PHOTOSYNTHETICA 41 (4): 551-557, 2003

Photosynthetic activity in seed wings of *Dipterocarpaceae* in a masting year: Does wing photosynthesis contribute to reproduction?

T. KENZO*, T. ICHIE**, I. NINOMIYA***, and T. KOIKE**

*United Graduate School of Agricultural Sciences, Ehime University, Matsuyama 790-8566, Japan**
*Hokkaido University Forests, FSC, Kita-9, Nishi-9, Sapporo, 060-0809, Japan***
*Faculty of Agriculture, Ehime University, Tarumi-3-5-7, Matsuyama, 790-8566, Japan****

Abstract

The photosynthetic rate of seed wings developed from sepals was compared with the leaf photosynthetic rate in nine dipterocarp tree species (*Dipterocarpus pachyphyllus, Dryobalanops aromatica, Dryobalanops lanceolata, Shorea beccariana, Shorea ferruginea, Shorea macroptera* ssp. *bailonii, Shorea macroptera* ssp. *macropterifolia, Shorea pilosa,* and *Vatica* spp.). The wings showed positive photosynthetic activity, but at much lower rates than in the leaves. The daily CO_2 uptake of wings showed slightly negative values in diurnal gas exchange measurements, even in *D. aromatica* that showed the highest photosynthetic capacity of all nine species. This low photosynthetic rate in the wings may be the result of low nitrogen and chlorophyll contents in the wing compared with leaves. However, the wings had a higher C/N ratio than leaves, and were thicker. Hence, dipterocarp wings have physical strength and defence against herbivores as higher priorities than photosynthetic activity.

Additional key words: chlorophyll; daily carbon gain; *Dipterocarpus*; *Dryobalanops*; respiration; Sarawak; sepal; *Shorea*; tropical rainforest; *Vatica*.

Introduction

Reproductive organs may contribute part of the carbon needed for flower and fruit production (Bazzaz *et al.* 1979, Watson and Casper 1984). Photosynthetic ability has been reported in a number of reproductive plant organs, including corn, sepal, fruit, and flower robe (*e.g.* Bazzaz *et al.* 1979, Linder and Troeng 1981, Blanke and Lenz 1989). These reproductive organs vary in photosynthetic ability from a close balance with their own respiration to greater photosynthetic capacity than leaves.

In Southeast Asia, dipterocarp species dominate the emergent canopy of most lowland rain forest (Ashton 1982). Most dipterocarp species have characteristic reproductive features: (*1*) They produce many large seeds with high density (Ashton 1982, Whitmore 1998, Curran *et al.* 1999). (*2*) They show synchronous mass flowering and consequent mass fruiting at community level, at irregular intervals of 2 to 10 years (Ashton *et al.* 1988, Yap and Chan 1990, Appanah 1993, Sakai *et al.* 1999, Sakai 2002). It is therefore possible that dipterocarp trees need large amounts of resources for reproduction in a masting year (Ashton 1982).

After flowering, most dipterocarp species bear relatively large seeds, and elongate two to five long wings from the sepals. These wings vary across species in colour (red, green, and yellow), size, and shape, and are exposed in the canopy (Ashton 1982). The function of the wing appears to be seed dispersal, by gyration (Chan 1980, Tamari and Jacalne 1984, Whitmore 1984, Suzuki and Ashton 1996, Osada *et al.* 2001). Ashton (1989) has also suggested that seed wings of dipterocarp species have the photosynthetic ability to support their own development from their morphological characteristics, which the fruit sepals of dipterocarp species fully enlarge before the embryo expands. This process occurs in most flowers following anthesis, even though most will abort without embryogenesis.

Little is known about the photosynthetic characteristics of seed wings because of difficulty in accessing the tree canopy and the irregular flowering interval. We consider three possible reasons why the wings have a relatively high net photosynthetic rate (P_N): (*1*) Leaf-shaped structures, such as winged carpels of *Acer*, bracts of *Tilia*, and the calyx of persimmon and apple, have a higher P_N than round fruits or those with small wings

---

Received 22 September 2003, *accepted* 24 October 2003.

Fax: +81-89-946-9868; e-mail: mona@agr.ehime-u.ac.jp

Acknowledgements: This research was partly supported by the Japan Science and Technology Corporation (JST) and JSPS Research Fellowships for Young Scientists (T.I.). Helpful comments were received from Dr. D. G. Sprugel.

(Bazzaz *et al.* 1979, Nakano *et al.* 1991, Vemmos and Goldwin 1994). (*2*) The dipterocarp wing develops in the canopy, where there are sufficient photons for photosynthesis. (*3*) Since dipterocarp trees need large amounts of resources for reproduction, dipterocarp wings may be an important carbon source during seed development if they have photosynthetic ability.

