Liana abundance and colonization in a tropical moist secondary lowland rainforest in Nigeria

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ABSTRACT: Studies on the influence of host tree successional status on liana infestation are few or lacking in regenerating forests in Africa. This study examined some likely predictors of the abundance of dominant lianas in a regenerating lowland rainforest in Ile-Ife, Nigeria. Six sample plots (0.25 ha each) were sampled in the secondary forest in the Biological Gardens of Obafemi Awolowo University, Ile-Ife, Nigeria. All trees and shrubs (≥ 2 m in height) and lianas attached to the trees and shrubs, were enumerated and their girth sizes were measured. The successional status of the host and lianas was determined. A chi-square analysis was carried out to determine the preferential liana infestation on host species in the forest while logistic binary regression analysis was used to determine the probability of infestation of the host species by each liana species. Liana colonization was species-specific with *Chasmanthera dependens, Combretum* sp. and *Motandra guineensis* being the only lianas that preferentially infested specific host species. *Senegalia ataxacantha* and *Combretum* sp. were the only lianas that preferred both late- and early-successional host species while *Motandra guineensis* was the only liana species that preferred both small and large host species. Since late-successional host species are gradually replacing the early-successional hosts in the forest, this makes it more necessary to monitor the tree regeneration process in the forest closely especially because most of the dominant lianas are early-successional species that would impede the regeneration of the trees and shrubs in the forest.

KEY WORDS: binary regression, biological garden, colonization probability, host-specific, successional status.

INTRODUCTION

Lianas are key features of tropical rainforests and constitute from 10–45% of all woody plants and species (Schnitzer and Bongers, 2002). They reduce growth, fecundity, survival, and recruitment of trees (Schnitzer and Carson, 2010; Yorke *et al.,* 2013) by using them as structural support and resource competition and as a result, they can have a considerable impact on forest dynamics and tree species composition (Schnitzer and Bongers, 2002; 2011). Schnitzer *et al.* (2000) suggested that the ability of lianas to colonize and proliferate allows them to alter tree regeneration in gaps for many years and cause the pattern of tree regeneration to proceed on an altered successional path. Lianas colonize disturbed areas faster than trees and often have higher abundance following disturbance, especially along forest edges and within forest gaps (Schnitzer *et al.,* 2000; Allen *et al.,* 2005; Allen *et al.,* 2007; Estrada-Villegas *et al.*, 2020). Ladwig and Meiners (2010) suggested that to understand potential liana impacts on the regenerating forest community, we need to first know the location and intensity of liana burdens on host trees.

Because lianas are abundant in many tropical forests (Clark and Clark, 1990; Uwalaka and Muoghalu, 2017), the potential for lianas to alter gap-phase regeneration could be frequent and widespread, but data on the prevalence or duration of stalled gaps remain scarce.

Factors such as host tree size (Nabe-Nielsen, 2001), bark texture (Campanello *et al.,* 2007), host tree identity and availability (Ibarra-Manriquez and Martinez-Ramos, 2002; Muoghalu and Okeesan, 2005) and host tree allelopathy (Talley *et al.,* 1996) have been suggested as determinants of the infestation of lianas on host tree species with only a few studies examining the influence of host tree successional status on liana infestation in regenerating forests (e.g., Ladwig and Meiners, 2010), although colonization of forests by lianas is dominated by a few competitively colonizing species, which recruit early (in high density), and are able to persist in high abundance (Barry *et al.*, 2015). Such studies are either lacking or non-existing in the African forest formation (e.g., Kirika *et al.,* 2010). This study examined the colonization probability of dominant liana species in a regenerating lowland rainforest in Ile-Ife, Nigeria. The questions asked in this study are:
1. Do lianas preferentially infest trees of early- or late-successional status?
2. What factor(s) best explain the colonization of a liana on a host species in a Nigerian regenerating rainforest?

