

SHORT COMMUNICATION

Myrmecochory in the Zingiberaceae: seed removal of *Globba franciscii* and *G. propinqua* by ants (Hymenoptera – Formicidae) in rain forests on Borneo

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The Old-World tropics encompass one of the floristically richest zones of the world and some of the hot spots of ant diversity. This results in a large variety of ecological interactions between both groups. One of them is the phenomenon of myrmecochory, seed dispersal by ants, which is also well known from temperate forests (Gorb & Gorb 2003, Ulbrich 1919), and which is most prominent in sclerophyll shrublands of Australia and southern Africa (Andersen 1988). Beattie (1983), who reviewed the distribution of ant-dispersed plants (at least 80 plant families worldwide) proposed that species richness and abundance of myrmecochores and diaspore-dispersing ants increases with decreasing latitude and thus predicted a greater variety of ant-dispersal systems in the tropics. However, up to now, few tropical myrmecochores have been described (Horvitz 1981, Horvitz & Schemske 1986), especially in the palaeotropics (Kaufmann *et al.* 2001). Here we report myrmecochory in two species of rain-forest herb of the Zingiberaceae, give the first evidence for seed dispersal by ants in this plant family and present a list of seed-dispersing ant species. An important benefit of myrmecochory is the dispersal distance of the ant-transported seeds (Andersen 1988), that has been found to be positively correlated with ant size (Gomez & Espadaler 1998a, Pudlo *et al.* 1980). In this study, we checked whether this correlation is also true for the conditions of the tropical rain forest, where *Globba* plants occur.

Bornean *Globba* (Zingiberaceae) species are plants of the primary rain forest usually found in moist, shady places along streams and waterfalls. The slender herbs

are 0.5–1 m high, with delicate small, yellow, white or violet inflorescences and flowers on the top of the leafy shoots. *Globba* species produce fruits infrequently but often reproduce vegetatively by bulbils or vegetative miniature plantlets (Larsen *et al.* 1999, Smith 1996). Their inflorescences often point downwards or are pendulous (Weber 1995), which may hint towards myrmecochory, as many ant-dispersed plant species have limp fruit stalks that facilitate the collection of seeds by ants (Ulbrich 1919).

We studied two species: *Globba franciscii* Ridl. and *G. propinqua* Ridl. Seeds of both species are embedded in a fruit capsule including a mean of 13 diaspores in *G. propinqua* (SD = 5.83, n = 20) and 33 diaspores in *G. franciscii* (SD = 7.33, n = 6) (photographs of plants ants and seeds can be obtained at: <http://www.antbase.de/myrmecochory.htm>). Fruiting occurs over a long period as several capsules may form on one shoot while the plant is still flowering. When fruits are ripe, the capsule bursts open to present the seeds. As commonly occurs in the Zingiberaceae, the seeds of *Globba* have an aril, a fleshy appendage that partially encloses the seed and attaches to the seed coat at the micropylar region (Liao & Wu 2000). Aril cells are usually rich in lipids and also contain proteins, starch grains and other polysaccharides (Liao & Wu 2000).

Field work was conducted from January to March 2000 and from February to March 2001 in the Kinabalu National Park (N 6°2', E 116°42') and in the Tawau Hills Park (N 4°23', E 117°53'), both in Sabah, Malaysia (see also Smith 1996). We observed seed handling by ants under natural conditions and experimentally studied removal of seeds. In each of the experiments (n = 46) we presented 10 seeds of one of the examined *Globba* species

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Table 1. Ant species that removed seeds of *Globba franciscii* and *G. propinqua* during our experiments and all other observations (pooled). The mean tibia length of ant species, number of removed seeds, mean transport distances, standard deviations of transport distances (SD), and number of measured seed transports (N) are provided. Species in bold contribute to the regression analysis (Figure 1). Direct observations of feeding on the seed arils are marked with X. Subfamilies are coded as follows: Dol = Dolichoderinae, For = Formicinae, Myr = Myrmicinae and Pon = Ponerinae.