We studied the photosynthetic abilities of dipterocarp wings and their contribution to reproduction in a masting year. We first measured P_N, the concentrations of chlorophyll (Chl), nitrogen (N), and carbon (C) in the seed wing and leaves of nine dipterocarp tree species during seed development. Second, we estimated the daily carbon balance of seeds, wings, and leaves.

Materials and methods

Study site: The study was carried out in the mixed dipterocarp forest of Lambir National Park, Sarawak, Malaysia (4°12'N, 114°00'E, 150–250 m a.s.l.), in November 2001. Observations were made in the Canopy Biology Plot (8 ha: 200×400 m; Inoue and Hamid 1995) and the Crane Site (4 ha: 200×200 m). To reach the tree canopy, we used a tree tower and a crane (Sakai *et al.* 2002). The climate is humid tropical, with a weak seasonal change in rainfall and temperature (Kato *et al.* 1995). The mean annual rainfall and temperature collected at Miri Airport, 20 km from the research site, are about 3 200 mm and 27 ºC (Kumagai *et al.* 2001).

Plants: In August 2001 we observed a synchronous mass flowering event in Lambir National Park. The mature fruits were dropped from January to March 2002. We selected seven species and two subspecies for this study (Table 1). All trees measured reached the canopy layer (50–70 m). Table 1 shows the wing colour and the numbers of measured individuals, wings, and leaves. Although the wing colour varies between species, it is uniform within a species and individual trees. From the microscopic observation, we observed some poles in the wings of all species.

Gas exchange rate of leaf and wing: We measured wing and leaf P_N in November 2001, in the middle of fruit development and when the wing area had just reached its maximum, based on the growth curves for wing area and seed mass of *D. aromatica* (Fig. 1). This was believed to be the time of greatest carbon activity in the wings, because the expansion stage involves a high dark respiration rate (R_D) for such wing-like reproductive organs as the winged carpels of *Acer* and the bracts of cotton (Bazzaz *et al.* 1979, Wullschleger and Oosterhuis 1990). Our preliminary measurements also determined a very low P_N at the expanding stage of wings in *D. aromatica* and *Dryobalanops lanceolata* [–2.1 to –2.4 µmol(CO_2) m^{-2} s^{-1}, wing area of about 50 % of full expansion]. The carbon requirement for seed development is high at this time, since the seed growth rate is large around the middle of seed development (Fig. 1). Both maximum carbon export and maximum P_N of a leaf occur when the leaf reaches its maximum size (for review see Šesták 1985). Therefore, we considered that the period was suitable to estimate maximum contribution of wing photosynthesis for dipterocarp species during seed developmental stage.

To measure P_N of wings and leaves in the canopy, we used a portable photosynthesis meter (*LI-6400*, *Li-Cor*, Lincoln, NE, USA). All measurements were taken from 08:00 to 11:00 to avoid the midday reduction in photosynthesis (Hiromi *et al.* 1999). Measurements were made on the enlarged wings and on the third leaf from the top of shoots. Relations between the photon flux density (PFD) and P_N were studied for the leaves and wings of four species. The irradiance and temperature at measurement were chosen as 0–1 200 µmol m^{-2} s^{-1} and 30 ºC. For the five other species, we measured P_N at saturating PFD (P_{Nmax}) and R_D. These measurements were made at 1 200 µmol m^{-2} s^{-1} and 30 ºC. The gross photosynthetic rate (P_{Gmax}) was calculated as the sum of P_{Nmax} and R_D.

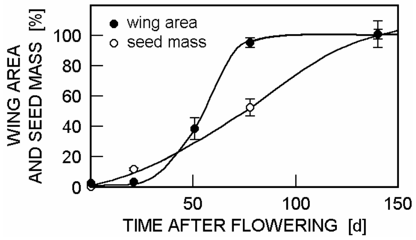

Fig. 1. Growth curves for wing area and seed mass after anthesis in *Dryobalanops aromatica*. *Bars* show the standard error. The curve is fixed by sigmoid growth curve (Zhao and Oosterhuis 1999).

Chlorophyll (Chl), nitrogen (N), and carbon (C) contents: Chl was extracted with DMSO (Barnes *et al.* 1992, Shinano *et al.* 1996), and the absorbances at 664.9 and 648.2 nm were determined by a spectrophotometer (*UV-1400*, *Shimadzu*, Kyoto, Japan). The nitrogen and carbon contents were determined by an *NC* analyser (*NC-900*, *Shimadzu*, Kyoto, Japan). The wing area, thickness, and dry mass of the samples were also measured (Table 2).

