Received: 18 August 2020 | Accepted: 27 November 2021
DOI: 10.1111/afe.12478

ORIGINAL ARTICLE

Agricultural and Forest Entomology

Host plants and associated trophobionts of the weaver ant *Oecophylla longinoda* Latreille (Hymenoptera Formicidae) in Benin

Jean-François Vayssières[1,2] | Isabelle Grechi[2,3] | Antonio Sinzogan[4] | Issa Ouagoussounon[4] | Raymond Todjihoundé[4] | Soumanou Modjibou[4] | Jean-Claude Tossou[4] | Appolinaire Adandonon[5] | Cinthia Kikissagbé[6] | Manuele Tamò[7] | Georg Goergen[7] | Anaïs Chailleux[2,8] | Jean-François Germain[†] | Aristide Adomou[4]

[1]CIRAD Persyst, UPR HortSys, Kourou, French Guiana
[2]HortSys, Univ Montpellier, CIRAD, Montpellier, France
[3]CIRAD, UPR HortSys, Saint-Pierre, France
[4]UAC, Université d'Abomey Calavi, Cotonou, Bénin
[5]ENSTA, Université d'Agriculture de Kétou, Kétou, Bénin
[6]FAO, Cotonou, Bénin
[7]IITA, Biological Control Unit for Africa, Cotonou, Benin
[8]BIOPASS, ISRA-IRD-UCAD, Dakar, Sénégal

Correspondence
Jean-François Vayssières, "Ri-Biocontrol" Program, Kourou, B.P. 701-97387, French Guiana.
Email: jeanfrancoisvayssieres@gmail.com

Abstract

1. The African weaver ant *Oecophylla longinoda* builds woven leaf nests inside tree canopies and is a major conservation biocontrol agent in sub-Saharan Africa. Weaver ant colonies provide well-protected and resource-rich environments for many associated trophobionts, thereby boosting their establishment on host plants.
2. There is very little published literature on *O. longinoda*, their hosts plants and their associated trophobionts in West Africa. These tri-trophic interactions were studied over a period of four consecutive years (2010–2013) from south to north Benin.
3. Our fieldwork revealed that all *O. longinoda* colonies were consistently associated with trophobionts. *Oecophylla longinoda* nests were recorded on 82 plant species belonging to 30 families, with 35 associated trophobiont species representing 11 families.
4. Among cultivated plants, *Mangifera indica* was the most common species hosting *O. longinoda*, while *Sarcocephalus latifolius* the most frequent native one. Among trophobionts, *Parasaissetia nigra*, *Udinia catori*, *Udinia farquharsoni* (Coccidae) and *Stictococcus sjostedti* (Stictococcidae) were the most common hemipterans associated with *O. longinoda*.
5. We identified a wide range of host plants that could be preserved (or planted) to promote the establishment of weaver ants to control different insect pests in fruit plantations in sub-Saharan Africa. When planted around fruit plantations with their nests and tended hemipterans, these host plants could facilitate biocontrol of mango fruit flies (Tephritidae) and cashew bugs (Coreidae, Miridae), by *O. longinoda* in the fruit plantations.

Résumé

1. La fourmi tisserande africaine, *Oecophylla longinoda*, construisant et vivant dans des nids de feuilles tissées à l'intérieur de la canopée, est un agent majeur de lutte biologique de conservation en Afrique sub-Saharienne. Les colonies de fourmis

[†]To our great sadness Jean-François GERMAIN passed away.

tisserandes fournissent un environnement bien protégé et riche en ressources pour de nombreux insectes trophobiontes associés, renforçant ainsi leur établissement sur certaines espèces de plantes-hôtes.
2. Très peu de publications sont disponibles concernant *O. longinoda*, ses plantes hôtes et ses insectes trophobiontes associés en Afrique de l'Ouest. Au Bénin, ces interactions tri-trophiques ont été étudiées sur une période de quatre années consécutives (2010–2013) le long d'un transect sud-nord.
3. Notre travail de terrain a révélé que toutes les colonies d'*O. longinoda* étaient systématiquement associées à des insectes trophobiontes. Les nids d'*O. longinoda* ont été répertoriés sur 82 espèces végétales appartenant à 30 familles, en symbiose avec 35 espèces d'insectes trophobiontes associés représentant 11 familles d'insectes.
4. Parmi les plantes cultivées, *Mangifera indica* était l'espèce la plus commune hébergeant *O. longinoda*, tandis que *Sarcocephalus latifolius* était la plante indigène la plus fréquente. Parmi les espèces de trophobiontes, *Parasaissetia nigra*, *Udinia catori*, *Udinia farquharsoni* (Coccidae) et *Stictococcus sjostedti* (Stictococcidae) étaient les espèces d'hémiptères les plus communes associées à *O. longinoda*.
5. Nous avons identifié un large éventail de plantes-hôtes qui pourraient être protégées (ou plantées) pour promouvoir l'établissement de fourmis tisserandes afin de lutter contre différents insectes ravageurs dans les plantations fruitières d'Afrique sub-Saharienne. Lorsqu'elles sont présentes autour des plantations fruitières avec leurs nids et leurs hémiptères associés, ces plantes-hôtes pourraient grandement faciliter la lutte biologique vis-à-vis des mouches des fruits ravageurs du manguier (Tephritidae) comme des punaises ravageurs de l'anacardier (Coreidae, Miridae), grâce à *O. longinoda* dans les plantations fruitières.

KEYWORDS
conservation biocontrol, mutualism, *Oecophylla longinoda*, tritrophic interactions, trophobiosis

INTRODUCTION

Given their feeding habits, their resilience and their high contribution (nearly 15%) inside animal biomass, ants have a key influence in many kinds of habitats (Hölldobler & Wilson, 1990). Many studies have identified ants as important control agents of insect pests (Offenberg, 2015; Way & Khoo, 1989). On the other hand, ants can indirectly induce crop damage by facilitating infestation with trophobiont hemipterans (Gullan, 1997; Way, 1963). Because weaver ants are associated with coccids and mealybugs, they are often alleged to be responsible for the proliferation of pests of economic importance on fruit trees. For instance, *Udinia catori*, a common coccid species listed among the most frequently encountered trophobionts (Photo 1) that mainly occur in mango plantations is occasionally considered as a fruit pest.

In traditional farming systems, farmers were first to recognize ants as biocontrol agents of pest insect species, namely in main five genera of dominant ants in the tropics: *Anoplolepis* (Khoo & Chung, 1989; Van der Goot, 1917), *Azteca* (Overal & Posey, 1984; Vandermeer et al., 2002), *Dolichoderus* (Van Mele & Cuc, 2001; Way & Khoo, 1989), *Oecophylla* (Dejean, 1991; Huang & Yang, 1987) and *Wasmania* (Bruneau de Miré, 1969). One major interest of studying plant/ant/hemipterans interactions is that *Oecophylla longinoda* (Latreille) (Hymenoptera Formicidae) is used as a biocontrol agent against crop-damaging insects in some fruit plantations throughout sub-Saharan Africa. Successful application of the African weaver ant, *O. longinoda*, as an endemic natural auxiliary has been demonstrated in Benin (Anato et al., 2015, 2017; Van Mele et al., 2007; Wargui, 2010; Wargui et al., 2018) versus tephritids, cashew mirid and coreid bugs, in Ghana (Ativor et al., 2012; Ayenor et al., 2007; Dwomoh et al., 2008), Senegal (Diamé et al., 2015) versus tephritids, and, in Tanzania (Abdulla et al., 2015; Vanderplank, 1960; Way, 1953) versus coconut coreid and cashew mirid bugs. Similar to historical use of *O. smaragdina* in the Australasian region, *O. longinoda* is also a compelling example of conservation biocontrol throughout sub-Saharan Africa.

Initially, about ∼100 mya ago, ants were ground-dwelling or litter-dwelling predators or/and scavengers. They became arboreal with the rise of angiosperms and provided plants a biotic defence by foraging for various arthropods on their foliage (Dejean et al., 2007). Plants provide ants opportunities (i) to forage on their leaves and branches, (ii) to look for food rewards (extra-floral nectar, pollen, etc.) and (iii) to attend diverse hemipterans for their honeydew. For this last reason they are "cryptic herbivores" on hemipteran honeydew (Blüthgen et al., 2004; Dejean et al., 2007; Tobin, 1994). In tree-crop plantations, particularly in mango-citrus plantations in West Africa, territorially dominant arboreal *Oecophylla* ants have large colonies with large and/or polydomous nests. As biocontrol agents they are closely adapted to many species of fruit-trees where several ant species Territories marked by workers with their deposits or landmarks are distributed in a mosaic pattern creating what has become known as "arboreal ant mosaics" (Dejean et al., 1997; Hölldobler & Wilson, 1990; Leston, 1973; Majer, 1972; Room, 1971). They are effective predators that have developed strategies allowing them to attack other arthropods on their host trees as to feed on some of their associated hemipteran also called trophobionts (Vanderplank, 1960).

