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REGULAR PAPER

Hemi-epiphytic *Ficus* (Moraceae) in a Congolese forest

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Background and aims – *Ficus* species exhibit a variety of morphological habits (tree, hemi-epiphyte, shrub, climber, creeping shrub and rheophytic shrub) but their description, and especially the difference between tree and hemi-epiphyte, has led to confusion in previous works. In this paper the terms tree, free-standing strangler, hemi-epiphyte, trunk and pseudo-trunk are defined, discussed and illustrated. The aim in this study was to build on these definitions and document how many tree and hemi-epiphytic *Ficus* species occur at one site in northern Congo; investigate how many hemi-epiphytic species reach the free-standing strangler habit at that site and provide data on host tree species for the hemi-epiphytic *Ficus*.
Results – In the Goualougo Triangle in the southern part of the Nouabalé-Ndoki National Park (Republic of Congo), 285 *Ficus* individuals belonging to 19 species were studied, one of which was a tree while the remaining 18 were hemi-epiphytes of which only six reached the free-standing strangler habit. The host species on which the *Ficus* grew were also recorded; 244 individuals of 69 species were found, one of which, *Petersianthus macrocarpus*, was the most common support for hemi-epiphytic *Ficus* species. Two *Ficus* species, *F. elasticoides* and *F. burretiana,* were also found as hosts for other species of *Ficus* species. A field method for determining whether an adult specimen was a free standing hemi-epiphyte or a tree was tested and proved reliable; this is to knock the trunk to see if it sounds hollow or not.
Conclusion – The differences observed between *Ficus* species in tree and free-standing stranglers, the stages they can reach in the hemi-epiphytic habit and the different host species, indicate that the *Ficus* species play very different roles in the ecosystem. It is likely that the species will vary in response to climate or land-use changes that are happening in tropical forests.

Key words – *Ficus*, free-standing strangler, habit, hemi-epiphyte, pseudo-trunk, Goualougo Triangle Nouabalé-Ndoki National Park.

INTRODUCTION

Ficus L. (Moraceae) commonly called figs is a pantropical genus with at least 735 species (Berg & Corner 2005, Rønsted et al. 2008, Sonibare et al. 2004) that can be trees, hemi-epiphytes, climbers, or shrubs, including creeping or rheophytic shrubs, often with adventitious roots (Berg & Corner 2005, Condit 1969, Datwyler & Weiblen 2004, Putz & Holbrook 1989). Hemi-epiphytic figs, including free-standing stranglers, represent at least fifty percent of the total number of *Ficus* species worldwide (Berg & Corner 2005, Berg & Wiebes 1992) but this percentage is higher in African tropical rain forests (Gentry & Dodson 1987, Harris 2002, Ndolo Ebika 2010).

In previous works on *Ficus* (Berg & Wiebes 1992, Burrows & Burrows 2003, Corner 1940, Harris 2002, Ndolo Ebika 2010, Turner 2001), there has been a degree of confusion with regard to the description of *Ficus* species exhibiting the hemi-epiphytic habit. The same species can be described as "trees" by one author, "hemi-epiphytes" by another, and "trees and hemi-epiphytes" by others. The main confusion seems to be between the definition of "trees" and that of hemi-epiphytes which have become "free-standing strangler figs". Species in one case have quite different life cycles from species in the other case. The true tree species germinate in or on the ground like most other trees. The hemi-epiphyte species germinate on a host tree and become hemi-epiphytes before strangling their hosts and then becoming free-standing individuals. Calling both of these cases "trees", while understandable, hides fundamental differences in germination and establishment, differences in what is stem versus root, ignores the structural difference of a hollow centre versus a solid trunk and obscures the different stages of the highly specialized hemi-epiphytic habit.

Given the confusion over the use of the term "tree" in the genus *Ficus*, we aim in this paper to (1) clearly define both a tree and a free-standing strangler in *Ficus*; (2) explain the transition in habit from an epiphyte to a free-standing strangler; (3) document how many tree and hemi-epiphytic *Ficus* species occur at one site in northern Congo; investigate how many hemi-epiphytic species reach the free-standing strangler habit at that site; and (4) provide data on host tree species for the hemi-epiphytic *Ficus* that occur there.