Diurnal gas exchange rate and daily carbon gain: The diurnal gas exchange rate for leaf, wing, and seed were measured for *D. aromatica*, which has the greatest P_N of wings of the nine species. Three individuals that had reached emergence (about 50 m) were measured on 11, 16, and 18 November, 2001. Measurements were made on the upper sun-exposed crown using a portable photosynthesis meter (*LI-6400*). The rate of gas exchange was recorded every 30 min over an interval of about 12 h (08:30 to 20:00 on November 11 and 16, 07:20 to 20:00

Table 1. The studied plant species and the number of individuals, with wing and leaf numbers, and wing colour.

Species	Code	Number of individuals	wings	leaves	Colour
Dipterocarpus pachyphyllus	DP	2	4	3	red
Dryobalanops aromatica	DA	4	21	17	green
Dryobalanops lanceolata	DL	3	11	12	green
Shorea beccariana	SB	3	9	6	red
Shorea ferruginea	SF	1	3	3	red
Shorea macroptera ssp. *bailonii*	SMB	1	3	3	yellow
Shorea macroptera ssp. *macropterifolia*	SMM	1	1	3	yellow
Shorea pilosa	SP	1	3	3	green
Vatica spp.	V	1	4	4	yellow

Table 2. Wing area [cm^2 per seed], wing dry mass [g per seed], and wing and leaf thickness [mm].

Species code	Wing area	Wing dry mass	Thickness of	
			wing	leaf
DP	45.2±3.1	0.45±0.01	0.513±0.016	0.246±0.005
DA	27.4±1.7	0.31±0.02	0.439±0.008	0.303±0.006
DL	37.8±4.4	0.64±0.05	0.639±0.021	0.289±0.007
SB	66.5±8.5	1.11±0.08	0.901±0.030	0.369±0.008
SF	28.2±1.5	0.20±0.02	0.571±0.053	0.321±0.025
SMB	36.0±4.3	0.60±0.02	0.441±0.003	0.245±0.007
SMM	19.0	0.41	0.661	0.272±0.002
SP	123.0±10.2	2.14±0.22	1.211±0.095	0.324±0.009
V	29.9±1.8	0.33±0.01	0.413±0.005	0.267±0.003

on November 18). Gas exchange was measured for the fully expanded leaf, the elongated wing, and seed with the wing removed. In each case, four samples were used.

Results

Gas exchange of leaf and wing: P_N was photon-saturated at around 400 to 500 µmol m^{-2} s^{-1} for wings, and 700 to 1 200 µmol m^{-2} s^{-1} for leaves. P_{Nmax} was –0.7 to 0.7 µmol(CO$_2$) m^{-2} s^{-1} for wings and 6 to 19 µmol(CO$_2$) m^{-2} s^{-1} for leaves (Fig. 2).

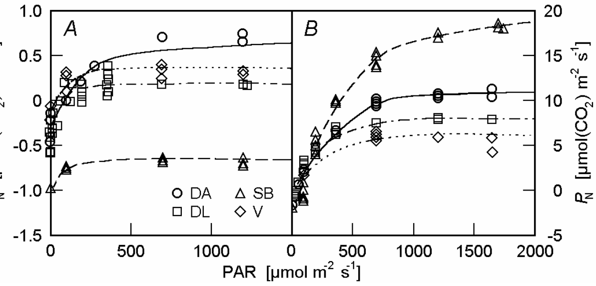

Fig. 2. Relation of net photosynthetic rate (P_N) and irradiance (PAR) for wing (*A*) and leaf (*B*) of four plant species (for name abbreviations see Table 1). These curves are fitted by an asymptotic equation (Boote and Loomis 1991).

P_{Nmax}, R_D, and P_{Gmax} values for wings and leaves of all nine species (Table 3) show that the wings of dipterocarp fruit have photosynthetic capability, although at a significantly lower rate than in leaves. A positive P_{Nmax} was observed for wings of DA, DL, SMM, and V, ranging from 0.19 to 0.26 µmol(CO$_2$) m^{-2} s^{-1}. Wings of DP, SB, SF, SP, and SMB showed negative P_{Nmax} from –0.09 to –1.10 µmol(CO$_2$) m^{-2} s^{-1}.

In all wings, P_{Gmax} showed interspecific trends similar to P_{Nmax}. The P_{Gmax} of wings was relatively high in two *Dryobalanops* species [0.93 µmol(CO$_2$) m^{-2} s^{-1} in DA and 0.68 µmol(CO$_2$) m^{-2} s^{-1} in DL]. In contrast, wings of SB and SF had very low P_{Gmax}, 0.14 and 0.07 µmol(CO$_2$) m^{-2} s^{-1}, respectively. P_{Nmax} and P_{Gmax} for leaves of all species were significantly higher than for wings. In particular, the leaf P_{Gmax} was 15 to 158 times larger than the wing P_{Gmax}.