Colonies of weaver ants are arboreal and their populations build large silky nests (Photo 2) in colonized trees. The genus *Oecophylla* is represented by two tropical species, *O. longinoda* originating from Africa and *Oecophylla smaragdina* (Fabricius) from Australasia. Societies of *O. longinoda* are very populous, monogynous and have polydomus colonies with a high level of intraspecific competition. As dwellers of natural forests, they require thick vegetation, particularly perennial species, usually with an interconnected canopy, to provide nesting sites and that allow them to forage over large territories (Dejean, 1991; Taylor & Adedoyin, 1978).

PHOTO 1 Very common association *O. longinoda* – *Udinia catori* (Coccidae) on *Mangifera indica* (Anacardiaceae) in all agroecological zones of Benin

PHOTO 2 Making the nest of weaver ants *O. longinoda*: leaves drawn together by workers with a worker carrying in its mandibles a larva which secreted silk (to secure the edges of the leaves)

The *O. longinoda* colonies play a key role in the African ecosystems in which they occur. In West Africa, *O. longinoda* nests are usually found in humid forests up to the dry savannahs in the southern Sahelian zone on both wild hosts (trees, shrubs and lianas) and cultivated fruit trees. In Benin, *O. longinoda* are widespread on many cultivated trees including cashew, guava, soursop, and especially citrus and mango trees (Vayssières et al., 2016). A colony of weaver ants may remain on one tree with a small number of nests or extend over several trees with a large number of nests (Hölldobler, 1979; Way, 1954a). The process of nest building is highly organized and was first described more than 60 years ago (Chauvin, 1952; Ledoux, 1950; Way, 1954a). Most weaver ants' nests are located below a height of two metres. Food availability, nesting space on host plants with associated trophobionts and management practices are crucial factors that affect *O. longinoda* performance (Wargui et al., 2018; Way, 1963).

Hemipterans are tended by weaver ants as a source of both carbohydrates and proteins in many host species (Lim et al., 2008; Way, 1954a). Ant-hemipteran mutualism is one of the most famous examples of food-for-protection mutualism between ants and honeydew-producing hemipterans (Hölldobler & Wilson, 1990; Way, 1963). Mutualism includes several representatives of the suborders Auchenorrhyncha (leafhoppers, planthoppers and treehoppers) and Sternorrhyncha (aphids, psyllids, scales and mealybugs, white flies) formerly grouped as Homoptera. The literature on *O. longinoda*, their host plants and trophobiotic mutualisms in the Afrotropical region is poor despite the use of this ant in fruit protection (Kenné et al., 2003; Lim et al., 2008; Way & Khoo, 1992).

Attended Homoptera are protected by ants but provide honeydew and sometimes solid protein food (Way, 1963). Weaver ants play a biocontrol role against fruit-pests by preventing the number of trophobionts from rising above certain levels (Way, 1954b). On the other hand, the *Oecophylla* ant has one major drawback: it bites people. Perception of this slight nuisance, and its response, is influenced by the frequency of encounters and the perceived benefits gained from *Oecophylla* (Van Mele et al., 2009). About the key question of potential vectors of diseases it seems that hemipteran species attended by African weaver ants are not disease vectors of fruit trees (Kenné, 2006; Way, 1963). In any case, the consistent positive effects of *O. longinoda* in reducing pest populations are very likely to outweigh a few negative effects such as presence of trophobionts, ant bites and eventual plant physiological disruptions due to ant nests.

The aim of the present study was to answer four questions: (a) Which host plant species are most commonly used by *O. longinoda*? (b) Do ant trophobionts differ in their occurrence between host plants? (c) Does the spatial position on host plants differ between trophobiont species? (d) Does the distribution of host plants or trophobionts differ between agroecological zones?

Characterizing the food web structures involving African weaver ants will advance our understanding of the mechanisms that drive their population dynamics, a prerequisite for the introduction of colonies of this beneficial ant species in previously uncolonized fruit plantations.

MATERIALS AND METHODS

Study area

We investigated the three main agroecological zones in Benin, which are from north to south: (i) the southern Sudan, (ii) the Sudan-Guinean, (iii) Guineo-Congolian zone, in four consecutive years (2010–2013). Fifty sites were sampled per zone each year giving total of 150 sites sampled four times, that is 600 replicates over time and space.

Data collection

The methodology was the same at each site (i) three "quadrats" per site were defined, the quadrats being located randomly in areas with trees, shrubs and lianas, (ii) each quadrat measured 10 × 10 m, (iii) quadrats were GPS referenced, (iv) botanical and entomological data were collected in each quadrat. A total of 1800 quadrats were studied in both natural and cultivated areas.

The following facts were recorded in every quadrat: (i) the number of individual specimens of each species of tree, shrub, and liana present, (ii) individual plants containing *Oecophylla* nests, (iii) the presence of trophobionts with information concerning their species and their position (within the nest (Photo 3), on the stem or on the fruit). Adult specimens of hemipteran trophobionts were collected and preserved in alcohol-filled vials for further identification.

PHOTO 3 Association *O. longinoda* – Coccidae (located in the open nest) on *Psydrax horizontalis* (Rubiaceae) in south of Benin

Photographs were taken of all the trophobionts of *Oecophylla* encountered and the majority of their host plants were identified with available references (Arbonnier, 2004). Unknown plant species were placed between sheets of paper in an herbarium and subsequently identified by A. Adomou (National Herbarium of Benin, University of Abomey Calavi, Benin). All weaver ant trophobionts were mounted on slides and identified by J.-F. Germain (French National Health Security Agency, for food, the environment and work [French acronym ANSES], Montpellier, France). All weaver ant trophobionts were also barcoded and their nucleotide sequence referenced at the French Center for Biology and Population Management (French acronym CBGP) laboratory.

Data analysis

Host plant

Weaver ant occurrence was defined at the plant scale as a binary variable corresponding to whether the sampled plant hosted weaver ants. To test the null hypothesis that weaver ant occurrence was the same in all the plant groups (i.e., species, genus or family) and all plant types (i.e., cultivated, local non-cultivated or exotic-non-cultivated), we used a generalized linear model (GLM) with binomial error distribution followed by an analysis of deviance with a χ^2 test. When these tests were significant, we performed post-hoc pairwise comparisons using Fisher's exact test with the Holm method to correct p-values.

Trophobiont species and host plant species relationship

A χ^2 test was used to test the null hypothesis that trophobionts were equally distributed among host plant species. The tests were only applied to frequently observed trophobiont and host plant species (i.e., trophobiont species with at least 15 occurrences and host plant species related to ≥5% of trophobiont occurrences in at least one of these frequent trophobiont species). Since Cochran conditions could be not satisfied due to the small number of individuals and the large number of plant groups, *p*-values of χ^2 tests were computed using Monte Carlo simulations with 2000 permutations.

Trophobiont species position and agroecological zones

An exact multinomial test was used to test the null hypothesis that trophobionts were equally distributed among the positions on the host plants. The same test was used to test the null hypothesis that host plants and trophobionts were equally distributed among agroecological zones. The tests were applied to each species (or genus) that occurred at least 15 times. The exact multinomial test was used in preference to the χ^2 test as the numbers of individuals and groups were small and Cochran conditions could be not satisfied. When these tests were significant, we performed post-hoc pairwise comparisons using exact binomial tests with the Holm method to correct *p*-values.

All the statistical tests and figures were performed using R statistical software version 3.5.0 (R Core Team, 2018). Exact multinomial tests and pairwise comparisons were performed using functions in the "RVAideMemoire" (Hervé, 2018) and "fifer" (Fife, 2014) R packages.

RESULTS

We found 4045 *O. longinoda* colonies, all of which were associated with hemipteran and/or lepidopteran trophobionts. Ant colonies were recorded on 82 plant species belonging to 30 families (Table 1), with 35 associated trophobiont species representing 11 insect families (Table 2). Among these insect families, Coccidae were associated with 79 different plant species, Stictococcidae with 18 plant species, Pseudococcidae with 12 plant species, Monophlebidae with six plant species, Lycaenidae, Membracidae, Psyllidae and Tettigometridae with two plant species, Delphacidae, Diaspididae and Margarodidae with one plant species (Table 3). The main insect family was Coccidae, represented by 17 species (Table 3). Several families of trophobionts were recovered inside *Oecophylla* nests including 17 species of scale insects (Coccidae), four species of mealybugs (Pseudococcidae) and stictococcids (Stictococcidae), two species of typical tree-hoppers (Membracidae) (Photo 4) and tettigometrid plant-hoppers (Tettigometridae), one species of armoured scale insects (Diaspididae), ground pearls (Margarodidae), giant coccids (Monophlebidae), delphacids (Delphacidae), jumping plant lice (Psyllidae) and young caterpillars (Lycaenidae).