Species	Subfamily	Tibia length of minors (mm)	No. of removed seeds	Mean distance of seed transport (\pm SD) (cm)	N	Feeding on aril (direct obs.)
Dolichoderus sp. 1	Dol	2.0	10	10 \pm 0	9	X
<i>Dolichoderus</i> sp. 2	Dol	1.0	9	–	0	X
Camponotus (Colobopsis) sp. 1	For	2.1	14	48.8 \pm 2.5	10	X
<i>Camponotus (Colobopsis)</i> sp. 2	For	–	4	6 \pm 0	4	X
Camponotus gigas Latreille	For	7.3	5	> 437 \pm 346	5	–
Camponotus sp. 3	For	3.2	9	170 \pm 0	3	–
Oecophylla smaragdina Fabricius	For	3.6	27	> 500	5	–
Paratrechina sp.	For	0.9	15	72 \pm 5.35	15	–
Polyrhachis sp. 1	For	3.8	44	184 \pm 174	27	X
<i>Polyrhachis</i> sp. 2	For	–	10	7 \pm 4.2	4	X
Crematogaster inflata Smith	Myr	1.1	10	6.8 \pm 2.3	6	X
Lophomyrmex bedoti Emery	Myr	0.3	18	11 \pm 1.7	9	X
<i>Pheidole aristotelis</i> Forel	Myr	0.4	2	–	0	–
Pheidole quadrensis Forel	Myr	0.8	13	40 \pm 0	7	X
Pheidole cariniceps Eguchi	Myr	0.6	9	20 \pm 10	4	–
<i>Pheidole</i> sp. 1	Myr	–	10	10 \pm 0	4	X
Pheidologeton affinis Jerdon	Myr	0.6	5	35 \pm 21	4	–
<i>Pheidologeton pygmaeus</i> Emery	Myr	–	2	–	–	–
Pheidologeton sp. 1	Myr	0.8	16	99 \pm 65	16	X
Diacamma cf. rugosum Le Guillou	Pon	3.5	18	193 \pm 144	6	–
Leptogenys sp. 1	Pon	2.1	1	150 \pm 0	1	–
Leptogenys sp. 2	Pon	2.1	10	150 \pm 70.7	2	–
Odontoponera cf. transversa Smith	Pon	2.3	66	105 \pm 15.1	11	–

on a small wooden tray (10 \times 10 cm) on the forest floor to attract terrestrial ant species. Seed depots were randomly placed along walking trails with a minimum distance of 15 m between them, so that each seed pile constituted an independent sample. The behaviour of the ants towards the seeds was observed and we recorded the number of seeds they removed within 1 h. Seed transport distances of different ant species were noted as beeline over ground. In only two of the observed 152 cases were seeds dropped to the ground before ants reached their nests, however, in some cases we lost the foragers after several metres. Ants were collected with forceps and stored in vials with 85% alcohol. Determination to subfamilies took place according to the key of Bolton (1994), then specimens were assigned to morphospecies that could partly be identified at species level. Many ant species show positive allometry for leg size with body mass and longer leg sizes (or tibia lengths) are an indicator for better mobility of the species (Kaspari & Weiser 1999). To obtain mean tibia lengths ten worker ants of most of the observed ant species were measured using a Wild M5A binocular scope (Wild Ltd., Switzerland). Statistical analyses were performed using the STATISTICA 6.1 package (Statsoft, Inc. 2003, Tulsa, USA, <http://www.statsoft.com>).

In both *Globba* species examined the fleshy aril formed a large elaiosome (ant fruit) that served as food for ants and allowed them to handle the seed easily. Generally, ants removed seeds from trays rapidly after their encounter and

transported them directly back to their nests. However, one species (*Camponotus (Colobopsis)* sp. 2) fed on the seed arils and also transported separate aril pieces into the nest, but mostly without taking away seeds from trays. In total, in 11 experiments with *Globba propinqua*, 77 seeds were removed by seven ant species (removal rate = 7 seeds h⁻¹, n = 11, SD = 4), while in 35 samples with *Globba franciscii* 228 seeds were removed by 17 species of ants (mean removal rate = 6.51 seeds h⁻¹; n = 35, SD = 3.7). The removal rates for the two species of *Globba* did not differ statistically (Mann–Whitney U-test, U = 174, Z = 0.49, P > 0.05).

Altogether, we observed 23 species of ant from 12 genera and 4 subfamilies that transported the seeds (or fed on the seed arils) of these two *Globba* species (see Table 1). We noted Formicinae, Dolichoderinae and Myrmicinae and also mainly carnivorous species such as Ponerinae. Ant species that removed seeds in our experiments comprised ground-living as well as predominantly arboreal species that were recorded near the base of tree trunks where they descended to the ground. Only one species, *Polyrhachis* sp. 2, a widely distributed arboreal ant, was observed to remove seeds directly from the dehisced fruit capsules. Dispersal distances achieved by this ant were notably long and reached more than 800 cm. However, we lost most individuals of arboreal species before they reached their destination.

