

# Chemical contents of *Macaranga* food bodies: adaptations to their role in ant attraction and nutrition

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## Summary

1. *Macaranga* (Euphorbiaceae) is a paleotropical tree genus comprising myrmecophytic and non-myrmecophytic species. All species are presumed to possess food bodies (FBs) to maintain or attract ants as anti-herbivore defence.

2. The hypothesis was tested that *Macaranga* species differing in their mode of association with ants would produce FBs differing in their chemical composition. We investigated contents of carbohydrates, proteins and lipids in FBs of four myrmecophytic and one non-myrmecophytic *Macaranga* as well as one *Parthenocissus* (Vitaceae) species.

3. On a dry weight basis, FBs of myrmecophytes contained relatively higher amounts of proteins compared to carbohydrates than those of non-myrmecophytes. Soluble carbohydrates showed species-specific patterns and were found in especially high amounts in both non-myrmecophytes. Furthermore, *Parthenocissus* FBs contained higher amounts of soluble compared to polymeric substances not only in carbohydrates but also in proteins.

4. FBs seem to be specifically adapted to their respective role in ant attraction and nutrition, with myrmecophytes providing ants with high amounts of lipids and proteins and non-myrmecophytes mainly offering carbohydrates in the form of common soluble sugars.

*Key-words:* Ant–plant interaction, insect nutrition, mutualism, myrmecophytism

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## Introduction

*Macaranga* (Euphorbiaceae) is a genus of important pioneer trees, having its centre of distribution in South-East Asia. Nine of the 27 *Macaranga* species of Peninsular Malaysia are true myrmecophytes, regularly inhabited by ants nesting in the hollow stems and twigs of the plants (so-called ‘domatia’) (Fiala & Maschwitz 1992a). All myrmecophytes produce food bodies (FBs) on different parts of the plant (Fiala & Maschwitz 1992b). These associations are highly specific with the ants living only on one or a few plant species (Fiala, Linsenmair & Maschwitz 1994). Ants effectively protect their host against, for example, insect herbivores and climbers (Fiala *et al.* 1989). Because the ants feed only on FBs and honeydew from scale insects, which they keep in the interior of the inhabited internodes, FBs must be considered a very important source of nutrients for the ants.

Non-myrmecophytic *Macaranga* species possess no domatia and therefore cannot house ants. However, several are ‘myrmecophilic’ and produce FBs as well as extrafloral nectar on their surface and thus attract generalistic ants (Fiala & Maschwitz 1991, 1992b).

Because of their foraging activities, these provide at least some protective effect for the plants (Fiala, Grunsky *et al.* 1994).

FBs are produced at different parts of the plant surface, the anatomical properties of the FB-producing parts depend on the degree of the plants’ association with ants (Fig. 1). We determined the main nutrients of FBs (carbohydrates, proteins and lipids) in myrmecophytic and non-myrmecophytic *Macaranga* species. If FBs have evolved any chemical properties to meet the respective nutritive requirements of harvesting ants, differences should become obvious when obligate myrmecophytes are compared to facultative myrmecophilic species.

## Materials and methods

FBs were collected at different sites in Peninsular Malaysia from four myrmecophytic *Macaranga* species [*Macaranga triloba* (Bl.) Muell. Arg., *M. hullettii* King ex Hook., *M. hosei* King ex Hook. and *M. pruinosa* (Miq.) Muell. Arg.] and from the non-myrmecophytic *M. tanarius* (L.) Muell. Arg. Additionally, FBs from the non-myrmecophytic



*Parthenocissus tricuspidata* (Sieb. et Zucc.) Planch. (Vitaceae) grown in gardens in Germany were collected. One sample sufficient for analyses of all three nutrient classes consisted of at least 4000–5000 FBs and was, whenever possible, collected from one individual plant. Occasionally, FBs of several plants growing at the same location had to be pooled in one sample.