The relevance of habit in *Ficus*

The importance of the genus *Ficus* in tropical ecosystems has been emphasized in many publications, most of which have focused on the role of *Ficus* in providing a rich food resource for vertebrates. However there are many other aspects of the ecology of the genus which are worth investigating, for various reasons. If one is interested in α-diversity, for example, then it is useful to know that *Ficus* is the genus of flowering plants with the largest number of species at some sites (Gillet & Doucet 2012, Harris 2002, Ndolo Ebika 2010). Given the importance of *Ficus* for feeding ecology of vertebrates and its high number of species, it is important to understand the differences between these species and their different ecological roles rather than to treat them all as "*Ficus* sp." As land-use changes become more and more widespread over the tropics the difference between true trees and hemi-epiphytes in *Ficus* will become more important in the modelling of change under different scenarios. For example when forest is logged it appears from our observations in the north of the Republic of Congo that there is a change in the frequency of *Ficus* species and habits. Secondary forests have been reported in Makokou (Gabon) and Taï (Ivory Coast) to have higher proportion of hemi-epiphytes on trees than old growth forest (Gauthier-Hion & Michaloud 1989).

MATERIAL AND METHODS

Study area

The Goualougo Triangle is located in the southern part of the Nouabalé-Ndoki National Park (2.05′–3.03′N 16.51′–16.56′E; see fig. 1) and covers 310 km^2 of lowland forest occurring at a range of altitudes between 330 and 600 m (Morgan et al. 2006). The climate is equatorial (Moutsambоté et al. 1994), characterized by alternating rainy and dry seasons. The main rainy season is typically from August through November, and the main dry season from December to February. A short rainy season and a short dry season occur in the intervening months. Annual rainfall averaged (± SD) 1689.6 ± 27 mm between 2007 and 2011, with average minimum and maximum daily temperatures (± SD) of 21.5 ± 0.6°C and 23.7 ± 0.8°C during the same period (Sanz & Morgan 2013).

The vegetation of the Goualougo Triangle is forest of three main types: mixed species semi-evergreen forest (*sensu* White 1986), swamp forest and *Gilbertiodendron dewevrei* forest. There is no evidence of the site being used by people for the last fifty years and human influence appears to have been minimal over a much longer period.

Methods

Data on *Ficus* and their host species were collected opportunistically while conducting research on apes and botanical inventories at the study site from December 2010 to February 2011. All individual *Ficus* found during daily reconnaissance surveys and in botanical plots were included in this study (285 observations, table 1). For epiphytes and hemi-epi-