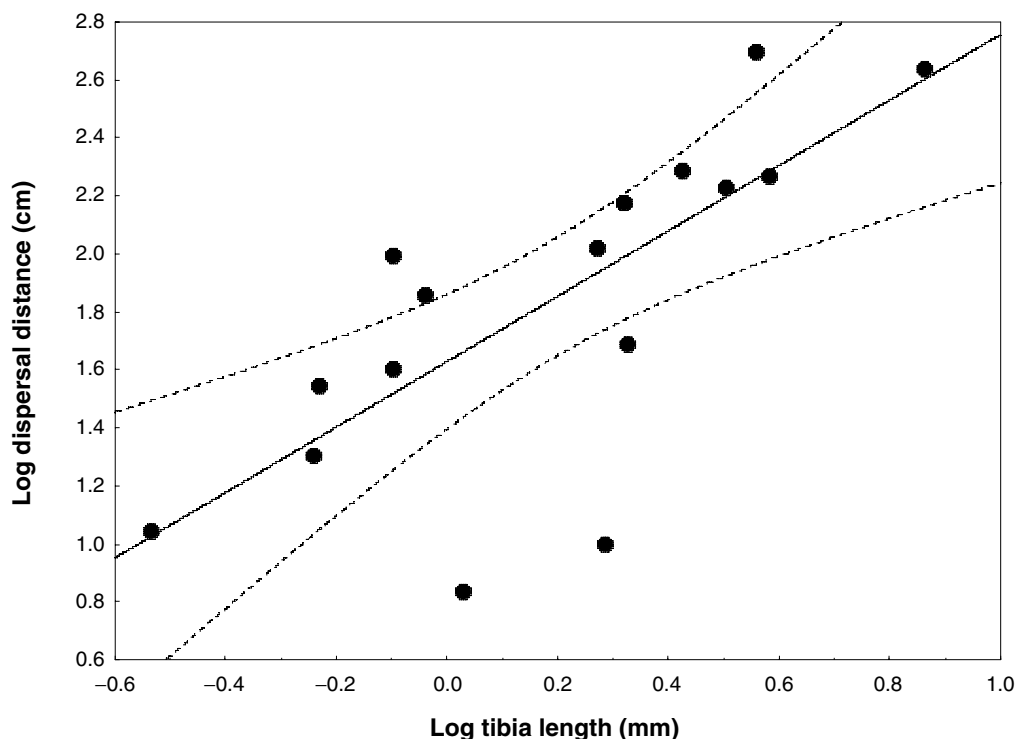


Figure 1. Relationship between logarithm of tibia lengths of ant species that transported seeds and logarithm of their dispersal distances. A linear regression line is shown, together with its 95% confidence interval (linear regression equation: $Y = 1.63 + 1.13 X$, $F(1,15) = 17.1$; adjusted $r^2 = 0.50$, $P < 0.001$).

Our measurements of mean tibia lengths of the transporting ant species ranged from 0.3 to 7.3 mm ($n = 19$, median = 2.1). Logarithms of dispersal distances were significantly correlated with logarithms of tibia lengths of the transporting ant species ($n = 17$, $r = 0.73$, $P < 0.001$, Figure 1). The median dispersal distance of all seeds was 55 cm ($n = 132$, range 4–800 cm, mean = 112 cm, SD = 143). Though in most species (including tiny *Pheidole*) single workers removed seeds, in some ant species, e.g. *Paratrechina*, cooperative seed transport was performed by several workers.

Among the forest herbs that occur in tropical Asia, the Zingiberaceae are an especially rich group with about 1000 species (Larsen *et al.* 1999). As they flower near to or directly at the ground and do not possess specialized dispersal mechanisms except arillate seeds, animals may play an important role as their potential seed dispersal vectors. Here we show for the first time that the seed aril in *Globba* indeed functions as an elaiosome and that myrmecochory can serve as a mechanism of seed dispersal in the Zingiberaceae. Seed collecting behaviour of ants in the Palaetropics has already been observed in ant-gardens on the giant bamboo, *Gigantochloa scortechinii*, in West Malaysia (Kaufmann *et al.* 2001). However, diaspores of the vascular epiphytes that had been tested in that study had no elaiosomes and the ants' carrying

behaviour was only released by chemical cues, not by food rewards (Kaufmann *et al.* 2001). Our experimental results in *G. propinqua* and *G. franciscii* are consistent with occasional observations of arillate seed dispersal by ants in *G. pendula* Roxb. and in other species of ginger (e.g. *Zingiber pseudopungens* R. M. Smith) (M. Pfeiffer, unpublished data) and demonstrate that ant-dispersal due to elaiosomes is a potential mechanism of seed distribution in the Old World tropics.