All FBs were stored in 100% ethanol and freeze-dried before analysis. For analysis of carbohydrates, about 10 mg FB tissue (dry weight) was homogenized by grinding and was subsequently extracted twice in a total of 1.5 ml water. After centrifugation, the supernatant was cleared further by micro-membrane filtration (Spartan 30/B filters, 0.45  $\mu\text{m}$ , Schleicher & Schuell, Germany) and stored at  $-20^{\circ}\text{C}$  until use. Polysaccharides in the pellet were hydrolysed by boiling for 1 h at  $100^{\circ}\text{C}$  in 1n HCl. Sugars were separated by isocratic (0.1n NaOH) HPLC on an anion exchange column, and quantified by pulsed amperometric detection (Dionex Series 4500 Chromatography System, Dionex, Idstein, Germany).

For the analysis of proteins and soluble amino acids, about 20 mg of ground tissue was extracted with 1.5 ml water. After centrifugation and membrane filtration, soluble amino acids were directly determined in the supernatant. Proteins were hydrolysed for 4 h at  $100^{\circ}\text{C}$  with 6n HCl. Amino acids were separated and measured with an Amino Acid Analyzer LC 5001 (Biotronic, Maintal, Germany).

Total lipids were analysed with the method described by Merck (1970, pp. 237–239). FB tissue was extracted in isopropanole (about 50 mg tissue with 5 ml solvent). By addition of 1 ml 1n alkaline hydroxylamine solution, free fatty acids as well as those from di- or triglycerides were converted to hydroxamic acids. After adding a solution of  $\text{FeCl}_3$  (about 10% Fe), the resulting complexes were measured colorimetrically in a PMQ 2 Photometer (Zeiss, Germany) at a wavelength of 515 nm.

At least two parallel analyses were carried out for each sample. Therefore, a mean had to be calculated from these parallels for each detected substance to obtain the results for one distinct sample. Further calculations were based on these results. The compo-

**Fig. 1.** Food bodies of three *Macaranga* species differing in their degrees of association with ants: (a) in the non-myrmecophyte *M. tanarius* FBs are produced on the whole plant surface; (b) production of FBs in the myrmecophytic species *M. hosei* is mainly restricted to the upper surface of stipules; (c) *M. triloba* produces its FBs to more than 99% on the inner surface of recurved and stem-clasping stipules. The anatomical properties of the FB-producing organs and surfaces therefore show close dependencies on the taxonomic relationships within the genus *Macaranga* as well as on the various degrees in the plants' associations with ants. The ants on *M. triloba* and *M. hosei* are about 4 mm in length, the diameter of the FBs is up to 800  $\mu\text{m}$  for the largest FBs of *M. tanarius*, up to 650  $\mu\text{m}$  for *M. hosei* and up to 300  $\mu\text{m}$  for *M. triloba*.

sition of a 'typical FB' for each species was assessed by calculating the mean for each substance from all respective samples. Because samples with differences of more than 10% between the parallels were excluded, calculations were based only on valid measurements. Thus, extreme values represent true, existing data. The number of valid samples per substance class and species ranged from three to 17.

## Results

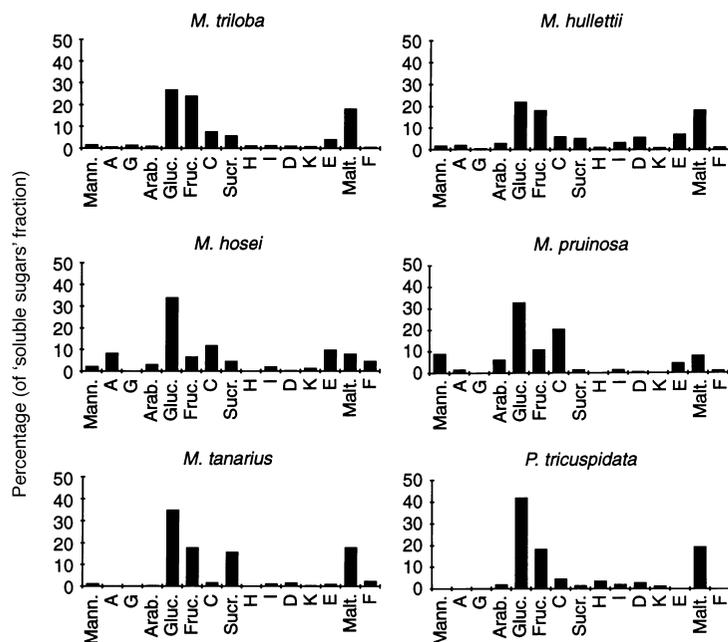
In the analysis of nutrients two tendencies became obvious. First, especially for soluble sugars, species-specific patterns in the percentage composition were found (Fig. 2). These patterns showed high similari-