Host plant

Occurrence probability of *O. longinoda* varied significantly among the host plant species (GLM Binomial, $\chi^2 = 868.9$, d.f. $= 81$, $p < 0.001$), genera (GLM Binomial, $\chi^2 = 707.3$, d.f. $= 66$, $p < 0.001$) and families (GLM Binomial, $\chi^2 = 343.4$, d.f. $= 29$, $p < 0.001$). To ensure clarity, only plants with an occurrence probability ≥0.10 for plant families and ≥0.20 for plant species and genera are presented in Figure 1. The most common plant species used by *O. longinoda* in Benin, with an occurrence probability >0.40, were the African peach *Sarcocephalus latifolius* (Rubiaceae), Angolan Berlinia *Isoberlinia doka* (Caesalpinioideae), mango tree *Mangifera indica* (Anacardiaceae), *Opilia celtidifolia* (Opiliaceae), *Maranthes polyandra* (Chrysobalanaceae), *Uapaca togoensis* (Euphorbiaceae), African bark *Crossopteryx febrifuga* (Rubiaceae), *Margaritaria discoidea* (Euphorbiaceae), wild custard apple *Annona senegalensis* (Annonaceae) and *Aidia genipiflora* (Rubiaceae) (Figure 1a). The plant genera with the highest frequency of *O. longinoda* in Benin were *Sarcocephalus*, *Mangifera*, *Uapaca*, *Crossopteryx*, *Margaritaria* and *Opilia* (Figure 1b). The most common plant families used by *O. longinoda* in Benin were Opiliaceae and Rubiaceae with an occurrence probability >0.40 (Figure 1c). The occurrence probability was more than two times higher on native non-cultivated plant species than on exotic non-cultivated plants species (Appendix), with cultivated plant species in between (GLM Binomial, $\chi^2 = 35.7$, d.f. $= 2$, $p < 0.001$; Figure 2). Occurrence probability of *O. longinoda* was <0.10 on non-cultivated exotic plant species and was not significantly different between these species (GLM Binomial, $\chi^2 = 4.55$, d.f. $= 3$, $p = 0.21$), whereas it varied significantly among cultivated (GLM Binomial, $\chi^2 = 48.2$, d.f. $= 7$, $p < 0.001$) and non-cultivated native plant species (GLM Binomial, $\chi^2 = 780.4$, d.f. $= 69$, $p < 0.001$). Except for mango, *O. longinoda* occurrence was three times more likely on native non-cultivated plant species than on cultivated plant species.

Trophobiont species and host plant species relationship

Data on host plants and trophobionts showed that the five most frequent trophobiont species (Figure 3) were not equally associated with the different host plants (all $p < 0.001$). Thus, *U. farquharsoni* (Coccidae) was mostly associated with *M. polyandra* (>30%) and to a lesser extent with West African ebony *Diospyros mespiliformis* (>10%). *Parasaissetia nigra* (Coccidae) and *S. sjostedti* (Stictococcidae) were mostly associated with the African peach (>20%). *Udinia catori* (Coccidae) was associated with both the African peach (>10%) and *O. celtidifolia* (>10%) and to a lesser extent with Senegal mahogany *Khaya senegalensis*, the mango tree and others.

Trophobiont species distribution on plants

With regard to within-plant distribution, most trophobionts were observed in the weaver ants' nest (55.7%) followed by the stem (36.3%). A few trophobionts were located on the fruit (6.2%) and only 1.7% were found both in the weaver ants' nest and on the stem. Considering the most common trophobiont species (i.e., those with at least 15 occurrences), there was no significant difference between the position of *S. sjostedti*, *U. catori and U. farquharsoni* in the weaver ants' nest and on the stem of the host plants (Figure 4a). The relationship of each trophobiont genus according to its position on the plant confirms the same relationships with colonies of *Stictococcus* spp. and *Udinia* spp. also mostly found in the nests of weaver ants or on the stem, and those of *Coccus* spp. and *Parasaissetia* spp. that are mostly only positioned in the weaver ants' nests (Figure 4b).

Agroecological zones

The majority (61.7%) of the plants most frequently used by *O. longinoda* were located in the Sudan-Guinean zone with the remaining plants distributed between the southern Sudan (20.7%) and Guineo-Congolian (17.6%) zones (Figure 5a). Among the most common weaver ant host plant species (i.e., those with at least 15 occurrences), *Combretum nigricans*, *M. polyandra*, *O. celtidifolia* and the

TABLE 1 Host plants of *O. longinoda* observed in Benin

Genus	Species		Families		Nbr_plant_with *O. longinoda*	Nbr_plant_sampled
Anacardium	*occidentale*	(A.occ)	Anacardiaceae	(Anac)	11	88
Lannea	*acida*	(L.aci)	Anacardiaceae	(Anac)	1	47
Mangifera	*indica*	(M.ind)	Anacardiaceae	(Anac)	18	25
Spondias	*mombin*	(S.mom)	Anacardiaceae	(Anac)	2	15
Annona	*senegalensis*	(A.sen)	Annonaceae	(Anno)	15	49
Annona	*squamosa*	(A.squ)	Annonaceae	(Anno)	1	26
Artabotrys	*velutinus*	(A.vel)	Annonaceae	(Anno)	1	41
Hexalobus	*monopetalus*	(H.mon)	Annonaceae	(Anno)	2	14
Monodera	*tenuifolia*	(M.ten)	Annonaceae	(Anno)	3	52
Holarrhena	*floribunda*	(H.flo)	Apocynaceae	(Apoc)	1	30
Rauvolfia	*vomitoria*	(R.vom)	Apocynaceae	(Apoc)	4	21
Strophantus	*sarmentosus*	(S.sar)	Apocynaceae	(Apoc)	1	37
Cussonia	*arborea*	(C.arb)	Araliaceae	(Aral)	13	58
Ehretia	*cymosa*	(E.cym)	Borraginaceae	(Borr)	4	27
Afzelia	*africana*	(A.afr)	Caesalpinioideae	(Caes)	3	39
Berlinia	*grandiflora*	(B.gra)	Caesalpinioideae	(Caes)	3	41
Daniellia	*oliveri*	(D.oli)	Caesalpinioideae	(Caes)	2	55
Isoberlinia	*doka*	(I.dok)	Caesalpinioideae	(Caes)	24	32
Isoberlinia	*tomentosa*	(I. tom)	Caesalpinioideae	(Caes)	1	44
Piliostigma	*thonningii*	(P.tho)	Caesalpinioideae	(Caes)	7	85
Gymnosporia	*senegalensis*	(G.sen)	Celastraceae	(Cela)	1	30
Maranthes	*polyandra*	(M.pol)	Chrysobalanaceae	(Chry)	23	38
Maranthes	*robusta*	(M.rob)	Chrysobalanaceae	(Chry)	1	37
Parinari	*curatellifolia*	(P.cur)	Chrysobalanaceae	(Chry)	4	54
Combretum	*collinum*	(C.col)	Combretaceae	(Comb)	1	93
Combretum	*fragans*	(C.fra)	Combretaceae	(Comb)	3	74
Combretum	*glutinosum*	(C.glu)	Combretaceae	(Comb)	1	109
Combretum	*nigricans*	(C.nig)	Combretaceae	(Comb)	16	87
Terminalia	*avicennoides*	(T.avi)	Combretaceae	(Comb)	5	124
Terminalia	*laxiflora*	(T.lax)	Combretaceae	(Comb)	2	94
Dioscorea	*alata*	(D.ala)	Dioscoreaceae	(Dios)	2	25
Diospyros	*mespiliformis*	(D.mes)	Ebenaceae	(Eben)	9	42
Alchornea	*cordifolia*	(A.cor)	Euphorbiaceae	(Euph)	8	75
Antidesma	*venosum*	(A.ven)	Euphorbiaceae	(Euph)	2	37
Bridelia	*ferruginea*	(B.fer)	Euphorbiaceae	(Euph)	4	90
Hura	*crepitans*	(H.cre)	Euphorbiaceae	(Euph)	3	34
Margaritaria	*discoidea*	(M.dis)	Euphorbiaceae	(Euph)	10	21
Uapaca	*togoensis*	(U.tog)	Euphorbiaceae	(Euph)	10	19
Dialium	*guineense*	(D.gui)	Fabaceae	(Faba)	1	25
Lonchocarpus	*sericeus*	(L.ser)	Fabaceae	(Faba)	4	42
Parkia	*biglobosa*	(P.big)	Fabaceae	(Faba)	1	86
Pericopsis	*laxiflora*	(P.lax)	Fabaceae	(Faba)	8	66
Senna	*siamea*	(S.sia)	Fabaceae	(Faba)	3	95
Irvingia	*gabonensis*	(I. gab)	Irvingiaceae	(Irvi)	1	33
Anthocleista	*nobilis*	(A.nob)	Loganiaceae	(Loga)	1	29
Strychnos	*spinosa*	(S.spi)	Loganiaceae	(Loga)	11	71

(Continues)

TABLE 1 (Continued)