MATERIALS AND METHODS

Study area

The study was carried out within a 20.5 hectare secondary rain forest in the Biological Gardens of the
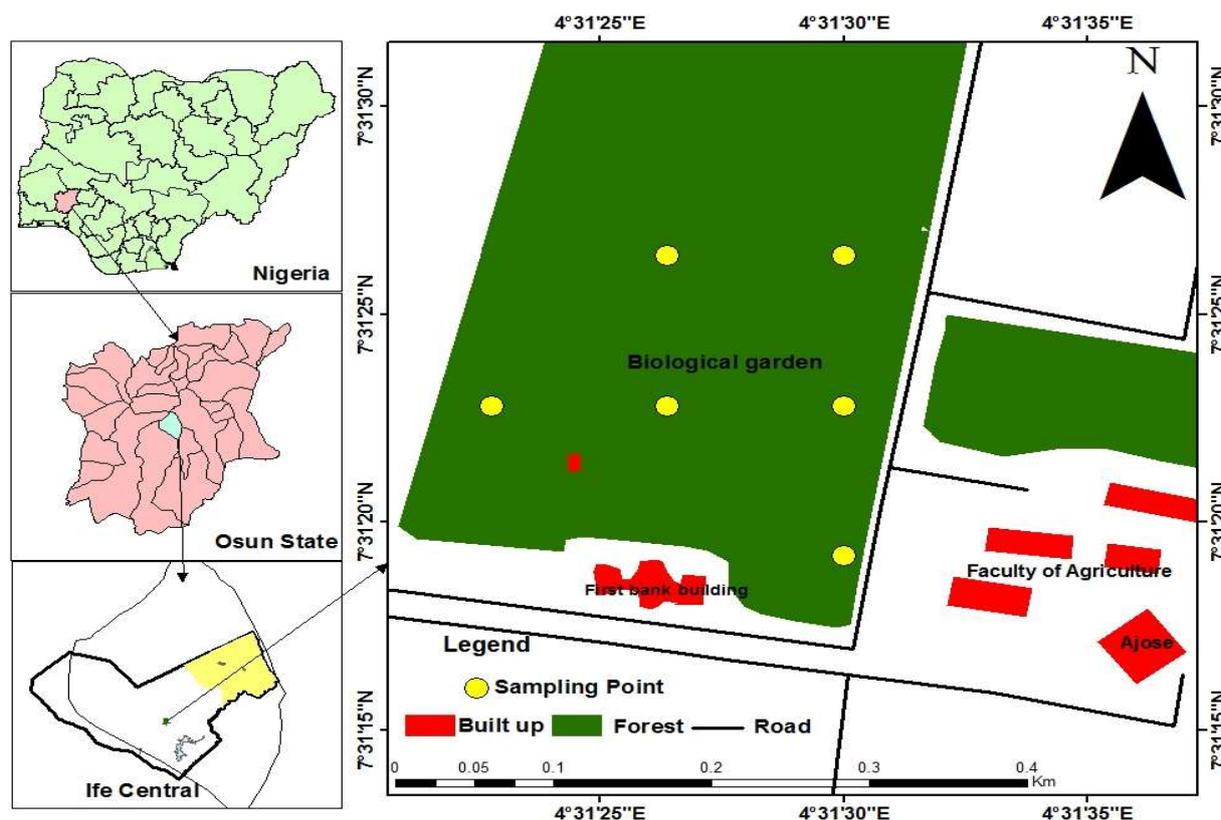
Fig. 1. Map of the Biological Gardens of Obafemi Awolowo University, Ile-Ife, with the Sampling location where the Study was carried out.

Obafemi Awolowo University, Ile-Ife, Nigeria (7° 30' to 7° 35' N and 4° 30' to 4° 35' E) (Fig. 1). The elevation ranges from 213 m to 457 m above sea level (Hall, 1969). Ile-Ife has a short dry season and longer rainy season (average temperature: 25.5 °C; average rainfall: 1302 mm per year; relative humidity: 82.80%; solar radiation: 164.30Wm^{-2}) (Atmospheric Physics Research Group, 2013). The city is underlain by rocks of the Basement Complex of Precambrian age (De Swardt, 1953). The soil which is of the Ultisols class (USDA, 1975), has an Isohyperthermic temperature regime, ustic soil moisture and kaolinite clay mineral content (Ayodele, 1986). The forest is a natural regrowth under conservation within and outside the Gardens with minimal human disturbance.