ties within the three pairs *M. triloba*/*M. hullettii*, *M. hosei*/*M. pruinosa* and *M. tanarius*/*P. tricuspidata*, respectively.

In FBs of the two non-myrmecophytic species, the common sugars glucose, fructose, sucrose and maltose made up about 85% of the soluble sugar fraction (Table 1), with *P. tricuspidata* showing very low sucrose levels. In myrmecophytic *Macaranga* species, other sugars or sugar alcohols (arabinose, mannitol and nine unidentified mono- or oligosaccharides) made up from 24% to 46% of the soluble sugar fraction. Most of these substances were found in higher amounts only in one or in closely related species. For example, a peak designed 'sugar A' appeared in high amounts only in FBs from *M. hosei* (8.5% compared to 0–2.3% in other species). 'Sugar C' was the substance with the second highest relative amounts in *M. hosei* and *M. pruinosa* (proportions of 12.1% and 20.5%, respectively), while we did not find more than 5–8% of 'sugar C' in *M. triloba* and *M. hullettii*. *Macaranga tanarius* and *P. tricuspidata* contained about 2–4% 'sugar C' (Fig. 2).

Substantial differences were also found for the absolute and relative amounts of polymeric carbohydrates, proteins and soluble amino acids (Table 2). Most striking are the differences in the ratio of total carbohydrates to total proteins (including soluble amino acids) in *M. tanarius* and *P. tricuspidata* (6.40 and 2.47, respectively) as compared to the other species, which showed proportions ranging from 0.70 up to a maximum of 1.11. FBs of *P. tricuspidata* contained considerable more soluble components than macromolecules. Furthermore, FBs of *M. tanarius* and *P. tricuspidata* contained the highest amounts of soluble sugars (44.8 and 96.2 mg g<sup>-1</sup> dry weight, respectively, compared to 10.4 to 14.6 mg in myrmecophytes).

When quantities were calculated per fresh weight, the differences became even more obvious: owing to very high water content in FBs of *P. tricuspidata* and *M. tanarius*, the FBs of these two species showed the lowest contents of total proteins in fresh FBs (Table 3), while total carbohydrate contents were still comparable to or higher than those of myrmecophytes.



**Fig. 2.** Percentage composition of the soluble sugar fraction of all six study species. Bars indicate the mean proportion of the respective substance in use (%), for number of samples see Table 1. The order of the substances on the x-axis follows their original order as they appear on the chromatograms. Species pairs showing highest similarities in their sugar patterns are arranged in one line. Names of identified sugar and sugar alcohols are abbreviated (Mann., mannitol; Arab., arabinose; Gluc., glucose; Fruc., fructose; Sucr., sucrose; Malt., maltose), unidentified substances are indicated by single letters.

**Table 1.** Relative composition of the soluble sugar fraction of four myrmecophytic *Macaranga* species and two non-myrmecophytes. The proportions of the various substances are expressed as percentage of the total soluble sugar fraction of the regarded species. The class 'others' comprises mannitol, arabinose and nine unidentified mono- or oligosaccharides or sugar alcohols. The number of samples (*n*) is indicated for each species as well as the association with ants (M for myrmecophyte and NM for non-myrmecophyte). The values are given as mean ± standard deviation calculated from all respective samples