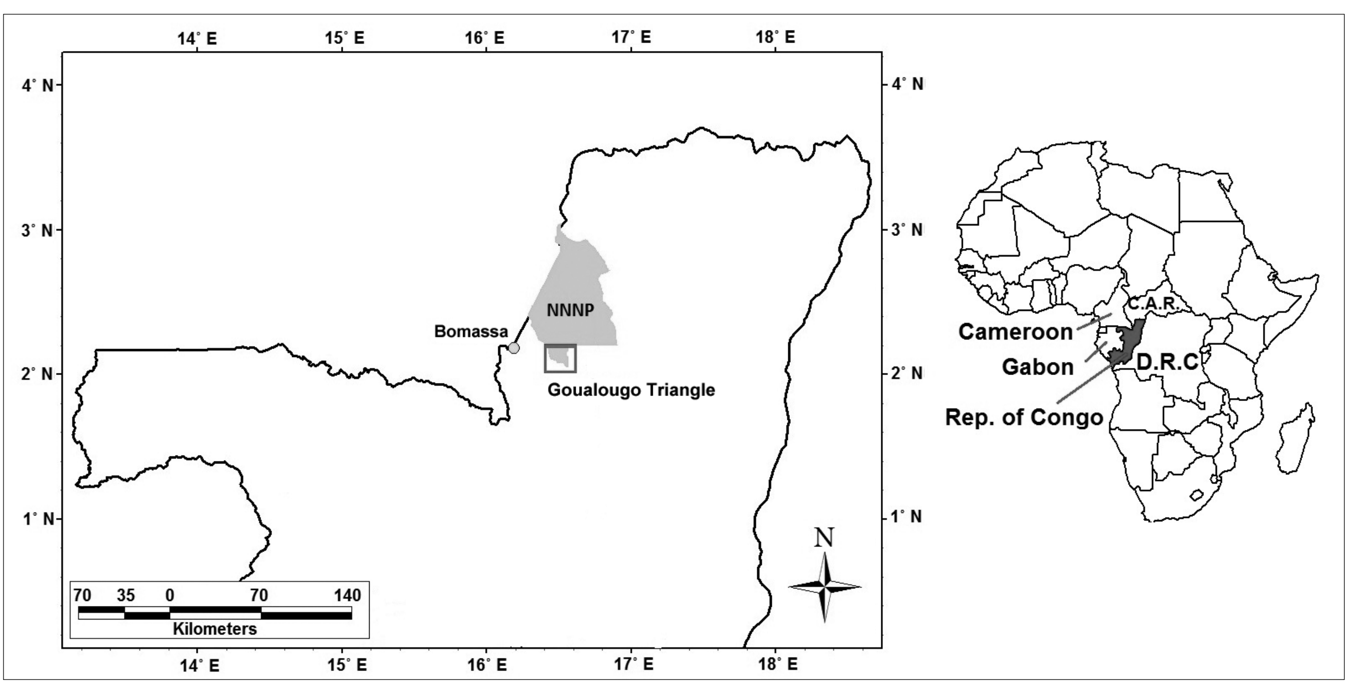

Figure 1 – Location of the Goualougo Triangle Area.

Table 1 – Nineteen *Ficus* species recorded from Goualougo Triangle during this study.
The number of individuals for each species is given under their life-form.

Species and subspecies	Epiphyte	Hemi-epiphyte	Free-standing strangler	Tree	Total
Ficus elasticoides De Wild.	0	49	16	0	65
F. wildemaniana De Wild. & T.Durand	1	45	1	0	47
F. kamerunensis Mildbr. & Burret	0	39	0	0	39
F. craterostoma Warb. ex Mildbr. & Burret	0	25	0	0	25
F. calyptrata Vahl	0	19	0	0	19
F. burretiana Hutch.	0	16	4	0	20
F. lingua De Wild. & T.Durand	0	11	0	0	11
F. lutea Vahl	0	7	1	0	8
F. preussii Warb.	0	7	0	0	7
F. natalensis Hochst.	0	6	0	0	6
F. dryepondtiana De Wild.	0	5	0	0	5
F. polita Vahl subsp. *polita*	0	5	2	0	7
F. adolfi-friderici Mildbr.	0	2	0	0	2
F. barteri Sprague	0	2	0	0	2
F. conraui Warb.	0	2	0	0	2
F. sansibarica Warb. subsp. *macrosperma* (Mildbr. & Burret) C.C.Berg	0	2	0	0	2
F. ardisioides Warb. subsp. *ardisioides*	0	1	0	0	1
F. recurvata De Wild.	0	0	12	0	12
F. variifolia Warb.	0	0	0	5	5
Total	**1**	**243**	**36**	**5**	**285**

phytes, we recorded whether or not the roots had reached the ground. If roots had not yet reached the ground, the individual was recorded as an epiphyte and if there was contact with the soil, it was noted as a hemi-epiphyte, as defined below. When the host was dead or decayed and the *Ficus* was still standing, the latter was recorded as a free-standing strangler. Information recorded for host trees included whether the host was alive, dead but intact or entirely decayed; the species and the approximate diameter at 1.3 m above the ground. In the case of trees and free-standing stranglers, there was no host information to record. Voucher specimens were made for both the *Ficus* and the host if the latter was still alive. The specimens were identified at the herbaria at Edinburgh and Kew using named specimens and literature (Berg & Wiebes 1992, Berg et al. 1984, 1985, Harris 2002). We excluded dead trees and unidentified live species from our analysis. We mapped the distribution of all *Ficus* and host individuals found in the study area.

RESULTS

Definitions

A *tree* in the genus *Ficus* is a non-climbing plant developing from a seed germinated on or in the ground and from which a full trunk greater than 10 m tall has developed in the adult individual above the point of germination (fig. 2A).

A *free-standing strangler* in the genus *Ficus* is a plant which begins its life as an epiphyte with a seed germinating on another plant (Benzing 1987, Fedorov 1959, Gentry 1991, Ingrouille & Eddie 2006, Richards 1964) and which in the adult individual develops a pseudo-trunk below the point of germination. This *pseudo-trunk* is formed from the fusion of aerial roots and has in its centre the trunk of the host tree (figs 2B–C & 3B–D). After death and decay of the host the pseudo-trunk is usually hollow (figs 3E & 4C). The *true trunk* of the hemi-epiphyte is situated above the point of germination (fig. 4). Berg & Wiebes (1992) described the pseudo-trunk as a ‘secondary’ trunk which is able to support the true trunk and branches after the host trunk has decayed.

The term *hemi-epiphyte* is used here, and elsewhere, as both (a) a stage in the life cycle of many *Ficus* species and (b) a description of the species which have this stage in their life cycle. The hemi-epiphytic stage is defined as the one that begins after the roots of the epiphyte reach the ground, the host is still alive. Hemi-epiphytism is discussed in a broader context by Benzing (1987, 2004), Ingrouille & Eddie (2006) and Putz & Holbrook (1986).