Ile-Ife lies in the lowland rainforest zone (Keay, 1959) and Guineo-congolian forest drier type (White, 1983). The most frequently occurring woody plant families are Apocynaceae, Euphorbiaceae, Fabaceae, Moraceae, and Sterculiaceae (Uwalaka *et al*., 2018). Six sample plots (0.25 ha each) were established using a measuring tape in the secondary rain forest in the Biological Gardens.

Data collection

Vegetation sampling

In each sample plot, all the tree and shrub species ≥ 2 m in height were identified to species level and enumerated. The girths were measured at 1.3 m height (girth at breast height) or above the buttresses. They were marked to avoid double enumeration. The successional status of each tree/shrub species followed the method of Ademoh *et al*. (2017) while the method described by Aubréville (1957) was used to categorize the lianas. In each sample plot, all liana individuals were identified to species level. All liana individuals climbing or attached to a host species in each sample plot were sampled according to the method of Uwalaka and Muoghalu (2017). The enumeration and measurements of both lianas and host species were done simultaneously. Voucher specimens of the species which could not be identified in the field were collected, preserved and identified in the IFE Herbarium of the Department of Botany, Obafemi Awolowo University, Ile-Ife, Nigeria.

However, some of the lianas could only be identified up to the family level. Such species were not included in the data matrix. The species composition of the plots was established by listing all the species encountered in each plot. Species nomenclature follows those of Plant List database (The Plant List, 2013).

Data and statistical analysis

The girth measurements of the plant species (trees, shrubs, and lianas) were taken. The girth sizes of all lianas

attached to or climbing each host species were used to establish the relationship between the girth sizes of the lianas and their host species.

The successional status of the host species was determined. It was revealed that all the dominant lianas were native and most of them were early colonizers (PROTA, 2012; Table 1) indicating that the forest in the biological gardens was still at its early stage of secondary succession. To determine the preferential infestation rate of lianas on the host species, the host species were sorted into different successional guilds; late- and early-successional hosts. Those whose guilds could not be determined were classified as "unknown" (This special class was not, however, used in the chi-square analysis). The data collated for these different infestation statuses were then determined by first sorting the frequencies into a contingency table before a chi-square analysis was carried out using two criteria of classification (successional status of hosts and liana infestation on hosts). The host species with unknown successional status were used as a reference category for further binary logistic regression analysis. Also, correlation analysis was carried out to test the relationship between successional host girth size and corresponding liana girth sizes. Based on the presence or absence of a liana of interest on dominant tree species, logistic binary regression analysis was used to determine the probability of colonization of the host tree species by each liana using tree girth size as standard. The girth sizes were used to categorize the tree species into small, medium and big. Trees of 0 - 30.9 cm girth sizes were designated as "small", those of 31–60.9 cm girth size were designated as "medium" while those of girth size ≥ 70 cm were termed "big". The "medium-sized" girth size class was used as the dummy variable in the logistic regression analysis. The percentage infestation of lianas on host species in the forest was calculated as the number of lianas on each species divided by the sum of the number of lianas on all species in the forest multiplied by 100. The frequency of species (host and liana) was recorded based on the presence of each species in the forest. Species presence ranged from + to ++++++ since six plots were used for this study. The analyses were carried out using STATA 14 software package (StataCorp, 2015).

RESULTS

A total of 119 plant species (67 tree, 10 shrub and 42 liana species) were present in the forest. Out of the 77 host species, more early-successional host species were recorded (44 early-successional species, 21 late-successional while the status of 12 species could not be ascertained) (Table 1). Of all the 584 host individuals examined in the forest, 452 individuals (77.4%) were infested by at least one liana individual. Only the successional status of 390 individuals out of the 452

individuals that hosted lianas in the forest were known. The most affected of these host species were *Lecaniodiscus cupanioides*, with 13.59% liana infestation and *Funtumia elastica*, with 12.65% liana infestation which are late- and early-successional species respectively. The least affected of the host species were *Blighia* sp., *Blighia unijugata*, *Bridelia ferruginea*, *Canarium schwenfurttii*, *Carpolobia lutea*, *Celtis* sp., *Cleistopholis patens*, *Cola acuminata*, *Dialium guineense*, *Ficus sur*, *Garcina kola*, *Mallotus mildbraedii*, *Morus mesozygia*, *Piptadenastrum africanum* and *Rauvolfia vomitoria*, all with 0.11% liana infestation.