Genus	Species		Families		Nbr_plant_with *O. longinoda*	Nbr_plant_sampled
Azadirachta	*indica*	(A.ind)	Meliaceae	(Meli)	2	128
Khaya	*senegalensis*	(K.sene)	Meliaceae	(Meli)	12	56
Trichilia	*emetica*	(T.eme)	Meliaceae	(Meli)	3	17
Acacia	*auriculiformis*	(A.aur)	Mimosoidae	(Mimo)	2	23
Albizia	*glaberrima*	(A.gla)	Mimosoidae	(Mimo)	4	47
Albizia	*zygia*	(A.zyg)	Mimosoidae	(Mimo)	1	56
Ficus	*ingens*	(F.ing)	Moraceae	(Mora)	1	70
Ficus	*sur*	(F.sur)	Moraceae	(Mora)	3	52
Ficus	*sycomorus*	(F.syc)	Moraceae	(Mora)	3	33
Ficus	sp1	(F.sp1)	Moraceae	(Mora)	1	13
Ficus	sp2	(F.sp2)	Moraceae	(Mora)	1	16
Eucalyptus	sp.	(E.sp.)	Myrtaceae	(Myrt)	2	22
Psidium	*guajava*	(P.gua)	Myrtaceae	(Myrt)	3	45
Syzygium	*guineense*	(S.gui)	Myrtaceae	(Myrt)	3	58
Lophira	*lanceolata*	(L.lan)	Ochnaceae	(Ochn)	13	87
Ochna	*schweinfurthiana*	(O.sch)	Ochnaceae	(Ochn)	3	48
Ximenia	*americana*	(O.sch)	Olacaceae	(Olac)	2	71
Opilia	*amentacea*	(O.ame)	Opiliaceae	(Opil)	1	27
Opilia	*celtidifolia*	(O.ame)	Opiliaceae	(Opil)	31	49
Aidia	*genipiflora*	(A.gen)	Rubiaceae	(Rubi)	9	30
Crossopteryx	*febrifuga*	(C.feb)	Rubiaceae	(Rubi)	13	27
Gardenia	*erubescens*	(G.eru)	Rubiaceae	(Rubi)	16	86
Psydrax	*horizontalis*	(P.hor)	Rubiaceae	(Rubi)	5	70
Sarcocephalus	*latifolius*	(S.lat)	Rubiaceae	(Rubi)	79	85
Citrus	*limon*	(C.lim)	Rutaceae	(Ruta)	4	14
Citrus	*paradisi*	(C.par)	Rutaceae	(Ruta)	2	13
Citrus	*sinensis*	(C.sin)	Rutaceae	(Ruta)	6	26
Blighia	*unijugata*	(B.uni)	Sapindaceae	(Sapi)	1	34
Leucaniodiscus	*cupanioides*	(L.cup)	Sapindaceae	(Sapi)	3	21
Paullinia	*pinnata*	(P.pin)	Sapindaceae	(Sapi)	1	15
Vitellaria	*paradoxa*	(V.par)	Sapotaceae	(Sapo)	8	113
Hannoa	*undulata*	(H.und)	Simaroubaceae	(Sima)	7	47
Smilax	*anceps*	(S.anc)	Smilacaceae	(Smil)	3	84
Grewia	*barteri*	(G.bar)	Tiliaceae	(Tili)	1	39
Vitex	*doniana*	(V.don)	Verbenaceae	(Verb)	5	76
Clerodendrum	*thyrsoideum*	(C.thy)	Verbenaceae	(Verb)	1	11
					507	4065

Note: Abbreviations used for plant species, genus and family names are in parentheses.

African peach were significantly associated with the Sudan-Guinean zone. The other most common hosts such as wild custard apple, *Gardenia erubescens*, Angolan *Berlinia* and mango were also mainly located in the Sudan-Guinean zone (Figure 5a). Similarly, the most common trophobiont species including *S. sjostedti*, *U. catori and U. farquharsoni* were significantly associated with the Sudan-Guinean zone (Figure 5b). More generally, the African weaver ant was widespread in all agroecological zones of Benin.

DISCUSSION

Most studies on weaver ant ecology and ethology to date have been carried out in fruit plantations with *O. longinoda* and to a lesser extent with *O. smaragdina*. The patterns in more composite and species-rich natural ecosystems are certainly different. The originality of the present study conducted in Benin is that most of our sampling campaigns took place in mixed secondary and tertiary forests in: (a) humid

TABLE 2 Trophobionts observed in association with *O. longinoda* in Benin

Genus	Species		Families	Number	Orders
Ceroplastes	sp.	(Ce.sp)	Coccidae	6	Hemiptera
Coccus	*acaciae*	(Co.aca)	Coccidae	6	
Coccus	*hesperidum*	(Co.hes)	Coccidae	10	
Coccus	*subhemisphaericus*	(Co. sub)	Coccidae	1	
Coccus	sp.	(Co.sp.)	Coccidae	29	
Hemilecanium	sp.	(He.leu)	Coccidae	1	
Parasaissetia	*nairobica*	(Pa.nai)	Coccidae	8	
Parasaissetia	*nigra*	(Pa.nig)	Coccidae	117	
Parasaissetia	sp.	(Pa.sp.)	Coccidae	11	
Saissetia	*privigna*	(Sa.pri)	Coccidae	1	
Saissetia	sp.	(Sa.sp.)	Coccidae	10	
Udinia	*catori*	(Ud.cat)	Coccidae	148	
Udinia	*farquharsoni*	(Ud.far)	Coccidae	48	
Udinia	sp.	(Ud.sp.)	Coccidae	9	
Waxiella	*egbara*	(Wa.egb)	Coccidae	1	
Waxiella	*senegalensis*	(Wa.sen)	Coccidae	1	
Waxiella	*subsphaerica*	(Wa. sub)	Coccidae	2	
Lepidosaphes	*tapleyi*	(Le.tap)	Diaspididae	1	
Aspidoproctus	sp.	(As.sp.)	Margarodidae	1	
Ferrisia	*virgata*	(Fe.vir)	Pseudococcidae	3	
Formicoccus	*njalensis*	(Fo.nja)	Pseudococcidae	1	
Planococcus	*kenyae*	(Pl.ken)	Pseudococcidae	1	
Tylococcus	*westwoodi*	(Ty.wes)	Pseudococcidae	12	
Stictococcus	*intermedius*	(St.int)	Stictococcidae	2	
Stictococcus	*sjostedti*	(St.sjo)	Stictococcidae	38	
Stictococcus	*vayssieri*	(St.vay)	Stictococcidae	1	
Stictococcus	sp.	(St.sp.)	Stictococcidae	4	
Oxyrhachis	*tarandus*	(Ox.tar)	Membracidae	2	
Oxyrhachis	sp.	(Ox.sp.)	Membracidae	1	
Hilda	*funesta*	(Hi.fun)	Tettigometridae	2	
Hilda	*undata*	(Hi.und)	Tettigometridae	1	
Delphacidae	NK		Delphacidae	1	
Monophlebidae	NK		Monophlebidae	7	
Psyllidae	NK		Psyllidae	2	
Euliphyra	sp.	(Eu.sp.)	Lycaenidae	2	Lepidoptera

Note: Abbreviations for trophobiont species names are in parentheses.
Abbreviation: NK, not known.

forests, (b) dry savannas and (c) gallery forests along rivers. So, the majority of our sampling campaigns were conducted in wild zones, in fruit plantations and none in villages or towns. More generally, *Oecophylla* colonies are very seldom encountered in large villages or towns and, consequently, trophobionts are absent. Various types of human disturbance discourage weaver ants (Hölldobler & Wilson, 1990).

For *O. longinoda*, field results from Benin indicate a host range of 82 plant species belonging to 30 plant families along a latitudinal transect (around 1000 km) crossing three agroecological zones. Four plant species were investigated in the consecutive years 2010–2013. Many plant species are used by *O. longinoda* to build their nests in the foliage in all agroecological zones from the coast in the south to the borders with Burkina Faso and Niger in the north. Several of these plant species were already recorded in Tanzania by Way (1954a, 1963) while many others have not been recorded to date because Tanzania and Benin are geographically distant and have different agroecological zones (Vanderplank, 1960). According to our results, the occurrence probability of ant-nests was significantly higher on native non-cultivated plant species. The conservation of native plants

TABLE 3 Distribution of all the host plant species—trophobiont species associations and trophobiont species observed in Benin according to the trophobiont family. Number of trophobiont species and plant species–trophobiont family associations are in parentheses

Trophobiont superfamily	Trophobiont families	% host plant species—trophobiont family associations ($n = 126$)		% trophobiont species ($n = 35$)	
Coccoidea	Coccidae	62.70	(79)	48.57	(17)
Coccoidea	Diaspididae	0.79	(1)	2.86	(1)
Coccoidea	Margarodidae	0.79	(1)	2.86	(1)
Coccoidea	Monophlebidae	4.76	(6)	2.86	(1)
Coccoidea	Pseudococcidae	9.52	(12)	11.43	(4)
Coccoidea	Stictococcidae	14.29	(18)	11.43	(4)
Fulgoroidea	Delphacidae	0.79	(1)	2.86	(1)
Fulgoroidea	Tettigometridae	1.59	(2)	5.71	(2)
Membracoidea	Membracidae	1.59	(2)	5.71	(2)
Psylloidea	Psyllidae	1.59	(2)	2.86	(1)
Papilionoidea	Lycaenidae	1.59	(2)	2.86	(1)

Note: Number of trophobiont species and plant species–trophobiont family associations are in parentheses. N.B.: All belonging to the Hemiptera, except the last one that belongs to the Lepidoptera.

PHOTO 4 Common association O. *longinoda* – *Oxyrhachis* sp. (Membracidae) on *Albizia glaberrima* (Mimosoideae) in the south of Benin

around fruit plantations could therefore help biological pest control in fruit plantations. Native plants that should be preserved around fruit plantations are mainly the African peach, Angolan *Berlinia*, *O. celtidifolia*, African bark and wild custard apple.