Transition from an epiphyte to a free-standing strangler through the hemi-epiphyte stage

Ficus species depend on frugivorous animals such as bats, birds or primates for the dispersal of their seeds (Berg &

Wiebes 1992, Burrows & Burrows 2003, Corner 1940, Lomáscolo et al. 2010). Once the seed of a hemi-epiphytic *Ficus* species has landed on a part of the host (e.g. bark or a forked branch) and if all the conditions required for its germination are met, the seed germinates as an epiphyte (fig. 3A) and sends its roots straight down or twines around the host to reach the soil (fig. 3B). When the roots reach the soil the epiphyte stage ends and the individual becomes a hemi-epiphyte as it is no longer a true epiphyte. With time it develops a substantial network of aerial roots, some of which grow upward and others downward, forming a complex interlinked support structure (fig. 3C) which starts to develop into the pseudo-trunk. This may result in damage to and even the death of the host tree by strangulation (Berg & Wiebes 1992, Compton & Musgrave 1993, Kricher 1999, Richards 1964, Shaw 2004). If the host tree is killed by the *Ficus* or dies from other causes (fig. 3D) and then decays, some hemi-epiphytic fig species can become free-standing stranglers

Figure 2 – Trunk v. pseudo-trunk in a tree and a hemi-epiphyte: A, true trunk of the tree *Ficus mucuso* Ficalho; B, pseudo-trunk of the hemi-epiphyte *F. recurvata* De Wild. seen from the side; C, and from inside and below in a different individual.

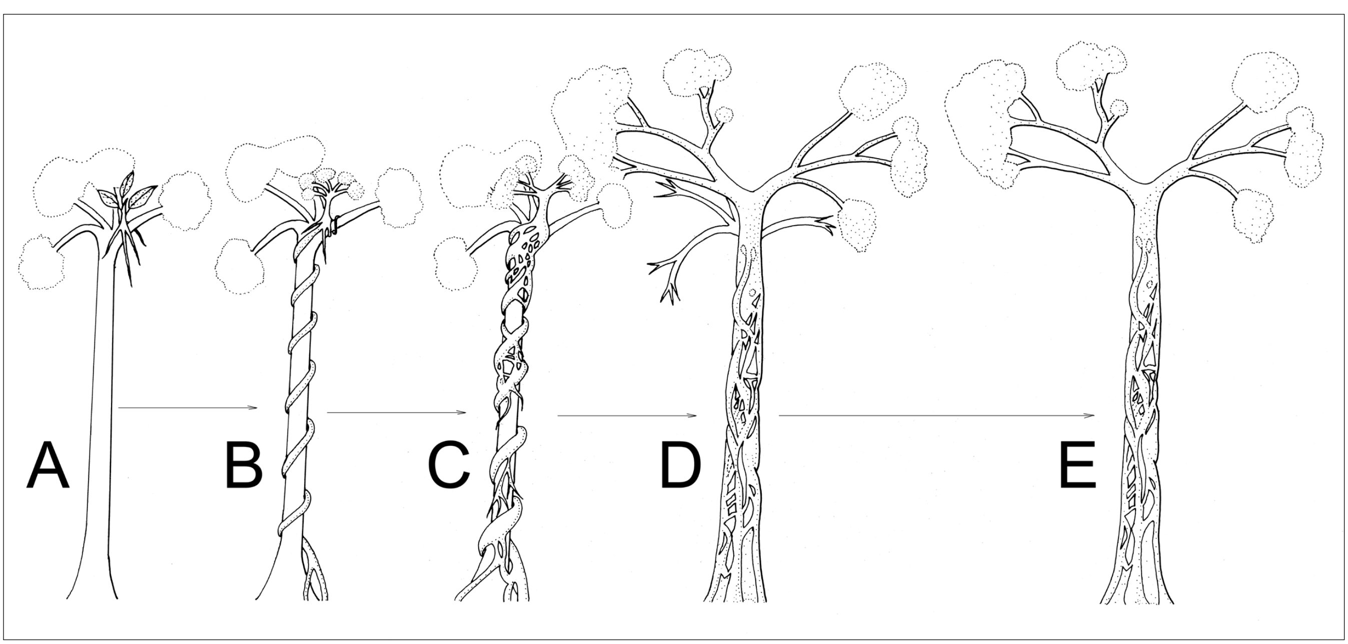

Figure 3 – Transitional habits of hemi-epiphytic *Ficus*: A, germination and establishment; B, root reaching the ground and beginning to wrap around the host, looking like a twining liana; C, strangler with a root network surrounding the trunk of the host, starting to form a pseudo-trunk; D, strangler with a pseudo-trunk and the dead host; E, free-standing strangler supported by hollow pseudo-trunk, host rotted away. Simplified after Fedorov (1959).

with a hollow pseudo-trunk (fig. 3E). Some hemi-epiphytic *Ficus* species apparently do not reach this free-standing strangler stage remaining one assumes as hemi-eiphyte until the host tree falls and they fall too.