N, C, and Chl contents (Table 4): N contents of wings and leaves ranged from 5.1 to 9.6 g kg^{-1} and 10.6 to 16.7 g kg^{-1}, respectively. The leaf N content was about two times higher than the wing N content, but there was no significant difference in C content. As a result, the C/N ratio of wings was higher than that for leaves (Table 4).

Chl was detected in wings of all species, regardless of wing colour (Table 4). The Chl content of wings was 2.2 to 12.6 times less than that of leaves. In particular, wing

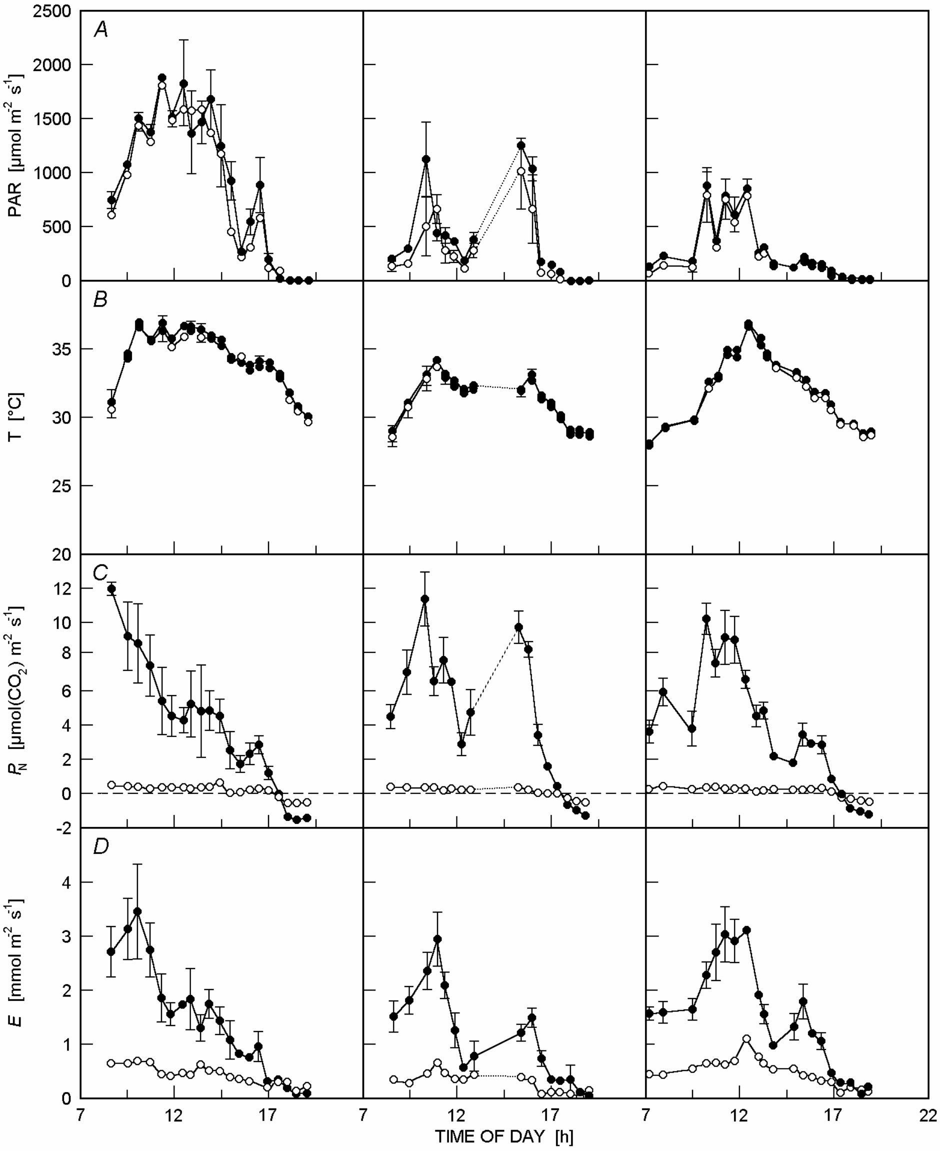

Fig. 3. Diurnal changes in photosynthetically active radiation, PAR (*A*), temperature on leaf and wing surface, T (*B*), net photosynthetic rate, P_N (*C*), and transpiration rate, *E* (*D*). *The dotted lines* for November 16 show an interruption by rain (13:00 to 15:00). *Bars* indicate the standard error.