Since there were more early-successional tree species in the forest, they hosted more lianas than the late-successional tree species. When the host tree species were sorted into successional status (late- and early-successional status), it was observed that their girth sizes were significantly correlated to those of the corresponding liana girth sizes; early-successional host species girth size vs liana girth size ($r = 0.34$; $P < 0.0001$; $df = 268$) (Fig. 2) and late-successional host species girth size vs liana girth size ($r = 0.53$; $P < 0.0001$; $df = 118$) (Fig. 3). Furthermore, number of liana was significantly correlated with the corresponding late- and early-successional host species girth sizes; early-successional host species girth size vs number of liana ($r = 0.32$; $P < 0.0001$; $df = 268$) (Fig. 4) and late-successional host species girth size vs number of liana ($r = 0.40$; $P < 0.0001$; $df = 118$) (Fig. 5).

The colonization probabilities of individual dominant lianas in the forest was host-specific. *Baissea campanulata, Mezoneuron benthamianum, Oncinotis gracilis, Periploca nigrescens, Senegalia ataxacantha* and *Smilax anceps* showed no affinity to colonize any particular host species while *Chasmanthera dependens* showed more affinity for *Milletia thonningii* ($P = 0.02$); *Combretum* sp. had more preference for *Ficus mucuso* ($P = 0.002$); and *Motandra guineensis* had more affinity for *Celtis zenkeri* ($P = 0.003$) (Table 2). Only *B. campanulata* and *S. anceps* infestation showed no preference for the girth size of host species. *S. ataxacantha* ($P = 0.04$), *C. dependens* ($P < 0.001$), *Combretum* sp. ($P < 0.001$), *M. benthamianum* ($P = 0.02$), *O. gracilis* ($P = 0.001$) and *P. nigrescens* ($P = 0.001$) preferred hosts with small girth sizes while *M. guineensis* was the only liana species that showed affinity to infest host species with both large ($P = 0.01$) and small girth sizes ($P < 0.001$) (Table 3). Using the successional status as factor, *B. campanulata, C. dependens, M. benthamianum, O. gracilis, P. nigrescens* and *S. anceps* showed no preference of colonizing any successional host species while *S. ataxacantha* preferred both late- ($P < 0.001$) and early-successional host species ($P < 0.001$), *Combretum* sp. preferred both early- ($P = 0.03$) and late-successional hosts ($P = 0.001$). However, *M. guineensis* preferred the late-successional host species ($P = 0.01$) (Table 4).