Although the African weaver ants may appear to favour plant species with the most leafy foliage (e.g., the African peach) to enable them to build their nests, we noted that trees with small leaves such as the African locust bean tree *Parkia biglobosa* or that have semi-rigid leaves as the cashew tree *Anacardium occidentale* can be also used for nest construction in Benin. A particularly curious observation was that some neems *Azadirachta indica* also host weaver ants and their nests despite their repellent properties (Viswanathan et al., 2002). For instance, we found that Hemipterans such as the common coccid *U. catori* can exploit neem trees in Benin in association with *O. longinoda*.

Field results concerning *O. longinoda* in Benin identified 35 associated trophobiont species representing 11 insect families. Our results concerning *O. longinoda* are partly comparable to those compiled by Lim et al. (2008) based on records of host plants of the two species of weaver ants between 1900 and 2006 in the literature. The fact that more *O. smaragdina* trophobionts (28 species) than *O. longinoda* trophobionts (17 species) are reported in Lim's review (2008) can be explained by the disproportionate number of studies of the two ant species (Van Mele, 2008). Basic studies and experimental manipulations with weaver ants in sub-Saharan Africa are relatively recent, but have witnessed a steady increase in the last decade (Offenberg, 2015; Vayssières et al., 2016).

In West Africa (Ghana), some trophobiont species such as *S. sjostedti* attended by *O. longinoda* have already been recorded in cocoa plantations (Strickland, 1950). References to host plants of trophobiont species are fragmented in sub-Saharan Africa. In Benin, we recorded a wide range of Homopterans that weaver ants use despite the absence of aphids. This wide range of potential trophobionts could help the first worker ants when a queen establishes a colony through honeydew provided. A review of the literature revealed that the majority of Hemipteran trophobionts identified in the present study are polyphagous, which may prove to be an advantage for the establishment of weaver ant colonies in Sudan zone and even in drier zones. It is known that plant species diversity decreases along the gradient from southern to northern areas across Benin (Adomou, 2005) and more generally throughout West Africa.

Way (1954b) suggested that *O. longinoda* regulates *Saissetia* populations in Tanzania. Similarly, Vanderplank (1960) also indicated that workers may kill different species of Homoptera including Membracidae. In Benin, we observed several cases of predation of *U. catori* on *S. latifolius* but also of the same trophobiont species on *M. indica* during the dry season (Vayssières et al., 2015). In this way,

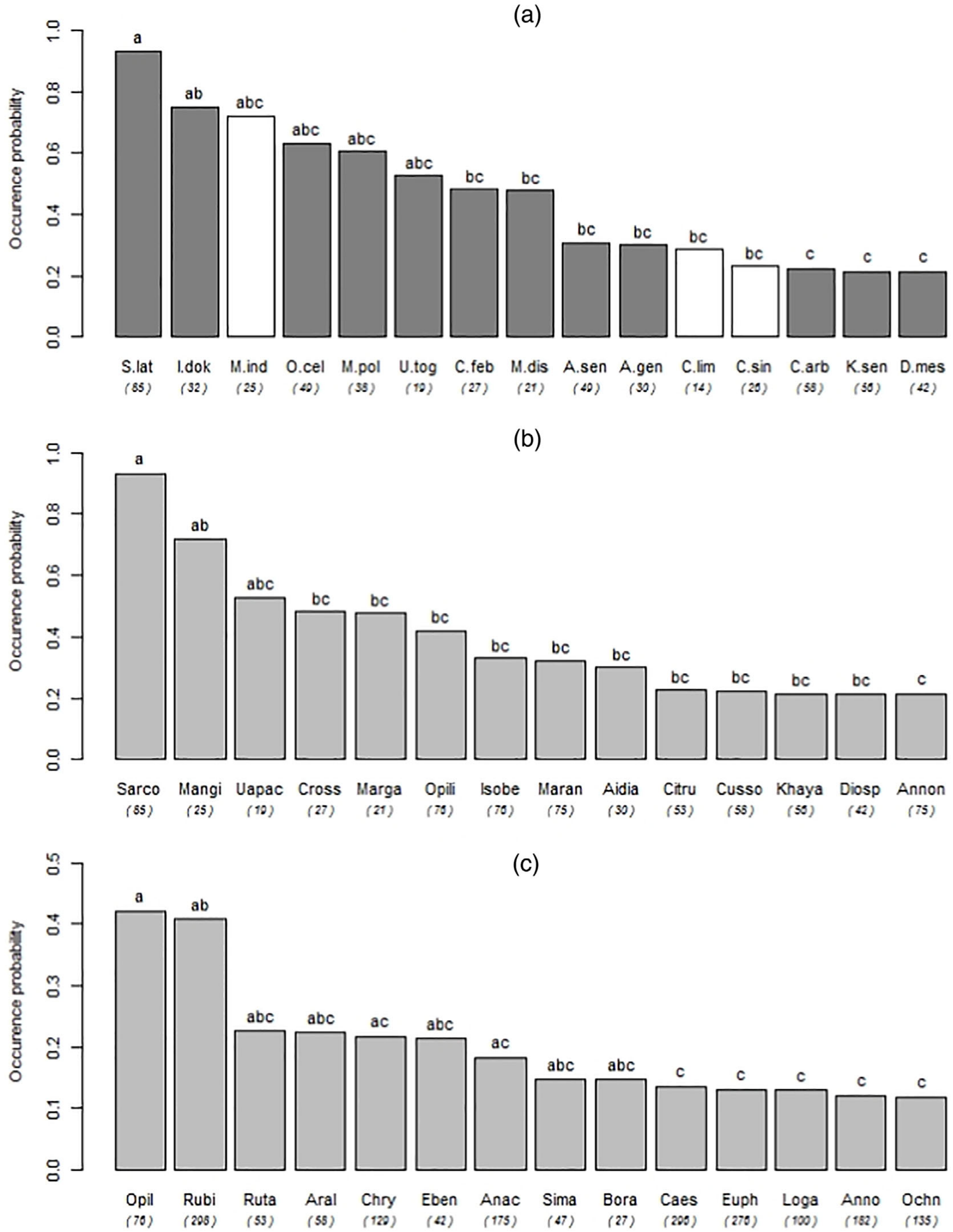

FIGURE 1 The most common host plant species (a), genera (b) and families (c) used by *O. longinoda* in Benin. Plant species: S.lat, *Sarcocephalus latifolius*; I.dok, *Isoberlinia doka*; M.ind, *Mangifera indica*; O.cel, *Opilia celtidifolia*; M.pol, *Maranthes polyandra*; U.tog, *Uapaca togoensis*; C.feb, *Crossopteryx febrifuga*; M.dis, *Margaritaria discoïdea*; A.sen, *Annona senegalensis*; A.gen, *Aidia genipiflora*; C.lim, *Citrus limon*; C.sin, *Citrus sinensis*; C.arb, *Cussonia arborea*; K.sen, *Kaya senegalensis* D.mes, *Diospyros mespiliformis*. Plant genus: Sarco, *Sarcocephalus* Mangi, *Mangifera* Uapac, *Uapaca*; Cross, *Crossopteryx*; Marga, *Margaritaria*; Opili, *Opilia*; Isobe, *Isoberlinia*; Maran, *Maranthes*; Citru, *Citrus*; Cusso, *Cussonia*; Diosp, *Diospyros*; Annon, *Annona*. Plant family: Opil, Opiliaceae; Rubi, Rubiaceae; Ruta, Rutaceae; Aral, Araliaceae; Chry, Chrysobalanaceae; Eben, Ebenaceae; Anac, Anacardiaceae; Sima, Simaroubaceae; Bora, Boraginaceae; Caes, Caesalpinioideae; Euph, Euphorbiaceae; Loga, Loganiaceae; Anno, Annonaceae; Ochn, Ochnaceae

African weaver ants may reduce the cost of hosting the trophobionts by balancing different trophobiont populations depending on abiotic-biotic factors fluctuating across the seasons (Way, 1954a). Weaver ants collect honeydew but, at the same time, they prey on and/or mostly deter many insect pests, resulting in a net positive effect for the host plant (Offenberg, 2015).