Mean observed seed dispersal distance of *Globba* spp. was 112 cm, about the global mean distance of myrmecochorous dispersal of 96 cm ($n = 2524$; range 0.01–77 m) (Gomez & Espadaler 1998b). As we have shown, dispersal distances were significantly correlated with tibia lengths of the transporting ant species: as larger ant species have larger foraging ranges, they are able to transport seeds over longer distances. Our results agree with those of Gomez & Espadaler (1998a), however, these authors showed that seed dispersal distances of ant species are also significantly influenced by their nest distances and nest densities; and as larger ants have lower nest densities than smaller ant species, their seed dispersal distances are longer (see also Andersen 1988).

In our study many of the larger ant species were partly arboreal and used trunk roads in the lower canopy to reach their foraging areas on the forest floor or in the

lower vegetation. But most of those species have nests in or near the ground (Pfeiffer & Linsenmair 2000, M. Pfeiffer *pers. obs.*), so discarded seeds will end up in the soil.

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LITERATURE CITED

- ANDERSEN, A. N. 1988. Dispersal distance as a benefit of myrmecochory. *Oecologia* 75:507–511.
- BEATTIE, A. J. 1983. Distribution of ant-dispersed plants. *Sonderbände naturwissenschaftlicher Verhandlungen* 7:249–270.
- BOLTON, B. 1994. *Identification guide to the ant genera of the World*. Harvard University Press, London.
- GOMEZ, C. & ESPADALER, X. 1998a. Seed dispersal curve of a Mediterranean myrmecochore: influence of ant size and the distance to nests. *Ecological Research* 13:347–354.
- GOMEZ, C. & ESPADALER, X. 1998b. Myrmecochorous dispersal distances: a world survey. *Journal of Biogeography* 25:573–580.
- GORB, E. & GORB, S. 2003. *Seed dispersal by ants in a deciduous forest ecosystem. Mechanisms, strategies, adaptations*. Kluwer Academic Publishers, Dordrecht. 225 pp.
- HORVITZ, C. C. 1981. Analysis of how ant behaviors affect germination in a tropical myrmecochore *Calathea microcephala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). *Oecologia* 51:47–52.
- HORVITZ, C. C. & SCHEMSKE, D. W. 1986. Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica* 18:319–323.
- KASPARI, M. & WEISER, M. D. 1999. The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology* 13:530–538.
- KAUFMANN, E., WEISSFLOG, A., HASHIM, R. & MASCHWITZ, U. 2001. Ant-gardens on the giant bamboo *Gigantochloa scortechinii* (Poaceae) in West-Malaysia. *Insectes Sociaux* 48:125–133.
- LARSEN, K., IBRAHIM, H., KHAW, S. H. & SAW, L. G. 1999. *Gingers of Peninsular Malaysia and Singapore*. Natural History Publications (Borneo), Kota Kinabalu. 135 pp.
- LIAO, J.-P. & WU, Q.-G. 2000. A preliminary study of the seed anatomy of Zingiberaceae. *Botanical Journal of the Linnean Society* 134:287–300.
- PFEIFFER, M. & LINSENMAIR, K. E. 2000. Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera/Formicidae). *Insectes Sociaux* 47:123–132.
- PUDLO, R. J., BEATTIE, A. J. & CULVER, D. C. 1980. Population consequences of changes in an ants seed mutualism in *Sanguinaria canadensis*. *Oecologia* 46:32–37.
- SMITH, R. M. 1996. Gingers. Pp. 244–257 in Wong, K. M. & Phillips, A. (eds). *Kinabalu summit of Borneo*. The Sabah Society & Sabah Parks, Kota Kinabalu.
- ULBRICH, E. 1919. *Deutsche Myrmekochoren. Beobachtungen über die Verbreitung heimischer Pflanzen durch Ameisen*. Verlag von Theodor Fisher, Leipzig und Berlin. 59 pp.
- WEBER, A. 1995. The Malayan species of *Globba*. *Nature Malaysiana* 20:114–121.