Trees, epiphytes, hemi-epiphytes and free-standing stranglers

A total of 285 individual *Ficus* from nineteen species were found in the Goualougo Triangle (see table 1, authors for the names are provided in that table). Almost all individuals had started their life as an epiphyte. The five individuals that were true trees were all the same species *Ficus variifolia*.

The epiphytic stage was represented by a single individual of *Ficus wildemaniana* which was found growing as a young epiphyte with no roots yet reaching the ground.

The hemi-epiphytic stage was represented by 243 individuals. *Ficus elasticoides* was the commonest species with 49 individuals representing 20% of the total number of hemi-epiphytes. *Ficus wildemaniana* followed with 45 individuals (19% of hemi-epiphytes) and *F. kamerunensis* with 39 individuals (16% of hemi-epiphytes). Four taxa at or below species rank, *F. adolfi-friderici*, *F. barteri*, *F. conraui* and *F. sansibarica* subsp. *macrosperma* were represented by two individuals each. *Ficus ardisioides* subsp. *ardisioides* was the rarest taxon with only one individual recorded. One species, *F. recurvata*, was not recorded at the epiphytic or hemi-epiphytic stages, although was represented by thirteen individuals at the free-standing strangler stage.

The free-standing strangler habit was only recorded for six of the eighteen species of *Ficus* which are hemi-epiphytes (*F. burretiana*, *F. elasticoides*, *F. lutea*, *F. polita*, *F. recurvata*, and *F. wildemaniana*), see table 2.

Three species were represented by a large number of individuals at the hemi-epiphytic stage but none that reached the free-standing strangler stage. These were *Ficus kamerunensis* (39 individuals), *F. craterostoma* (25 individuals) and *F. calyptrata* (19 individuals). In addition, *F. wildemaniana* had 45 individuals recorded at the hemi-epiphytic stage but only one free-standing strangler.

Host species diversity

Two-hundred and forty-four individual host trees were documented in this study, representing 69 species; one live and ten dead host trees were unidentified (table 3). *Petersianthus macrocarpus* (Lecythidaceae) was by far the most common host tree, representing 19% of the total number of identified host trees (N = 233). *Celtis mildbraedii* (Cannabaceae), *Klainedoxa gabonensis* (Irvingiaceae) and *Pterocarpus soyauxii* (Fabaceae) each accounted for 5% of host trees. Nearly fifty host species were represented by a single tree, each accounting for 0.4% of the total number of host individuals. *Ficus elasticoides* and *F. burretiana* were also identified as hosts with 1% and 0.4% of host individuals respectively.

The number of *Ficus* species per host species varied from one to ten (table 3). Of the 69 host species, *Petersianthus macrocarpus* was the only species hosting ten *Ficus* species. *Klainedoxa gabonensis* hosted seven species, followed by *Gilbertiodendron dewevrei* (Fabaceae) with six. Host species with a single *Ficus* species recorded represented 49% of the total number of host species in this study (N = 69).

Table 2 – Abundance of the six free-standing strangler *Ficus* species recorded during this study.
Species are arranged according to their abundance.

Free-standing strangler species	Number	Frequency (%)
Ficus elasticoides De Wild.	16	44
F. recurvata De Wild.	12	33
F. burretiana Hutch.	4	11
F. polita Vahl subsp. *polita*	2	6
F. wildemaniana De Wild. & T.Durand	1	3
F. lutea Vahl	1	3
Total	**36**	**100**

DISCUSSION

Trees and free-standing stranglers

The differences between trees and free-standing stranglers, and the stages in the hemi-epiphytic life-form have been illustrated, discussed and defined above.