Several points are worthy of note: (a) coccids were the most widespread and abundant group of the trophobionts recorded,

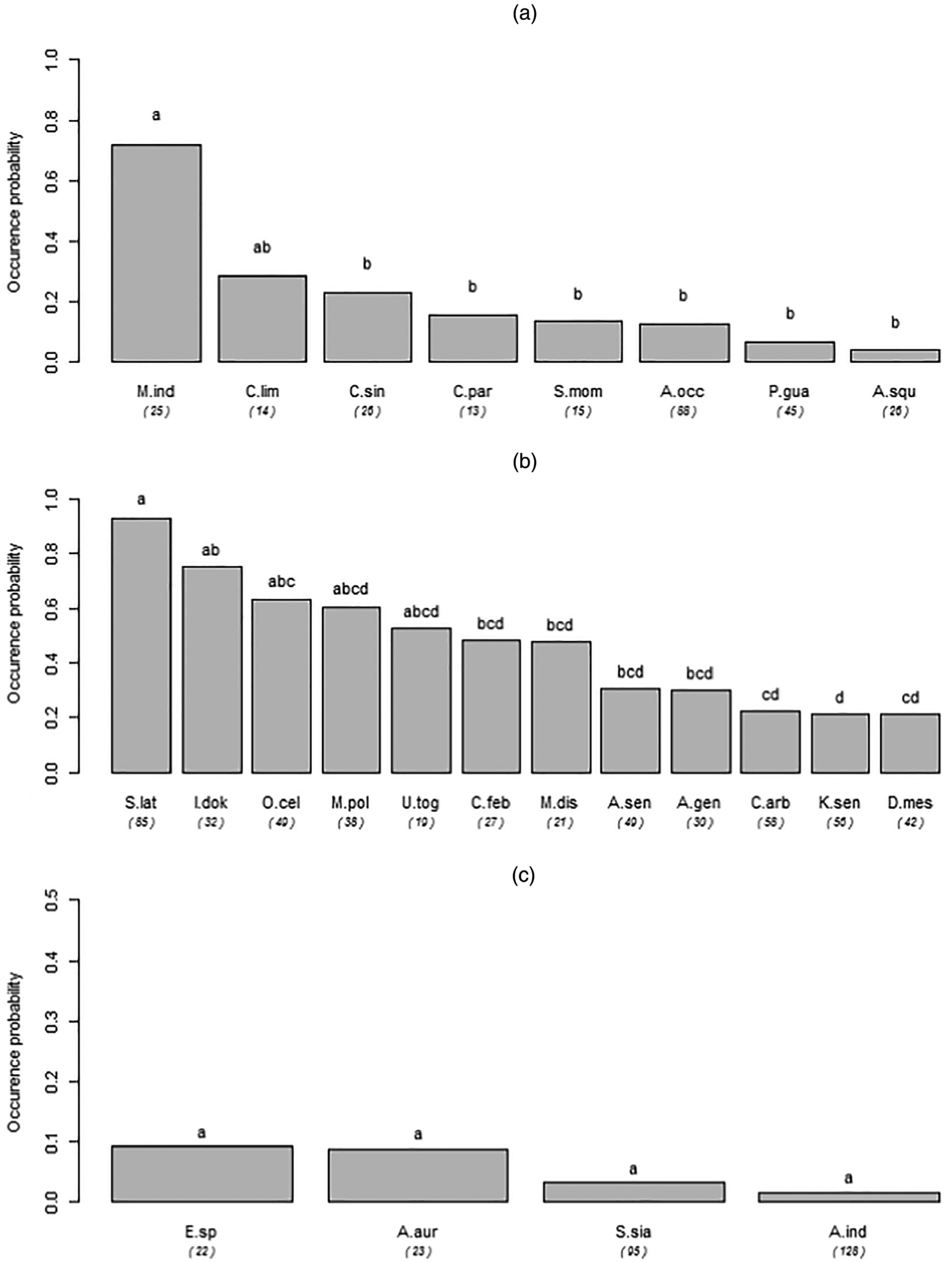

FIGURE 2 Differences of occurrence probability between cultivated and wild plants. Abbreviations used for plant species are explained in Figure 1. (a) Cultivated tree, shrub and liana species. (b) Non-cultivated local tree, shrub and liana species. (c) Non-cultivated exotic tree, shrub and liana species

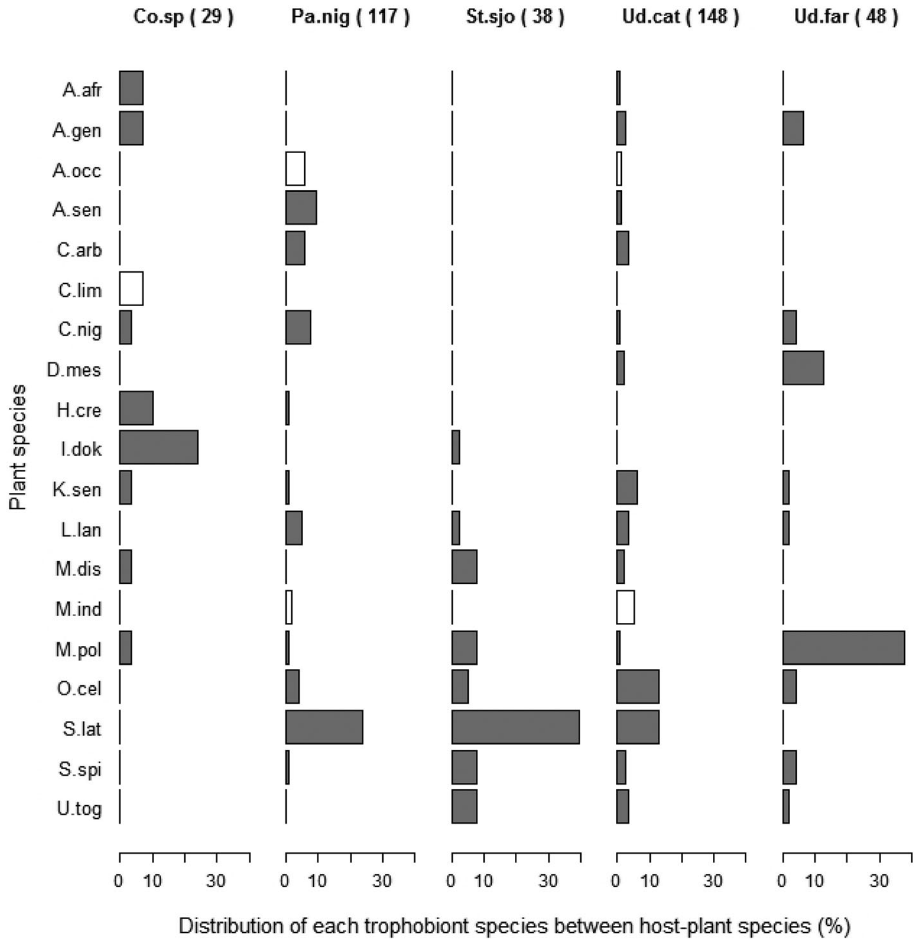

FIGURE 3 Associations between host plants and trophobionts species. Abbreviations used for plant species are explained in Figure 1. Trophobiont species: Co. sp, *Coccus* sp.; Pa.nig, *Parasaissetia nigra*; St.sjo, *Stictococcus sjostedti*; Ud.cat, *Udinia catori*; Ud.far, *Udinia farqharsoni*

especially *U. catori* and *P. nigra*, both of which are polyphagous; (b) *O. longinoda* attended several species of Pseudococcidae but not *Rastrococcus invadens*, which is a fruit pest of high economic significance; (c) different families of other trophobiont species (that are not fruit pests) show high diversity around weaver ant colonies. Concerning "mango mealybug" *R. invadens*, a high polyphagous pest of Indian origin accidentally introduced in West Africa in the 1980s, our observations did not reveal any associations with the ant: this is another key-point in favour of *O. longinoda*.

At the plant level, the effects of the interactions between honeydew-producing hemipterans and ants do not necessarily have negative consequences such as damage to the plant and reduced plant fitness. We observed that 56% of trophobionts were located in the weaver ants' nests and only 6% on the fruit. In a literature review by Styrsky and Eubanks (2007), in which the quantitative effects of various associations between ants and honeydew-producing hemipterans were analysed, 20 out of 30 associations were shown to exert a positive effect on the host plants. Among the trophobionts recorded in the present study, none of the species of associated hemipterans are known to be vectors of diseases of cultivated trees. Similarly, Way and Khoo (1992) also noted that *O. smaragdina* attended Stictococcidae and Coccidae on citrus trees, without any disease transmission.

Almost 62% of the plants used by weaver ants we recorded were located in the Sudan-Guinean zone, which also includes most mango and cashew plantations in Benin. This is not only the case in Benin but also in all other West African countries. The introduction of previously absent suitable host plants could trigger multiplication of weaver ant colonies around mango-cashew-citrus plantations throughout West Africa. In this way, our field work in wild areas could maybe explain the establishment of weaver ant colonies around and, later, in fruit plantations. The African weaver ant was also observed in south Burkina and south Niger in drier agroecological zones than those it mainly occurred in Benin.