Species	<i>n</i>	Associations with ants	Glucose	Fructose	Sucrose	Maltose	Others
<i>M. triloba</i>	9	M	27.2 ± 10.5	24.3 ± 13.0	6.0 ± 8.4	18.5 ± 23.1	24.0 ± 11.3
<i>M. hullettii</i>	9	M	22.4 ± 8.5	18.4 ± 7.4	5.4 ± 8.2	18.7 ± 15.1	35.1 ± 13.3
<i>M. hosei</i>	7	M	34.2 ± 5.3	6.8 ± 5.9	4.9 ± 6.0	8.2 ± 8.1	45.9 ± 10.7
<i>M. pruinosa</i>	4	M	33.0 ± 7.7	10.9 ± 6.2	1.7 ± 1.7	8.2 ± 8.5	46.2 ± 6.4
<i>M. tanarius</i>	5	NM	35.2 ± 11.7	18.2 ± 5.0	16.1 ± 13.6	18.2 ± 6.7	12.3 ± 9.7
<i>P. tricuspidata</i>	3	NM	42.2 ± 11.5	18.5 ± 19.1	1.7 ± 1.9	19.7 ± 10.2	17.9 ± 1.4

**Table 2.** Contents of soluble carbohydrates, polysaccharides, soluble amino acids and proteins in FBs of five *Macaranga* and one *Parthenocissus* species. Contents of all substances are expressed as mg g<sup>-1</sup> dry weight, values are given as mean ± standard deviation (*n* = number of samples). Total carbohydrates and total proteins are calculated as mean from the sums of soluble sugars and carbohydrates or from soluble amino acids and proteins, respectively. For this calculation, only samples which revealed valid results in both soluble and polymeric substances (parallels not differing more than 10%) are considered. The c/p-ratio indicates the quotient of total carbohydrates and total proteins and is calculated from the respective means as given in the table

Species	Soluble carbohydrates	Polysaccharides	Soluble amino acids	Proteins	Total carbohydrates	Total proteins	c/p-ratio
<i>M. triloba</i>	12.7 ± 12.4 (9)	18.3 ± 4.6 (4)	4.0 ± 2.2 (17)	32.0 ± 23.4 (15)	25.5 ± 3.2 (4)	28.2 ± 12.1 (11)	0.90
<i>M. hullettii</i>	10.4 ± 5.0 (9)	38.3 ± 9.2 (4)	4.2 ± 2.7 (4)	33.7 ± 19.1 (4)	50.4 ± 14.4 (4)	45.6 ± 18.8 (3)	1.11
<i>M. hosei</i>	14.6 ± 3.6 (7)	47.7 ± 17.8 (6)	12.3 ± 2.5 (6)	52.8 ± 10.1 (4)	62.5 ± 17.0 (5)	60.8 ± 7.4 (3)	1.03
<i>M. pruinosa</i>	13.8 ± 4.0 (4)	28.3 ± 6.4 (4)	10.1 ± 4.2 (5)	50.0 ± 19.0 (5)	42.1 ± 6.5 (4)	60.1 ± 19.7 (5)	0.70
<i>M. tanarius</i>	44.8 ± 24.4 (5)	80.7 ± 25.0 (4)	4.2 ± 1.0 (3)	16.0 ± 9.7 (2)	125.5 ± 42.5 (4)	19.6 ± 9.0 (2)	6.40
<i>P. tricuspidata</i>	96.2 ± 56.7 (3)	79.0 ± 13.6 (5)	53.2 ± 34.0 (6)	12.6 ± 12.0 (6)	162.6 ± 32.6 (2)	65.8 ± 31.4 (6)	2.47

Total lipids in dry FB tissue made up from 5.5% [*n* = 2, standard deviation (SD) 0.2] in *P. tricuspidata* to up to 40% (*n* = 3, SD 20.4) in *M. hullettii*, whereas total lipids in *M. hosei*, *M. triloba* and *M. tanarius* amounted to about 25% (25.5%, 26.0% and 26.4%, respectively, *n* = 4, 9 and 1, SD = 16.2, 11.6 and 0). The mean of *M. pruinosa* FBs was slightly lower (21.5%, *n* = 3, SD 4.1). When regarding total lipids in fresh FBs, the relations between the species are different. Here, *M. triloba* and *M. hullettii* had similar values (about 15%). The same holds true for the three other *Macaranga* species (about 8% to 9%), while *Parthenocissus* contained very low amounts (0.5%, see Table 3).