Chl *a* was lower than in leaves, so that the Chl *a*:*b* ratio was also lower in wings of all species (Table 4).

Diurnal gas exchange rate and daily carbon gain: November 11, 2001 was a fine day, but November 16 and 18 were partly cloudy and partly fine. Fig. 3 shows diurnal changes of PAR and temperature (T) on leaf and wing surfaces, and P_N and transpiration rate (*E*) on 11, 16, and 18 November 2001. The *dotted line* on Fig. 3 for November 16 shows interruption of the measurements by bad weather (13:00 to 15:00). Diurnal changes of PAR and temperature on both leaf and wing surfaces showed similar trends on all days of measurement (Fig. 3*A*,*B*). The daily total PAR was almost the same for surfaces of leaves and wings; values were 30 mol m^{-2} d^{-1} on November 11, and about 10 mol m^{-2} d^{-1} on November 16 and 18 (Table 5). The diurnal gas exchange rate on wings was usually much lower than that for leaves (Fig. 3*C*). However, the night-time R_D (19:00-20:00) of the wing was about 1/3 lower than that of leaves (Fig. 3*C*). P_N of leaves was maximum at around 10:00, whereas that of wings hardly changed during the daytime of all three days (Fig. 3*C*). P_{Nmax} was about 12 to 14 µmol(CO_2) m^{-2} s^{-1} for leaves, and 0.4 to 0.6 µmol m^{-2} s^{-1} for wings.

The diurnal course of *E* showed a trend similar to P_N (Fig. 3*D*), and values for wings were significantly lower than for leaves.

The daytime (07:00–18:00) carbon uptake ($P_{Ndaytime}$) of the wing was estimated as 512, 409, and 368 mg(CO_2) m^{-2} for 11 h on November 11, 16, and 18, respectively

(Table 5). These values are about 1/20 of those for leaves. Night-time respiration (R_{night}) was calculated from the mean R_{D} for 18:00 to 20:00 and R_{D} determined at the first measurement in the morning (Table 5). R_{night} for wings was about one-third of the value for leaves. The daily net carbon uptake (P_{Nday}) that subtracted R_{night} from P_{Ndaytime} was slightly negative [–90 to –472 mg(CO_2) m^{-2} d^{-1}] for all wings measured (Table 5). The value for leaves reached 3.65–9.63 g(CO_2) m^{-2} d^{-1}. The ratio of P_{Ndaytime} to R_{night} taken over all measurements was 43 to 87 % in wings, and 269 to 430 % in leaves. The total daytime transpiration (E_{day}) of wings was much lower than for leaves (Table 5).

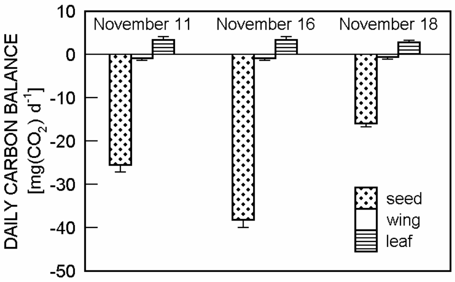

Fig. 4. Daily carbon balance in seed, seed wing, and leaf. Values are for a single seed and wings attached to one seed (27.4 cm^2 per seed), and for one leaf (5 cm^2). *Bars* indicate the standard error.

Discussion

P_{N} of wings was much lower than we expected and significantly lower than that of leaves (Table 3). Only four species showed even a slightly positive P_{N}. As P_{Nmax} was related linearly to the daily carbon uptake in canopy plants in the tropical rain forest of Panama (Zotz and Winter 1993), it is possible that the daily carbon balance for wings is negative in all species. In fact, even *D. aromatica*, the species with the highest P_{Nmax} in the present study, showed a negative daily carbon balance (Table 5, Fig. 4). The contribution of wing photosynthesis to seed growth is therefore small, and the small carbon gain from wings is used only to maintain the wings. Leaf photosynthesis is capable of providing almost all of the carbon needed for seed growth (Fig. 4).

Table 3. Maximum net photosynthetic rate (P_{Nmax}), dark respiration rate (R_{D}), and maximum gross photosynthetic rate (P_{Gmax}) [µmol(CO_2) m^{-2} s^{-1}] of wing and leaf.