Our use of the word "tree" for *Ficus variifolia* fits the descriptions provided by Berg & Wiebes (1992) and Burrows & Burrows (2003), who described it as a tree without any mention of the hemi-epiphytic habit. However, we disagree with these authors on also using the word "tree" for other species which are free-standing stranglers. For example, *F. lutea* is described by Burrows & Burrows (2003: 97, plate 117) as being a large tree starting as a hemi-epiphyte and becoming free-standing in the adult stage, and one can see in their illustration that just over half way up the pseudo-trunk, the anastomosed roots are clearly visible. This is also the case for *F. polita* subsp. *polita* which is described by Burrows & Burrows (2003: 215) as a tree while their plate 288 shows the anastomosed roots of the pseudo-trunk which means that it is in fact a hemi-epiphyte.

Globally the proportion of species expressing hemi-epiphytism in *Ficus* is about 50% (Berg & Corner 2005, Berg & Wiebes 1992), a figure that stands in contrast with the rate of 95% recorded at our study site. Harris (2002) reported 81% species of *Ficus* as being hemi-epiphytes in the nearby Dzanga-Sangha protected area. From Gabon, Berg et al. (1984) describe 71% of the species as having this habit. Within 50 km of the study area, at sites with more forest disturbance than in the Goualougo Triangle there are three other tree species of *Ficus*: *F. exasperata* Vahl*, F. mucuso* Ficalho and *F. sur* Forssk. (Gillet & Doucet 2012, Harris & Wortley 2008). The increase in proportion of *Ficus* species that are trees in forest with more disturbance is similar to what has been reported from Makokou (Gabon) and Taï (Ivory Coast) by Gauthier-Hion & Michaloud (1989).

When faced with a mature *Ficus* individual with no sign of a host, we agree that it can be easy to misinterpret the habit of a free-standing strangler that has lost its host and formed a cylindrical pseudo-trunk with the true tree habit. By exam-

Table 3 – List of host species.
Number of individuals is the number of each host species with a hemi-epiphytic *Ficus*.

Host species	Number of individual host plants recorded with *Ficus*	Number of *Ficus* species per host species
Petersianthus macrocarpus (P.Beauv.) Liben	45	10
Celtis mildbraedii Engl.	12	5
Klainedoxa gabonensis Pierre ex Engl.	12	7
Pterocarpus soyauxii Taub.	12	5
Dead, unidentified trees	10	7
Terminalia superba Engl. & Diels	9	5
Gilbertiodendron dewevrei (De Wild.) J.Léonard	8	6
Alstonia boonei De Wild.	7	3
Irvingia grandifolia (Engl.) Engl.	7	2
Erythrophleum suaveolens (Guill. & Perr.) Brenan	6	5
Blighia welwitschii (Hiern) Radlk.	5	5
Piptadeniastrum africanum (Hook.f.) Brenan	5	5
Detarium macrocarpum Harms	4	4
Duboscia spp.	4	2
Entandrophragma candollei Harms	4	4
Hexalobus crispiflorus A.Rich	4	4
Nesogordonia papaverifera (A.Chev.) Capuron	4	2
Pentaclethra macrophylla Benth.	4	3
Zanha golungensis Hiern	4	4
Amphimas pterocarpoides Harms	3	2
Chrysophyllum beguei Aubrév. & Pellegr.	3	2
Ficus elasticoides De Wild.	3	2
Funtumia elastica (Preuss) Stapf	3	3
Irvingia excelsa Mildbr.	3	3
Pausinystalia macroceras (K.Schum.) Pierre ex. Beille	3	1
Triplochiton scleroxylon K.Schum.	3	1
Angylocalyx pynaertii De Wild.	2	2
Antiaris toxicaria Lesch. subsp. *welwitschii* (Engl.) C.C.Berg	2	2
Celtis adolfi-friderici Engl.	2	2
Entandrophragma cylindricum (Sprague) Sprague	2	2
Manilkara mabokeensis Aubrév.	2	2
Milicia excelsa (Welw.) C.C.Berg	2	2
Pterygota bequaertii De Wild.	2	2
Pycnanthus angolensis (Welw.) Warb.	2	2
Scottellia klaineana Pierre	2	2
Sterculia oblonga Mast.	2	2
Strombosia pustulata Oliv.	2	2
Treculia africana Decne.	2	2
Afrostyrax lepidophyllus Mildbr.	1	1
Albizia ferruginea (Guill. & Perr.) Benth.	1	1
Albizia sp.	1	1
Anonidium mannii (Oliv.) Engl. & Diels	1	1

Table 3 (continued) – List of host species.