First results of GC/MS analyses indicate that the lipid fraction of FBs from myrmecophytic *Macaranga* species contained 80–90% triglycerides, compared to about 45% in the FBs from *Parthenocissus*. Additionally, up to 9% of diglycerides were found in the lipid fraction of the myrmecophytes' FBs, while none were detected in the FBs of *Parthenocissus*. On the other hand, the relative amount of free fatty acids was highest in *Parthenocissus* FBs (about 20% of the lipid fraction).

Because the mean energy content of pure fatty acids is about 38 kJ g<sup>-1</sup> compared to only about 17 kJ g<sup>-1</sup> for carbohydrates and proteins (Stryer 1990, p. 293), energy contents of FBs are mainly influenced by the amounts of incorporated lipids. Dry FBs from all species covered a total range from 6.0 kJ g<sup>-1</sup> dry weight to 16.8 kJ g<sup>-1</sup> dry weight (Table 4). When calculated per fresh weight, *M. triloba* and *M. hullettii* on the one hand and the other three *Macaranga* species on the other had nearly the same values (Table 4). In contrast, fresh FBs of *P. tricuspidata* had a very low energy content.

## Discussion

To our knowledge, these are the first quantitative data on the contents of all three major nutrient classes in FBs. O'Dowd (1980) presented some information on lipid contents in pearl bodies of *Ochroma pyramidale* and later reviewed dominating contents of pearl bodies from several genera (O'Dowd 1982). Rickson mainly used staining techniques to study FBs of *Macaranga* (Rickson 1980), *Acacia* and *Cecropia* (F. R. Rickson, personal communication).

Much more information exists on chemical contents of other types of plant-derived insect food, for example, on elaiosomes which have been studied in regard to their chemical composition and nutrient contents (Hocking & Kortt 1987), the costs emerging from their production (Hughes, Westoby & Johnson 1993) and to the adaptivity of incorporated compounds (Brew, O'Dowd & Rae 1989; Hughes, Westoby & Jurado 1994).

Our data indicate that FBs of the investigated non-myrmecophytes contain higher amounts of 'cheap'

**Table 3.** Mean contents of total protein and total carbohydrates (see Table 2) as well as lipids in relation to FB fresh weight. Calculations are based on mean contents per dry weight as given in Table 2 and the mean water content of each species as given here. Results are given as mg g<sup>-1</sup> fresh weight, number of samples (*n*) is given in brackets. Water content was determined gravimetrically and is given like the undetermined remaining mass in pro mille

Species	Total carbohydrates	Total protein	Lipids	Water	Remaining mass
<i>M. triloba</i>	10.3 ± 2.6 (4)	15.9 ± 6.9 (11)	146.9 ± 65.6 (9)	435 ± 99.5 (16)	391.9
<i>M. hullettii</i>	19.7 ± 5.6 (4)	17.8 ± 7.4 (4)	156.4 ± 79.8 (3)	609 ± 31.2 (4)	197.1
<i>M. hosei</i>	22.4 ± 6.1 (6)	21.8 ± 2.6 (3)	91.5 ± 58.0 (4)	641 ± 64.5 (4)	223.3
<i>M. pruinosa</i>	13.8 ± 2.1 (5)	19.8 ± 6.5 (5)	87.5 ± 16.7 (3)	671 ± 138.4 (7)	207.9
<i>M. tanarius</i>	39.3 ± 13.3 (4)	6.1 ± 2.8 (2)	82.6 ± 0.0 (1)	687 ± 92.6 (5)	185.0
<i>P. tricuspidata</i>	14.8 ± 3.0 (2)	6.0 ± 2.9 (6)	5.0 ± 0.2 (2)	909 ± 17.1 (3)	65.2

**Table 4.** Energy contents of FBs calculated for main nutrient contents using caloric values according to Stryer (1990) and mean values for total carbohydrates, proteins and lipids as given in Tables 2 and 3. Energy contents are given in Joules per g dry weight and, for estimation of the profitability of food body collection by ants, also in Joules per g fresh weight