The use of *O. longinoda* colonies is suitable for perennial cropping systems in sub-Saharan Africa because of the ants' effectiveness against highly damaging fruit pests such as fruit flies, sap-sucking bugs, weevils and caterpillars (Adandonon et al., 2009; Vayssières et al., 2015). Adverse perceptions are starting to change and there is currently a more positive attitude towards *O. longinoda* in some areas of certain West African countries such as Ghana, Guinea and Benin

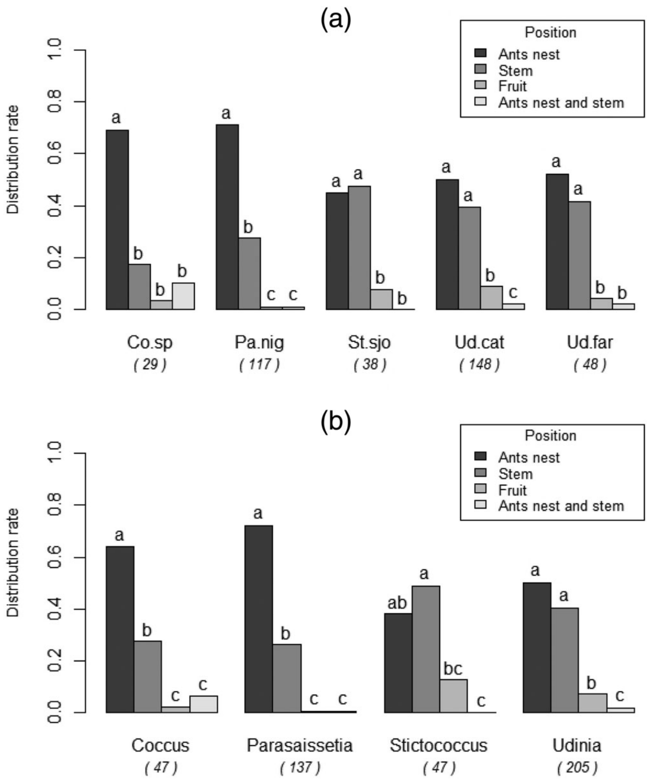

FIGURE 4 Distribution of each of the most common trophobiont species (a) and genera (b) according to their position on the host plant (1 = in the weaver ants' nest, 2 = on the stem, 3 = on the fruit, 4 = in the weaver ants' and on the stem). Abbreviations used for trophobiont species are explained in Figure 3

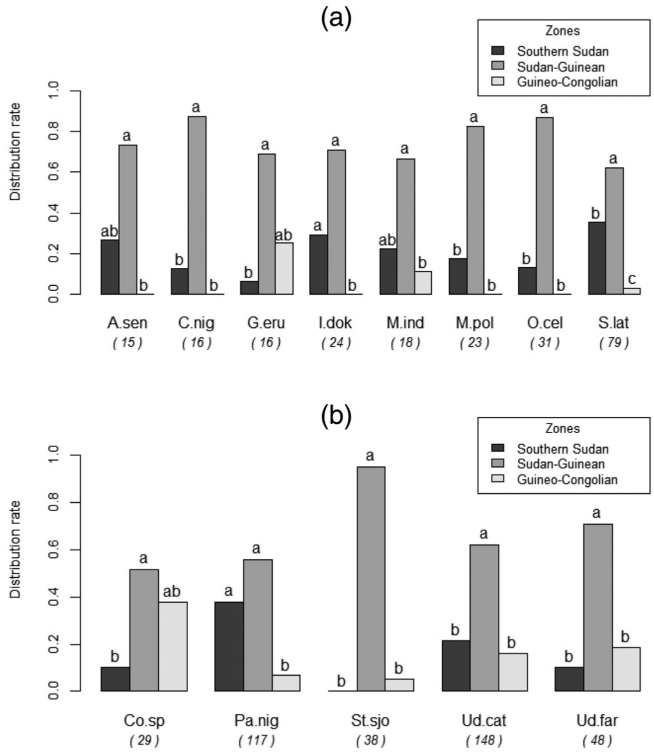

FIGURE 5 Repartition of each of the most common host plant (a) and trophobiont (b) species according to the Agroecological zones (1 = southern Sudan zone, 2 = Sudan-Guinean zone, 3 = Guineo-Congolian zone). Abbreviations used for plant species and trophobiont species are explained in Figures 1 and 3, respectively

(Ouagoussounon et al., 2015). Basic studies and R4D experiments with weaver ants in sub-Saharan Africa are relatively recent: there has been a significant increase of these studies in the last decade (Offenberg, 2015; Vayssières et al., 2016).

The present data contribute to a better understanding of the mechanisms driving these tri-trophic relationships and may promote the use of host plants that favour the establishment of weaver ant trophobionts. This could be a prerequisite for the introduction of populations of this beneficial weaver ant species in and around uncolonized fruit plantations. In plantations not treated with pesticides throughout Benin, 72% of cashew trees, 90% of citrus trees and 98% of mango trees are colonized by weaver ants. This is a good example of the equilibrium of food web structures under natural conditions that must be preserved and encouraged. The presence of these weaver ants in fruit plantations is also a bio-indicator of organic production that needs to be enhanced.

CONCLUSION

These first results highlight the fact that primarily host plants, and to a lesser extent *O. longinoda*, influence the distribution of various families of attended hemipterans throughout Benin. A wide range of native host plants could be preserved (or/and planted) to promote the establishment of weaver ants to control different insect pests in fruit plantations in sub-Saharan Africa. When planted (or preserved) around fruit plantations with their nests and tended hemipterans, these host plants could facilitate conservation biocontrol of mango fruit flies (Tephritidae), cashew bugs (Coreidae, Miridae) and other fruit pests by the presence *O. longinoda* in the plantations.

Trophobiont associations with honeydew producing hemipterans are a key component of weaver ant behaviour. It can be assumed that honeydew provision by associated trophobionts acts as a booster for *O. longinoda* to establish and develop new colonies.

ACKNOWLEDGEMENTS

This research was supported by the donor DANIDA, the institutions IITA (CGIAR), and CIRAD to whom the authors are very grateful. The present study on ants is part of research conducted in the framework of the West African Fruit Fly Initiative (WAFFI) and helped to promote the weaver ant component as a key element of conservative biological control activities in the IPM-package against mango fruit flies proposed to West African growers. We also thank Oswald Nobimé, Jean-Marcel Dèguénon, Alassane Seidou, Cyriaque Houndetounou, Cyrille Akponon and Lazard Adoho for their precious technical help in Benin. And we are grateful to Annie Boyer for help with bibliographic reference search and to Jérôme Orivel for useful advices on the manuscript.

DATA AVAILABILITY STATEMENT

Data available in my personal files.

REFERENCES

Abdulla, N., Rwegasira, G., Jensen, K.M., Mwatawala, M. & Offenberg, J. (2015) Effect of supplementary feeding of *Oecophylla longinoda* on their abundance and predatory activities against cashew insect pests. *Biocontrol Science & Technology*, 25, 1333–1345.

Adandonon, A., Vayssières, J.-F., Sinzogan, A. & Van Mele, P. (2009) Density of pheromone sources of the weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) affects oviposition behaviour and damage by mango fruit flies (Diptera Tephritidae). *International Journal of Pest Management*, 55, 85–292.

Adomou, A. (2005) *Vegetation patterns and environmental gradients in Benin. Implications for biogeography and conservation*. PhD Thesis, Wageningen University, Wageningen, p. 150.

Anato, F., Wargui, R., Sinzogan, A., Offenberg, J., Adandonon, A., Kossou, D. & Vayssières J.-F. (2015) Reducing losses inflicted by insect pests on cashew, using weaver ants as efficient biological control agent. *Agricultural Forest Entomology*, 17, 285–291.

Anato, F., Sinzogan, A., Offenberg, J., Adandonon, A., Wargui, R., Deguenon, J.-M. & Vayssières J.-F. (2017) *Oecophylla longinoda* (hymenoptera: Formicidae) lead to increased cashew kernel size and kernel quality. *Journal of Economic Entomology*, 110, 1133–1137.

Arbonnier, M. (2004) *Trees, shrubs and lianas of West African dry zones*. Cirad: Margraf publishers, GMBH, MNHN, p. 573.

Ativor, I.N., Afreh-Nuamah, K., Billah, M. & Obeng-Ofori, D. (2012) Weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera Formicidae) activity reduces fruit fly damage in citrus orchards. *Journal of Agricultural Science and Technology*, 2, 449–458.

Ayenor, G.K., Van Huis, A., Obeng Ofori, D., Padi, B. & Roeling, N.G. (2007) Facilitating the use of alternative capsid control methods towards sustainable production of organic cocoa in Ghana. *International Journal of Tropical Insect Science*, 27, 85–94.

Blüthgen, N., Gottsberger, G. & Fielder, K. (2004) Sugar and amino-acid composition of ant-attended nectar and honeydew sources from an Australian forest. *Austral Ecology*, 29, 418–429.

Bruneau de Miré, P. (1969) Une fourmi utilisée au Cameroun dans la lutte contre les mirides du cacaoyer *Wasmania auropunctata* Roger. *Café Cacao Thé*, 13, 209–212.

Chauvin, R. (1952) Sur la reconstruction du nid chez les fourmis oecophylles. *Behaviour*, 4, 190–201.

Dejean, A. (1991) Adaptation d'*Oecophylla longinoda* (Formicidae-Formicinae) aux variations spatio-temporelles de proies. *Entomophaga*, 36, 29–54.

Dejean, A., Djiéto-Lordon, C. & Durand, J.L. (1997) Ant-mosaic in oil palm plantations of the South-West Province of Cameroon: impact on a leaf miner chrysomelid beetle. *Journal of Economic Entomology*, 90, 1092–1096.

Dejean, A., Corbara, B., Orivel, J. & Leponce, M. (2007) Rainforests canopy ants: the implications of territorially and predatory behavior. *Global Science Book, Functional Ecosystems and Communities*, 1, 105–120.

