photosynthesis, light-limited photosynthesis and apparent quantum yield as dependent variables, and relative light intensity as regressor, for each species. For each regression, parameter estimate ("a" coefficient of the $y = ax + b$ equation), coefficient of determination (R^2) and significance probability (prob > F) are given.

Species	Specific leaf area			Light-saturated photosynthesis			Light-limited photosynthesis			Apparent quantum yield		
	a	R^2	prob > F	a	R^2	prob > F	a	R^2	prob > F	a	R^2	prob > F
Dacryodes excelsa	-7.08	0.55	0.0002	9.41	0.11	0.2371	-3.73	0.11	0.2533	-58.3	0.04	0.4987
Amanoa caribaea	-7.01	0.90	0.0001	-1.42	0.00	0.8787	-3.82	0.16	0.3188	-13.8	0.00	0.8648
Richeria grandis	-13.45	0.81	0.0001	12.45	0.34	0.0118	-4.47	0.58	0.0002	-66.1	0.20	0.0649
Simaruba amara	-11.15	0.74	0.0001	24.61	0.24	0.0207	-6.38	0.42	0.0011	-75.5	0.14	0.0848
Symphonia globulifera	-5.16	0.36	0.0011	-11.50	0.30	0.0437	-10.92	0.44	0.0088	-201.0	0.24	0.0729
Byrsonima coriacea	-9.78	0.67	0.0001	12.16	0.29	0.0563	-4.58	0.39	0.0231	-14.0	0.01	0.7522
Podocarpus coriaceus	-4.08	0.50	0.0005	10.37	0.36	0.0055	-7.89	0.49	0.0006	-142.0	0.30	0.0120

DISCUSSION AND CONCLUSION

Comparison between species

For the 7 species studied in Guadeloupe, maximum net photosynthesis in full sunlight was between 3.4 μmol m^{-2} s^{-1} for *D excelsa* and 7.9 μmol m^{-2} s^{-1} for *S amara*. The corresponding respiration values varied from 0.15 to 0.64 μmol m^{-2} s^{-1} depending on the species. Our results are compared (table VII) with the results of others studies including those by Stephens and Waggoner (1970), Bazzaz and Pickett (1980), Koyama (1981), Oberbauer and Strain (1984), Langenheim *et al* (1984), and Thompson *et al* (1988).

Pioneer trees in the early successional stages or young secondary formations generally have a high photosynthetic potential (14 μmol CO_2 m^{-2} s^{-1}) along with a high dark respiration (0.8 μmol CO_2 m^{-2} s^{-1}). Stable forest formations in the late successional species stages are composed of 3 main layers: an upper layer including emergent and dominant trees; a middle layer composed of average-sized trees which completely close the forest canopy; and a lower layer composed of understory species.

Among the emergent trees both "sun" species which are shade intolerant and "shade" species which are more or less tolerant to shade can be found. Sun species have an almost identical response to that of pioneer species (photosynthesis: 11 μmol CO_2 m^{-2} s^{-1} and dark respiration: 1.0 μmol CO_2 m^{-2} s^{-1}). An analogy can be made between these 2 groups as the emergent sun species appear very early in the first successional stages as do the pioneer species, but they have a much longer life than the latter which is why they can be found in the late successional stages.

The results for shade species from the upper layer and from the middle layer are close to 5 μmol CO_2 m^{-2} s^{-1} for maximum net photosynthesis and 0.6 μmol CO_2 m^{-2} s^{-1} for dark respiration. Large differences in shade tolerance can be seen between these species, but the knowledge of their photosynthetic potential is not sufficient to rank them according to an increasing order of shade tolerance. The understory species have a photosynthesis close to 2 μmol CO_2 m^{-2} s^{-1} and a respiration close to 0.2 μmol CO_2 m^{-2} s^{-1}.

These results give a good idea of the photosynthetic potential of tropical rainforest species. They are, in fact, very close to those for temperate forest species found by Bazzaz (1979), who gives photosynthetic potentials of 10.0 for species at the beginning of the succession, 5.7 for species at the end of succession, and 2.2 for understory species.