Host species	Number of individual host plants recorded with *Ficus*	Number of *Ficus* species per host species
Balanites wilsoniana Dawe & Sprague	1	1
Breviea sericea Aubrév. & Pellegr.	1	1
Chrysophyllum lacourtianum De Wild.	1	1
Chrysophyllum perpulchrum Mildbr. ex Hutch. & Dalziel	1	1
Chrysophyllum pruniforme Pierre ex Engl.	1	1
Chrysophyllum ubangiense (De Wild.) D.J.Harris	1	1
Cola lateritia K.Schum.	1	1
Croton sp.	1	1
Dialium pachyphyllum Harms	1	1
Dracaena arborea (Willd.) Link	1	1
Drypetes gossweileri S.Moore	1	1
Drypetes occidentalis (Müll.Arg.) Hutch.	1	1
Entandrophragma sp.	1	1
Fernandoa adolfi-friderici (Gilg & Mildbr.) Heine	1	1
Ficus burretiana Hutch.	1	1
Irvingia robur Mildbr.	1	1
Mammea africana Sabine	1	1
Myrianthus arboreus P.Beauv.	1	1
Nauclea diderrichii (De Wild.) Merr.	1	1
Panda oleosa Pierre	1	1
Parinari excelsa Sabine	1	1
Phyllocosmus africanus (Hook.f.) Klotzsch	1	1
Pteleopsis hylodendron Mildbr.	1	1
Santiria trimera (Oliv.) Aubrév.	1	1
Schrebera arborea A.Chev.	1	1
Staudtia kamerunensis Warb. var. *gabonensis* Fouilloy	1	1
Strombosia grandifolia Hook.f. ex Benth.	1	1
Strombosia nigropunctata Louis & J.Léonard	1	1
Alive, unidentified tree	1	1
Total	**244**	

ining the "trunk", however, to see if there is any evidence of root fusions such as fenestrations or scars one can usually differentiate the two habits quickly and accurately. We also found that tapping the trunk to tell whether it is hollow helped clarify whether it was a true tree or a free-standing strangler.

Only six of the eighteen hemi-epiphytic species at our site reached the free-standing strangler stage. This is a similar proportion to the five out of twenty hemi-epiphytic species reported by Gautier-Hion & Michaloud (1989) at M'passa in Gabon.

The absence of the free-standing strangler stage in *Ficus kamerunensis*, *F. craterostoma* and *F. calyptrata*, despite the presence of large numbers of individuals at the hemi-epiphytic stage, requires some explanation. This might be due to either: (1) a lack of development of the branching root network around the host tree to form a pseudo-trunk (remaining as in fig. 3B); or (2) a lack of strength in the pseudo-trunk, so that when the host dies the *Ficus* individual falls down with it and dies as well (remaining as in fig. 3C until the death of the host but then not progressing to fig. 3D). From our observations in the field, it appears that the first explanation hypothesis is more likely.

Ficus recurvata was found only as a free-standing strangler. This may be due to (1) faster growth during its early stage, compared to the other hemi-epiphytic species; (2) preferential selection of weaker hosts; (3) preferential selection of short lived hosts; or (4) a more deleterious effect on the host than that of other *Ficus* species, or a combination of the above.

The difference between true trees and free-standing stranglers is biologically important in several ways. One group of *Ficus* species establishes seedlings on the ground in soil and another group, the hemi-epiphytes establish above ground on other plants. Establishment is a key process in explaining the distribution of plants. The hemi-epiphytes will compete with their host trees more directly than *Ficus* trees with neighbors. If one is measuring diameter of trees to estimate carbon stocks, and tree free-standing stranglers in the same way, the hollow trunk of the free-standing stranglers will add an error. For several groups of vertebrates the hollow pseudo-stems of the free-standing stranglers provide important roosting sites.

Epiphyte stage

Given that nearly all *Ficus* species recorded in the Goualougo Triangle start their life as epiphytes, it was surprising that only one of the 280 individual *Ficus* observed in our study was found at the epiphytic stage. In contrast, Athreya (1999) reported a high number of young *Ficus* individuals in Karian Shola National Park, South India with no roots touching the ground. The fact that only a single individual epiphyte was observed in our study site may suggest rapid root growth to the ground in order to acquire nutrient access from the soil instead of relying on the nutrients found at the germination site on the host. However, it must be emphasized that no systematic surveying for epiphytes was carried out in our study. We suggest that the surveying of trees to record and measure individuals at the epiphytic stage may reveal a more complex situation, probably with different patterns in different species of *Ficus*.