Species	Energy (kJ g <sup>-1</sup> dry weight)	Energy (kJ g <sup>-1</sup> fresh weight)
<i>M. triloba</i>	10.8	6.0
<i>M. hullettii</i>	16.8	6.6
<i>M. hosei</i>	11.8	4.2
<i>M. pruinosa</i>	9.9	3.9
<i>M. tanarius</i>	12.5	3.9
<i>M. tricuspidata</i>	6.0	0.5

substances like carbohydrates, while N-containing proteins and energy-rich lipids are mainly incorporated into the FBs of myrmecophytic *Macaranga* species. Because Rickson (1971, 1980, personal communication) reported high amounts of lipids and proteins in FBs from three different myrmecophytic genera (*Acacia*, *Cecropia* and *Macaranga*), this property can be assumed to be a common feature of FBs produced by true myrmecophytes. Furthermore, the amounts of soluble (and thus presumably better tastable) carbohydrates were higher in FBs from non-myrmecophytes, with *P. tricuspidata* also showing very high amounts of soluble amino acids and free fatty acids.

The different patterns of soluble sugars reflect taxonomic relations within the genus *Macaranga* and may as well point to functional aspects. *Macaranga hullettii* and *M. triloba* belong to the same section of the genus (*Pachystemon* s. str., Whitmore 1973, 1975) and show high similarities in their sugar patterns, the same close correspondence is found in *M. hosei* and *M. pruinosa* (both *pruinosa* group). The sugar composition of *M. tanarius* FBs resembled those of *Parthenocissus* rather than its congeners. Furthermore, the latter two species mainly contained four or three different sugars, respectively, while the myrmecophytic ones provided up to 11 different substances. Similar results were found for the FBs of two non-myrmecophytic vines [*Cayratia mollissima* (Wall.) Gagnep. and *C. japonica*, (Thunb.) Gagnep., Vitaceae] growing in Malaysia (M. Heil & R. Rabenstein, unpublished results).

We assume that these patterns reflect different nutritive requirements of the respective consumers. Ants foraging on non-myrmecophytes collect the FBs in addition to their normal diet and are not exclusively dependent on this food source. High contents of common, soluble substances may serve as signals indicating the nutritional value of FBs.

In contrast to this, at least the ants associated with the obligate myrmecophyte *M. triloba* are able to live exclusively on FBs and thus seem to be absolutely dependent on this food source (Fiala 1988). High amounts of proteins and lipids have to be offered to satisfy the nutritional requirements of the inhabiting colony, while ant-attracting signals are not necessary here. In most cases carbohydrates can be derived from the honeydew of associated scale insects and the plants can reduce the carbohydrate provision via FBs. Field observations demonstrated that FBs from myrmecophytic species were not attractive to several ant species that visited extrafloral nectaries (B. Fiala & R. Rabenstein, unpublished results).

Similar adaptations can be seen in other plant tissues and excreted liquids provided as food source for animals. For example, correlations between nutritional requirements of the respective consumers and chemical contents of floral and extrafloral nectar were reported by Baker, Opler & Baker (1978), Koptur (1994) and Lanza *et al.* (1993). Rickson (1971) found glycogen to be the main storage carbohydrate in FBs of *Cecropia*. In a similar case, the fatty acid composition of elaiosomes was found to match most closely that of insects, not that of seeds (Brew *et al.* 1989; Hughes *et al.* 1993, 1994). A special diglyceride (1,2 Diolein) was found in both cases and could be demonstrated to cause the collecting behaviour in the ants tested (Brew *et al.* 1989; Hughes *et al.* 1994). First results based on GC/MS analyses also indicate the occurrence of diglycerides in *Macaranga* FBs.

All these data lead to the assumption that plant components produced to attract mutualistic animals show adaptive traits by possessing special contents matching special requirements of the consumers. Further studies are needed to elucidate whether this tendency is a general rule which is also valid for other species and genera.

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