Diamé, L., Grechi, I., Rey, J.-Y., Sané, C.A.B., Diatta, P., Vayssières, J.-F. et al. (2015) Influence of *Oecophylla longinoda* Latreille (hymenoptera: Formicidae) on mango infestation by *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) in relation to Senegalese orchard design and management practices. *African Entomologist*, 23, 294–305.

Dwomoh, E.A., Afun, J.V., Ackonor, J.B. & Agene, V.N. (2008) Investigations on *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) as a biocontrol agent in the protection of cashew plantations. *Pest Management Science*, 65, 41–46.

Fife, D. (2014) A collection of miscellaneous functions. R package version 1.0. https://CRAN.R project.org/package=fifer.

Gullan, P.J. (1997) Relationships with ants. In: Ben-Dov, Y. & Hogson, C.J. (Eds.) *Soft scale insects – their biology, natural enemies and control*. Amsterdam: Elsevier Science, pp. 351–377.

Hervé, M. (2018) RVAideMemoire: Testing and Plotting Procedures for Biostatistics. R package version 0.9-69-3. Available at: https://CRAN.R-project.org/package=RVAideMemoire.

Hölldobler, B. (1979) Territories of the African weaver ant *Oecophylla longinoda* (Latreille), a field study. *Zur Tierpsychologie*, 51, 201–213.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Cambridge, MA: Harvard University Press.

Huang, H.T. & Yang, P. (1987) The ancient cultural citrus ant, a tropical ant is used to control insect pests in southern China. *Bioscience*, 37, 665–671.

Kenné, M. (2006) Evaluation des possibilités d'utilisation d'une espèce de fourmi terricole dominante comme auxiliaire de lutte contre les insectes phytophages. HDR mémoire. Université de Toulouse, p. 105.

Kenné, M., Djiéto-Lordon, C., Orivel, J., Mony, R., Fabre, A. & Dejean, A. (2003) Influence of insecticide treatments on ant-hemiptera-associations in tropical plantations. *Journal of Economic Entomology*, 96, 251–258.

Khoo, K.C. & Chung, G.F. (1989) Use of the black cocoa ant to control mirid damage in cocoa. *Plant - Kuala lumpur*, 65, 370–383.

Ledoux, A. (1950) Recherche sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latreille). *Annales des Sciences Naturelles*, 12, 313–461.

Leston, D. (1973) The ant-mosaic, tropical tree crops and the limiting of pests and diseases. *Pest Articles and New Summaries*, 19, 311–341.

Lim, G.T., Kirton, L.G., Salom, S.M., Kok, L.T., Fell, R.D. & Pfeiffer, D.G. (2008) Host-plants and associated trophobionts of the weaver ants *Oecophylla* spp. (Hymenoptera Formicidae). *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Ressources*, 3, 35.

Majer, J.D. (1972) The ant-mosaic in Ghana cocoa farms. *Bulletin of Entomological Research*, 62, 151–160.

Offenberg, J. (2015) Ants as tools in sustainable agriculture. *Journal of Applied Ecology*, 52, 1197–1205.

Ouagoussounon, I., Offenberg, J., Sinzogan, A., Adandonon, A., Kossou, D. & Vayssières, J.-F. (2015) Founding weaver ant queens increase production and nanitic worker size. *Springerplus*, 4, 6. https://doi.org/10.1186/2193-1801-4-6

Overal, W.L. & Posey, P.A. (1984) Uso de formigas do genero Azteca por control de saúvas entre os indios Kaiapos do Brasil. *Attini*, 16, 2.

R Core Team. (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Room, P.M. (1971) The relative distribution of ant species in Ghana's cocoa farms. *Journal of Animal Ecology*, 40, 735–751.

Strickland, A.H. (1950) The entomology of the swollen shoot of cacao I – the insect species involved with notes on their biology. *Bulletin of Entomological Research*, 41, 725–748.

Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interaction between ants and honeydew-producing insects. *Proceedings of the Royal Society - Biological Sciences*, 274, 151–164.

Taylor, B. & Adedoyin, S.F. (1978) The abundance and interspecific relations of common ant species (Hymenoptera Formicidae) on cocoa farms in Western Nigeria. *Bulletin of Entomological Research*, 8, 105–121.

Tobin, J.E. (1994) Ants as primary consumers: diet and abundance in the Formicidae. In: Hunt, J.H. & Napela, C.A. (Eds.) *Nourishment and evolution in insect societies*. Colorado: Westview Press Boulder, pp. 279–307.

Van der Goot, P. (1917) De Zwarte cacao-mier (*Dolichoderus bituberculatus* Mayr.) en haar beteenkenis voor de cacao-cultuur op Java. *Medical Education Proefstn Mid Java*, 25, 1–141.

Van Mele, P. (2008) An historical review of research of the weaver ant *Oecophylla* in biological control. *Agricultural Forest Entomology*, 10, 13–22.

Van Mele, P. & Cuc, N.T.T. (2001) Farmers perception and practices in use of *Dolichoderus thoracicus* (smith) (hymenoptera Formicidae) for biological control of pests of sapodilla. *Biological Control*, 20, 23–29.

Van Mele, P., Vayssières, J.-F., Van Tellingen, E. & Vrolijks, J. (2007) Effects of an African weaver ant, *Oecophylla longinoda*, in controlling mango fruit flies (Diptera Tephritidae) in Benin. *Journal of Economic Entomology*, 100, 695–701.

Van Mele, P., Thi Thu Cuc, N., Seguni, Z., Camara, K. & Offenberg, J. (2009) Multiple sources of local knowledge: a global review of ways to reduce nuisance from the beneficial weaver ant *Oecophylla*. *International Journal of Agricultural Resources, Governance and Ecology*, 8, 484–504.

Vandermeer, J., Perfecto, I., Nuñez, G.I., Phillpott, S. & Ballinas, A.L. (2002) Ants (*Azteca* sp.) as potential biological control agents in shade coffee production in Chiapas, Mexico. *Agroforestry Systems*, 56, 271–276.

Vanderplank, F.L. (1960) The bionomics and ecology of the red ant tree, *Oecophylla* sp., and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). *Journal of Animal Ecology*, 29, 15–33.

Vayssières, J.-F., Ouagoussounon, I., Adandonon, A., Sinzogan, A., Korie, S., Todjihoundé, R. et al. (2015) Seasonal pattern in food gathering of the weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) in mango orchards in Benin. *Biocontrol Science & Technology*, 25, 1359–1387.

Vayssières, J.-F., Offenberg, J., Sinzogan, A., Adandonon, A., Wargui, R., Anato, F. et al. (2016) The use of weaver ants in the management of fruit flies in Africa. In: Ekesi, S., Mohamed, S. & de Meyer, M. (Eds.) *Fruit fly research and development in Africa, towards a sustainable management strategy to improve horticulture*, pp. 389–434. Switzerland: Springer International Publishing.

Viswanathan, G., Paul, C., Warier, N., Sampath, S. & Jha, S. (2002) Neem leaf extract as a natural plant pesticide in the control of fire ants. *Journal of Ecobiology*, 14, 131–135.

Wargui, R. (2010) Pheromonal effect of the weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) on citrus fruit flies (Diptera Tephritidae). IITA report, p. 14.

Wargui, R., Adandonon, A., Sinzogan, A., Anato, F., Vayssières, J.-F., Kossou, D. et al. (2018) Weaver ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) performance in mango and cashew trees under different management regimes. *Sociobiology*, 65, 208–214.

Way, M.J. (1953) The relationship between certain ant species with particular reference to biological control of the coreid, *Theraptus* sp. *Bulletin of Entomological Research*, 44, 669–691.

Way, M.J. (1954a) Studies on the life history and ecology of the ant *Oecophylla longinoda* Latreille. *Bulletin of Entomological Research*, 45, 93–112.

Way, M.J. (1954b) Studies on the association of the ant *Oecophylla longinoda* Latreille with the scale insect *Saissetia zanzibarensis* Williams. *Bulletin of Entomological Research*, 45, 113–134.

Way, M.J. (1963) Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology*, 8, 307–344.

Way, M.J. & Khoo, C. (1989) Relationships between *Helopeltis theobromae* and ants with special references to Malaysian cocoa smallholdings. *Journal of Plant Protection of the Tropics*, 6, 1–11.

Way, M.J. & Khoo, C. (1992) Role of ants in pest management. *Annual Review of Entomology*, 37, 479–503.

How to cite this article: Vayssières, J.-F., Grechi, I., Sinzogan, A., Ouagoussounon, I., Todjihoundé, R., Modjibou, S. et al. (2021) Host plants and associated trophobionts of the weaver ant *Oecophylla longinoda* Latreille (Hymenoptera Formicidae) in Benin. *Agricultural and Forest Entomology*, 1–15. Available from: https://doi.org/10.1111/afe.12478

APPENDIX

Mean occurrence probability across all species of each group with their probability of hosting *Oecophylla*:

A. Cultivated tree, shrub and liana species: mean = 0.22, SE = 0.077.
B. Non-cultivated native tree, shrub and liana species: mean = 0.14, SE = 0.022.
C. Non-cultivated exotic tree, shrub and liana species: mean = 0.06, SE = 0.019.