Species code	P_{Nmax} wing	 leaf	R_{D} wing	 leaf	P_{Gmax} wing	 leaf
DP	-0.22±0.08	10.05±0.90	-0.54±0.06	-1.07±0.05	0.32±0.05	11.12±0.86
DA	0.26±0.07	12.20±0.42	-0.67±0.05	-1.58±0.06	0.93±0.09	13.78±0.44
DL	0.24±0.06	10.22±0.44	-0.61±0.17	-1.33±0.06	0.68±0.10	11.55±0.48
SB	-0.86±0.08	15.55±0.83	-1.00±0-08	-1.73±0.10	0.14±0.04	17.28±0.85
SF	-1.10±0.33	9.94±0.63	-1.17±0.32	-1.13±0.05	0.07±0.04	11.07±0.68
SMB	-0.08±0.05	5.26±0.36	-0.32±0.13	-0.85±0.04	0.24±0.09	6.11±0.36
SMM	0.20	9.00±0-50	-0.25	-1.57±0.04	0.45	10.57±0.55
SP	-0.10±0.04	6.76±0.80	-0.37±0.02	-1.44±0.20	0.27±0.03	8.20±0.60
V	0.22±0.12	6.41±0.13	-0.23±0.03	-1.19±0.14	0.45±0.15	7.60±0.10

Table 4. Wing and leaf nitrogen (N) and carbon (C) contents [g kg^{-1}], C/N ratio, chlorophyll (Chl) content [g kg^{-1}], and Chl *a*:*b* ratio.

Code	N wing	 leaf	C wing	 leaf	C/N wing	 leaf	Chl wing	 leaf	Chl *a*:*b* wing	 leaf
DP	5.1±0.7	13.8±0.7	496.3±1.9	502.6±7.1	103.1±15.3	36.5±2.0	58.5±4.9	418.2±39.7	0.45±0.10	2.24±0.12
DA	7.9±0.1	14.8±0.4	542.9±2.4	528.9±0.9	69.6±1.2	36.0±1.0	51.1±2.5	566.2±34.0	0.76±0.18	2.67±0.10
DL	9.6±0.3	16.7±1.1	508.4±1.9	508.4±3.0	52.9±1.9	31.0±1.9	112.6±12.9	445.9±29.6	0.65±0.13	2.05±0.11
SB	7.6±0.4	12.8±0.3	497.0±12.6	505.1±4.1	67.1±4.9	39.7±1.1	71.0±5.0	444.7±27.8	0.65±0.17	2.13±0.07
SF	6.4±0.3	14.3±0.2	493.5±3.9	512.6±1.6	77.2±3.5	35.8±0.6	41.7±5.6	492.9±15.0	0.51±0.07	2.15±0.01
SMB	7.9±0.5	11.9±0.9	508.2±2.3	502.0±13.5	65.1±4.0	42.6±2.4	49.8±2.8	452.8±38.5	0.91±0.12	2.25±0.16
SMM	6.7±0.0	14.6±0.3	498.1±0.0	505.8±14.2	73.9±0.0	34.6±1.7	45.7±0.0	576.4±34.4	0.57±0.00	2.49±0.10
SP	7.9±0.6	13.7±0.1	478.4±6.5	494.7±0.1	61.5±6.1	36.0±0.1	81.3±7.4	702.9±3.0	1.46±0.20	2.59±0.01
V	8.1±0.3	10.6±0.4	505.1±3.1	467.9±3.5	62.4±2.9	44.4±1.8	79.1±9.9	193.0±19.0	0.68±0.06	1.40±0.16

The small photosynthesis in wings might be due to the low quantity of Chl and the low N content in the wing. Chl *a* is the main pigment for photon harvesting and transport (Lambers *et al.* 1998), but Chl *a* content was

Table 5. Daily photon flux density ($\mathrm{PAR_{day}}$) [mol $\mathrm{m^{-2}\ d^{-1}}$], day-time net photosynthesis (07:00-18:00, P_{Ndaytime}), night time respiration (18:00-06:00, R_{night}), daily net photosynthesis (P_{Nday}) [mg($\mathrm{CO_2}$) $\mathrm{m^{-2}}$], and daily transpiration (E_{day}) [mol $\mathrm{m^{-2}\ d^{-1}}$].

Day	$\mathrm{PAR_{day}}$		P_{Ndaytime}		$\mathrm{R_{night}}$		P_{Nday}		E_{day}	
	wing	leaf	wing	leaf	wing	leaf	wing	leaf	wing	leaf
11 Nov.	32.8±1.3	35.5±1.0	512±94	9046±2859	823±54	2540±145	-312±80	6506±1357	17.7±1.1	58.5±8.6
16 Nov.	10.9±2.0	15.0±1.5	409±112	8805±1834	674±39	2474±157	-265±55	4855±573	12.1±1.0	42.0±5.1
18 Nov.	9.5±0.5	10.5±1.0	368±73	7134±1162	691±56	2279±134	-323±81	6331±844	18.8±0.8	57.9±2.9

lower in the wing than in the leaf (Table 4). N is also closely related to photosynthetic activity (Björkman 1981). Field and Mooney (1986), Evans (1989), Larcher (2003), and others confirmed this positive correlation. The low Chl content, low Chl *a*:*b* ratio, and low N content of wings together account for the low photosynthetic rates.