Comparison of sun and shade phenotypes

For the 7 species studied, apparent quantum yield was higher for shade-grown plants (shade phenotypes) than for sun-grown plants (sun phenotypes). On the other hand, light-saturated photosynthesis on a leaf-area basis was higher for sun phenotypes than for shade phenotypes, except for *A caribaea* and *S globulifera*.

Similar results were reported by Logan (1970) for *Betula alleghaniensis*, by Tsel'Niker (1977) for 5 forest species, by Duba and Carpenter (1980) for *Platanus occidentalis*, by Bazzaz and Carlson (1982) for 12 herbaceous and shrub species and by Nygren and Kellomaki (1983) for 10 forest species. All the species studied by these authors belong equally to the early and late successional stages and thus both shade-tolerant and shade-intolerant species can be found.

Table VII. Photosynthetic characteristics of several tropical forest species. Species in bold are native, and species with standard type have been introduced into Guadeloupe. Numbers in brackets are maximum single values measured.

Species	Maximum photosynthesis $\mu mol\ m^{-2}\ s^{-1}$		Dark respiration $\mu mol\ m^{-2}\ s^{-1}$	References
Pioneer or early successional trees				
Macaranga hypoleuca	13.3		0.6	K
Mallotus paniculatus	13.9		1.2	K
Glochidion laevigatum	14.8		0.9	K
Cecropia peltata	16.4		0.5	S
Cecropia peltata	7.0	(15.8)	–	L
Anthocephalus cadamba	6.8		–	L
Ochroma lagopus	27.7	(32.7)	–	O
Emergent or dominant trees "Sun" type				
Shorea leprosula	12.7		1.3	K
Simaruba amara	8.2		0.6	D
Dipteryx panamensis	8.1	(9.6)	–	O
Bursera simaruba	11.8	(13.7)	–	O
Hampea appendiculata	13.9	(17.7)	–	O
"Shade" type				
Shorea macroptera	6.7		0.5	K
Shorea pauciflora	6.3		0.5	K
Dipterocarpus crinitus	8.8		1.3	K
Dipterocarpus sublamellatus	5.6		0.6	K
Parashorea densiflora	4.7		0.5	K
Cinnamomum parthenoxylon	5.4		0.8	K
Goethalsia meiantha	4.1		0.4	S
Sloanea berteriana	3.3		–	L
Dacryodes excelsa	1.4		–	L
Dacryodes excelsa	3.4		0.2	D
Amanoa caribaea	4.2		0.2	D
Symphonia globulifera	4.6		0.2	D
Hymenaea courbaril	5.0		–	LA
Hymenaea parviflora	2.5		–	LA
Copaifera venezuelana	7.6		–	LA
Pentaclethra macroloba	5.6	(6.2)	–	O
Gnetum leyboldi	8.5	(9.4)	–	O
Flindersia brayleyana	7.2		1.3	T

Table VII. *Continued*

Middle layer trees

Alangium ridleyi	4.4		0.8	K
Virola koschnyi	3.9		0.5	S
Virola koschnyi	6.3	(6.9)	–	O
Cordia alliodora	5.3		0.8	S
Richeria grandis	5.0		0.3	D
Byrsonima coriacea	4.5		0.3	D
Podocarpus coriaceus	5.1		0.6	D

Understory plants

Croton gabellus	1.6	0.2	S
Protium glabrum	2.1	0.2	S
Alocasia macrorrhiza	1.9	0.1	B
Cordyline rubra	1.9	0.1	B

B: Björkman *et al,* 1972; D: Original data from present paper. K: Koyama, 1981; L: Lugo, 1970; LA: Langenheim *et al,* 1984; O: Oberbauer and Strain, 1984; S: Stephens and Waggoner, 1970; T: Thompson *et al,* 1988.

The commonly accepted explanation for these results is that shade and sun phenotypes are well adapted to the light environment in which they grow and that the light level at which photosynthesis reaches its saturation plateau corresponds to the light conditions most commonly found by the plant in its natural environment (Tsel'Niker, 1977). Under these conditions, shade phenotypes have higher quantum yield and lower light-saturated photosynthesis.