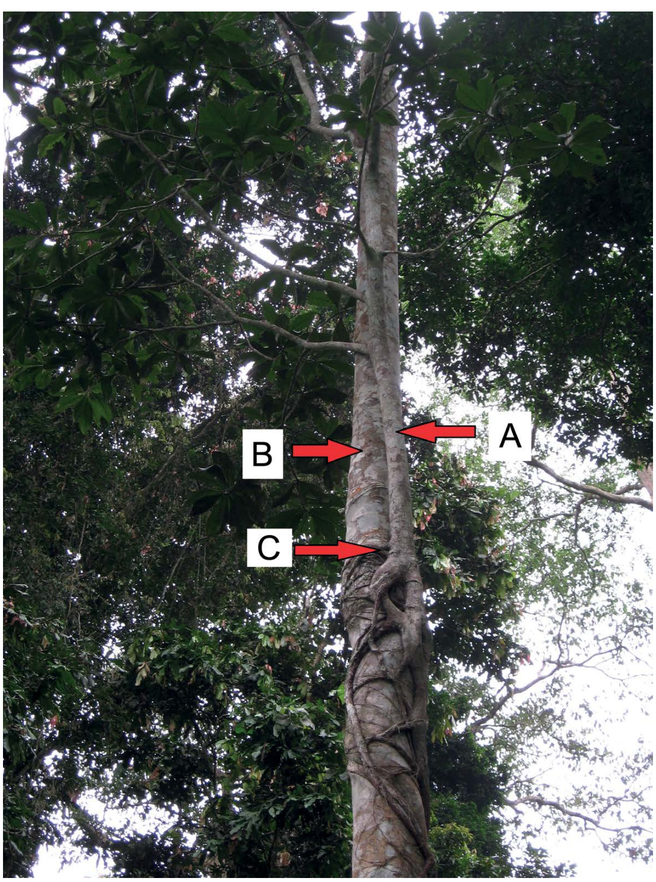

Figure 4 – A young hemi-epiphyte (*Ficus wildemaniana* De Wild. & T.Durand) with its host tree. Label A, true trunk of the *Ficus* individual; label B, trunk of the host; label C, germination point from which the pseudo-trunk will develop downwards.

Host species

This study shows that some host species used by *Ficus* are more colonized than others, a result that is similar to previous studies on fig-host preferences (Athreya 1999, Michaloud & Michaloud-Pelletier 1987, Patel 1996). *Petersianthus macrocarpus* was the most frequently colonized species, hosting 45 of the 244 epiphytic and hemi-epiphytic *Ficus* individuals documented in the Goualougo Triangle study area. This situation coincides with that in Makokou (Gabon) where *P. macrocarpus* was also the most common host (23 of the 154 *Ficus* individuals studied), but contrasts with that in Taï (Ivory-Coast) where the same species was ranked eighth in the list of host species (Michaloud & Michaloud-Pelletier 1987). While there were no *Ficus* individuals found growing on *Pycnanthus angolensis* in Taï (Michaloud & Michaloud-Pelletier 1987), two individuals of this species each served as hosts to a single individual of *Ficus* (belonging to two different species) (table 3, and Michaloud & Michaloud-Pelletier 1987) found three *Ficus* species on this host in Makokou. It is interesting that *Panda oleosa* was the second most frequently colonized host species in Makokou (for thirteen of the 154 individual *Ficus* plants), whereas in Goualougo Triangle we only found one *Ficus* individual on this host and none were reported from Taï. It might be that such differences are due to the density of the host species at different sites, which we plan to investigate in future.

Two *Ficus* species (*F. elasticoides* and *F. burretiana*) were recorded in our study as hosts for other *Ficus* species, albeit with only four cases in total. These observations confirm previous reports that some *Ficus* species can be hosts for other species. This was reported by Patel (1996) as a novel discovery from Karnataka State, India. However, Corner (1960) had previously shown that one *Ficus* species could grow on another and that the entity referred to as *F. clarkeana* King actually consisted of a mixture of syconia from a host, *F. racemosa* L., and leafy twigs from the epiphyte *F. tinctoria* Forst. f. subsp. *parasitica* (Willd.) Corner.

CONCLUSION

It is important to differentiate between the different habits of *Ficus* species because there has been inconsistent usage of these terms in the literature and the different stages in the hemi-epiphytic life cycle are biologically meaningful. Future modelling of the growth and dynamics of tropical plants and the vegetation that they make up should incorporate these important differences. Once the different stages of the hemi-epiphytic habit were clearly defined and recorded we found clear differences between some species occurring at our site. Our results suggest that further studies will reveal more differences in the ecology of co-occurring species in this globally important genus.

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