The low Chl and N contents may be part of an anti-herbivore defence. Greater Chl and N contents, with the resulting cost of N acquisition, bring increased risk of herbivory (Fitter and Hay 1981, Coley and Barone 1996, Turner 2001, Wright *et al.* 2001). Our results show that wings have a higher C/N ratio (Table 4) and a greater thickness than leaves (Table 2), with a probably greater mechanical strength. These findings suggest that dipterocarp species favour structural strength and anti-herbivore defence over photosynthetic activity in their wings. Wings also showed low daily *E* and low N and Chl contents compared to leaves. These factors might also help to reduce water and nutrient consumption in dipterocarp trees.

Based on this study, we conclude that the dipterocarp wing has photosynthetic ability that makes it self-sufficient in carbon. However, any contribution of wings to seed growth is small.

References

Appanah, S.: Mass flowering of dipterocarp forests in the aseasonal tropics. – J. Biosci. **18**: 457-474, 1993.

Ashton, P.S.: Dipterocarpaceae. – Flora Malesiana, Ser. 1 Spermatophyta. Vol. **9**. Pp. 237-552. Martinus Nijhoff Publishers, Dordrecht 1982.

Ashton, P.S.: Dipterocarp reproductive biology. – In: Lieth, H., Werger, M.J.A. (ed.): Tropical Rain Forest Ecosystems. Pp. 219-240. Elsevier, Amsterdam 1989.

Ashton, P.S., Givnish, T.J., Appanah, S.: Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. – Amer. Naturalist **132**: 44-66, 1988.

Barnes, J.D., Balaguer, L., Manrique, E., Elvira, S., Davison, A.W.: A reappraisal of the use of DMSO for the extraction and determination of chlorophyll *a* and *b* in lichens and higher plants. – Environ. exp. Bot. **32**: 85-100, 1992.

Bazzaz, F.A., Carlson, R.W., Harper, J.L.: Contribution to reproductive effort by photosynthesis of flowers and fruits. – Nature **279**: 554-555, 1979.

Björkman, O.: Responses to different quantum flux densities. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology I. Pp. 57-107. Springer-Verlag, Berlin – Heidelberg – New York 1981.

Blanke, M.M., Lenz, F.: Fruit photosynthesis. – Plant Cell Environ. **12**: 31-46, 1989.

Boote, K.J., Loomis, R.S.: The prediction of canopy assimilation. – In: Boote, K.J., Loomis, R.S. (ed.): Modeling Crop Photosynthesis – From Biochemistry to Canopy. Pp. 109-140. Crop Science Society of America, Madison 1991.

Chan, H.T.: Reproductive biology of some Malaysian dipterocarps. 2. Fluting biology and seedling studies. – Malay. Forester **43**: 438-451, 1980.

Coley, P.D., Barone, J.A.: Herbivory and plant defenses in tropical forest. – Annu. Rev. Ecol. Syst. **27**: 305-335, 1996.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E., Haeruman, H.: Impact of El Niño and logging on canopy tree recruitment in Borneo. – Science **286**: 2184-2188, 1999.

Evans, J.R.: Photosynthesis and nitrogen relationships in leaves of $\mathrm{C_3}$ plants. – Oecologia **78**: 9-19, 1989.

Field, C., Mooney, H.A.: The photosynthesis-nitrogen relationship in wild plants. – In: Givnish, T.J. (ed.): On the Economy of Plant Form and Function. Pp. 25-55. Cambridge University Press, Cambridge – London – New York – New Rochelle – Melbourne – Sydney 1986.

Fitter, A.H., Hay, R.K.M.: Environmental Physiology of Plants. – Academic Press, New York 1981.

Hiromi, H., Ninomiya, I., Koike, T., Ogino, K.: Stomatal regulation of canopy trees in a tropical rain forest. – Jap. J. Ecol. **49**: 68-76, 1999.

Inoue, T., Hamid, A.A.: Introduction to the canopy biology program in Sarawak. – In: Lee, H.S., Ashton, P.S., Ogino, K. (ed.): Reports of New Program for Promotion of Basic Sciences: Studies of Global Environment Changes with Special Reference to Asia and Pacific Regions. Vol. 2-3. Long Term Ecological Research of Tropical Rainforest in Sarawak. Pp. 120-131. Ehime University, Matsuyama 1995.