For *A caribaea*, we found no effect of light growth conditions on light-saturated photosynthesis, whereas light-saturated photosynthesis of *S globulifera* was higher for shade-grown plants than for sun-grown plants. Similar results have also been found by various authors. For *Tilia americana*, Bazzaz and Carlson (1982) found that sun and shade phenotypes had identical rates of photosynthesis. For *Acer saccharum*, Logan and Krotkov (1969), and Bazzaz and Carlson (1982) found that photosynthesis of shade phenotypes was high-

er than that of sun phenotypes. Similar results were also found by Gatherum *et al* (1963) for 3 different forest species. Logan and Krotkov (1969) interpreted these results by saying that when plants of this type photosynthesize under the same light conditions, plants grown under low light use light more efficiently than those grown in full sunlight.

The 2 main types of results for shade and sun phenotypes are contradictory and many references could be quoted for each point of view. Logan and Krotkov (1969) tried to provide an explanation. They hypothesized that the photosynthetic mechanisms of tolerant species are better adapted to low rather to high light habitats, and conversely, that the photosynthetic mechanisms of intolerant species are better adapted to high rather than to low light habitats. This theory involves the degree of adaptation to shade and is not entirely convincing as both types of response can be found in tolerant and intolerant species.

When we expressed photosynthesis on dry leaf matter basis, it was found that, for all species, the highest values corresponded to shade phenotypes and the lowest to sun phenotypes (see table VI). Photosynthesis per unit dry weight can be considered to be the product of the specific leaf area by photosynthesis per unit leaf area. For the species studied, photosynthesis per unit leaf area decreased with shade while specific leaf area increased, and the final result, as we have seen, was an increase with shade of photosynthesis per unit dry weight. This result depends on the degree of variation between shade and sun for the 2 parameters studied. Thus, any result is possible and would depend on the morphological and photosynthetic plasticity of the species studied.

Photosynthetic plasticity and shade adaptation

Bazzaz and Carlson (1982) introduced the notion of photosynthetic flexibility (or plasticity) to interpret the range of variation, from dense shade to full sunlight, in parameters defining the photosynthetic activity of a given species. They concluded in their study that photosynthetic flexibility was higher for early pioneer successional species, average for intermediate species and lowest for late successional species.

The "a" coefficients from table VII may be considered as indicators of species plasticity. From the regressions between specific leaf area and relative light intensity, an index of morphological plasticity may be defined. According to this index, *R grandis* and *S amara* are the 2 most plastic species, immediately followed by *B coriacea*; *D excelsa* and *A caribaea* are less plastic; and *S globulifera* and *P coriaceus* are the least plastic species. These results agree with those obtained on a greater

plant sample from the same experiment (Ducrey, 1992).

From the regressions between light-saturated photosynthesis and relative light intensity, an index of photosynthetic plasticity may be defined. *S amara* appears as the most plastic species. The following are then found in decreasing order: *R grandis*, *B coriacea*, *P coriaceus*, *D excelsa* and *A caribaea*. *S globulifera* reacted negatively to increasing light intensity.

There is a good agreement between the different indexes of plasticity, the presumed degree of shade tolerance of Guadeloupe species and their place in the species' succession cycle in tropical rain forests. *Simaruba amara* and *Richeria grandis* are the most plastic species from a morphological and photosynthetic point of view. They are early successional species, but not really pioneer species, and were considered as light-intolerant species (Ducrey and Labbé, 1986). *Byrsonima coriacea* is also a plastic species. This makes it possible to rank this species among shade intolerant species even though little was previously known about its forest behavior. The 3 species *Podocarpus coriaceus*, *Dacryodes excelsa* and *Amanoa caribaea* had low morphological and photosynthetic plasticity indexes. They are more or less shade tolerant and are late succession species. A special emphasis should be made on *Symphonia globulifera*, a species with very low plasticity, and whose light-saturated photosynthesis decreased with increasing relative light intensity. This species should be a strict "shade species", but it is also a wet soil specialist, so it may be a dominant species in the late succession stages.

This work has made it possible to gain a basic knowledge about the photosynthetic potentials of the main commercially interesting forest species from the Guadeloupe tropical rain forest. It has also characterized the shade and sun phenotypes of

these species from the point of view of their photosynthetic activity. However, studying only photosynthetic activity seems to be insufficient to determine the degree of shade tolerance. It is nevertheless a useful element which, when added to other elements concerning the morphological and biochemical adaptation of the leaf apparatus, growth, and biomass production, will make it possible to increase our knowledge of the ecophysiological behavior of these species.

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