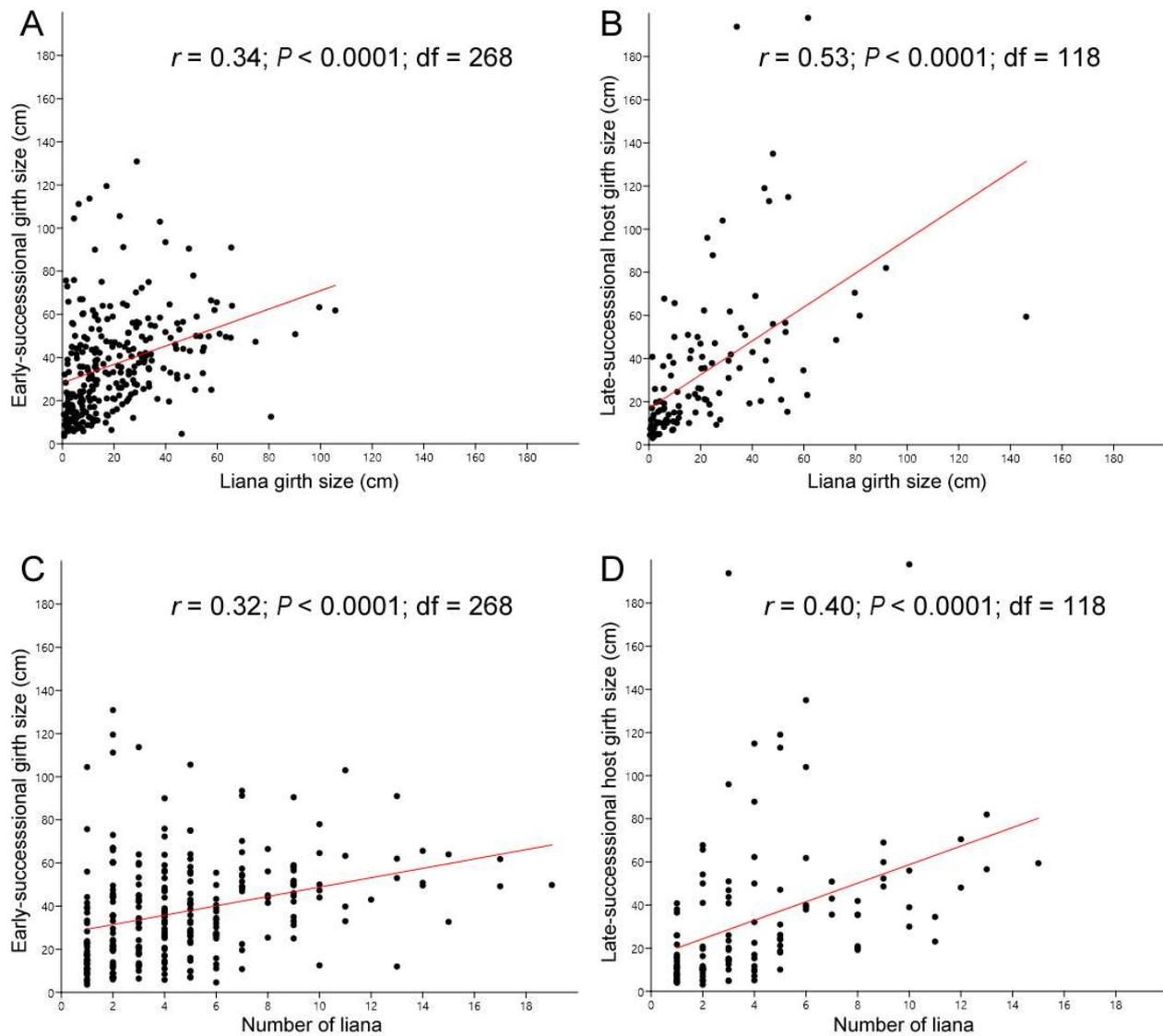
Fig. 2. The liana growth with successional stage in a regenerating forest in Nigeria. **A**. Relationship between early-successional host girth size and liana girth size. **B**. Relationship between late-successional host girth size and liana girth size. **C**. Relationship between early-successional host girth size and number of lianas. **D**. Relationship between late-successional host girth size and number of lianas

DISCUSSION

A part of the forest in the Biological Gardens of the Obafemi Awolowo University, Ile-Ife was damaged by surface fire three decades ago and is still undergoing some stages of regeneration as shown by the fewer number of late-successional host species compared to the early-successional host species. Liana infestation in the regenerating forest of the Biological Gardens of Obafemi Awolowo University, Ile-Ife had been found to increase with the abundance of host tree species, not considering the successional status of the host species (Muoghalu and Okeesan, 2005; Uwalaka and Muoghalu, 2017), although Uwalaka *et al*. (2018) had earlier reported a dominance of early-successional trees over late-successional trees in the

forest. The fewer number of late-successional host species compared to early-successional hosts is in contrast to the findings of Kirika *et al.* (2010) who reported a far higher number of late-successional tree species than early-successional tree species in the tropical forests of Budongo and Mabira in Uganda, and Kakamega in Kenya, respectively. This indicates that the forest used in this study is still young and undergoing regeneration. This is not surprising given the reduced canopy cover (although not considered in this study) as well as high liana infestation in the forest since it has been suggested that early-successional species can out-compete late-successional species, provided the canopy cover in the sites is open (Terborgh *et al.,* 2008; Kirika *et al.,* 2010).