Kato, M., Inoue, T., Hamid, A.A., Nagamitsu, T., Merdek, M.B., Nona, A.R., Itino, T., Yamane, S., Yumoto, T.: Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. – Res. Popul. Ecol. **37**: 59-79, 1995.

Kumagai, T., Kuraji, K., Noguchi, H., Tanaka, Y., Tanaka, K., Suzuki, M.: Vertical profiles of environmental factors within tropical rainforest, Lambir Hills National Park, Sarawak, Malaysia. – J. Forest Res. **6**: 257-264, 2001.

Lambers, H., Chapin, F.S., III, Pons, T.L.: Plant Physiological Ecology. – Springer-Verlag, New York 1998.

Larcher, W.: Physiological Plant Ecology. 4th Ed. – Springer-Verlag, Berlin 2003.

Linder, S., Troeng, E.: The seasonal course of respiration and photosynthesis in strobili of Scots pine. – Forest Sci. **27**: 267-276, 1981.

Nakano, R., Yonemori, K., Sugiura, A.: Photosynthesis by calyx lobes has no contribution to early fruit development in persimmon. – Acta Hortic. **436**: 345-353, 1997.

Osada, N., Takeda, H., Furukawa, A., Awang, M.: Fruit dispersal of two dipterocarp species in a Malaysia rain forest. – J. trop. Ecol. **17**: 911-917, 2001.

Sakai, S.: General flowering in lowland mixed dipterocarp forests of South-east Asia. – Biol. J. linnean Soc. **75**: 233-247, 2002.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A., Nakashizuka, T.: Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. – Amer. J. Bot. **86**: 1414-1436, 1999.

Sakai, S., Nakashizuka, T., Ichie, T., Nomura, M., Chong, L.: Lambir hills canopy crane, Malaysia. – In: Mitchell, A.W., Secoy, K., Jackson, T. (ed.): The Global Canopy Handbook. Pp. 77-79. Global Canopy Programme, Oxford 2002.

Šesták, Z. (ed.): Photosynthesis During Leaf Development. – Academia, Praha; Dr W. Junk Publ., Dordrecht – Boston – Lancaster 1985.

Shinano, T., Lei, T.T., Kawamukai, T., Inoue, M.T., Koike, T., Tadano, T.: Dimethylsulfoxide method for the extraction of chlorophylls *a* and *b* from the leaves of wheat, field bean, dwarf bamboo, and oak. – Photosynthetica **32**: 409-415, 1996.

Suzuki, E., Ashton, P.S.: Sepal and nut size of fruits of Asian Dipterocarpaceae and its implications for dispersal. – J. trop. Ecol. **12**: 853-870, 1996.

Tamari, C., Jacalne, D.V.: Fruit dispersal of dipterocarps. – Bull. Forest. Forest Prod. Res. Inst. **325**: 127-140, 1984.

Turner, I.M.: The Ecology of Trees in the Tropical Rain Forest. – Cambridge University Press, Cambridge 2001.

Vemmos, S.M., Goldwin, G.K.: The photosynthetic activity of Cox’s Orange Pippin Apple flowers in relation to fruit setting. – Ann. Bot. **73**: 385-391, 1994.

Watson, M.A., Casper, B.B.: Morphogenetic constraints on patterns of carbon distribution in plants. – Annu. Rev. Ecol. Syst. **15**: 233-258, 1984.

Whitmore, T.C.: Tropical Rain Forest of the Far East. 2nd Ed. – Oxford University Press, Oxford 1984.

Whitmore, T.C.: An Introduction to Tropical Rain Forests. 2nd Ed. – Oxford University Press, Oxford 1998.

Wright, I.J., Reich, P.B., Westoby, M.: Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. – Funct. Ecol. **15**: 423–434, 2001.

Wullschleger, S.D., Oosterhuis, D.M.: Photosynthetic and respiratory activity of fruiting forms within the cotton canopy. – Plant Physiol. **94**: 463-469, 1990.

Yap, S.K., Chan, H.T.: Phenological behaviour of some Shorea species in peninsular Malaysia. – In: Bawa, K.S., Hadley, M. (ed.): Reproductive Ecology of Tropical Forest Plants. Pp. 21-35. UNESCO, Paris; Parthenon Publishing Group, Paris 1990.

Zhao, D., Oosterhuis, D.M.: Photosynthetic capacity and carbon contribution of leaves and bracts to developing floral buds in cotton. – Photosynthetica **36**: 279-290, 1999.

Zotz, G., Winter, K.: Short-term photosynthesis measurement predict leaf carbon balance in tropical rain forest canopy plant. – Planta **191**: 409-412, 1993.