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Table 1: Plant species, habit, successional status and frequency of occurrence in a regenerating secondary forest in Nigeria.

Plant species	Family	Habit	Successional status	Frequency
Abrus precatorius Linn.	Fabaceae	Liana	Early	+
Adenia lobata (Jacq.) Engl.	Passifloraceae	Liana	Early	+
Agelaea obliqua (P. Beauv.) Baill.	Connaraceae	Liana	Early	++
Alafia barteri Oliv.	Apocynaceae	Liana	Early	++
Albizia sp.	Fabaceae	Tree	Early	+
Albizia zygia (DC.) J.F. Macbr.	Fabaceae	Tree	Early	++++
Alchornea laxiflora (Benth.) Pax & K. Hoffin.	Euphorbiaceae	Shrub	Early	++
Alstonia boonei De Wild.	Apocynaceae	Tree	Late	++
Antiaris africana Engl.	Moraceae	Tree	Early	+
Aristolochia ringens Vahl	Aristolochiaceae	Liana	Early	++
Baissea campanulata (K. Schum.) de Kruif	Apocynaceae	Liana	Early	++++++
Baphia nitida Load.	Fabaceae	Shrub	Late	+++++
Blighia sapida Konig	Sapindaceae	Tree	Early	++
Blighia sp.	Sapindaceae	Tree	Early	+
Blighia unijugata Bak.	Sapindaceae	Tree	Late	+
Bombax buonopozense P. Beauv.	Bombacaceae	Tree	Early	+++
Bridelia ferruginea Benth.	Euphorbiaceae	Shrub	Early	+
Bridelia micrantha (Hochst.) Baill.	Euphorbiaceae	Shrub	Early	+
Canarium schweinfurthii Engl.	Burseraceae	Tree	Late	+
Canthium vulgare (K.Schum.) Bullock.	Rubiaceae	Tree	Early	++
Carpolobia lutea G. Don	Polygalaceae	Shrub	-	+++
Celtis mildbraedii Engl.	Ulmaceae	Tree	Late	++++
Celtis sp.	Ulmaceae	Tree	Early	+
Celtis zenkeri Engl.	Ulmaceae	Tree	Early	++++++
Chasmanthera dependens Hochst.	Menispermaceae	Liana	Early	+++++
Chlamydocarya sp.	Icacinaceae	Liana	Early	++
Chassalia kolly (Schumach.) Hepper	Rubiaceae	Shrub	-	++
Chrysophyllum albidum G. Don	Sapotaceae	Tree	Late	++
Cissus petiolata Hook. f.	Vitaceae	Liana	Early	+++
Cleistopholis patens (Benth.) Engl. & Diels	Annonaceae	Tree	Early	+
Cnestis ferruginea DC.	Connaraceae	Liana	Late	++
Cola acuminata (P. Beauv.) Schott & Endl.	Sterculiaceae	Tree	-	+
Cola hispida Brenan & Keay	Sterculiaceae	Tree	Early	+
Cola millenii K. Schum	Sterculiaceae	Tree	Early	+++++
Cola nitida (Vent.) Schott & Endl.	Sterculiaceae	Tree	Late	+
Cola sp.	Sterculiaceae	Tree	Early	+++
Combretum racemosum P. Beauv.	Combretaceae	Liana	Late	+++
Combretum sp.	Combretaceae	Liana	Early	++++++
Dalbergia lactea Vatke	Fabaceae	Liana	Early	+++
Dialium guineense Willd.	Fabaceae	Tree	Late	+
Dracaena manii Bak.	Dracaenaceae	Tree	Early	++
Elaeis guineensis Jacq.	Aracaceae	Tree	Early	++
Ficus exasperata Vahl	Moraceae	Tree	Early	++
Ficus mucuso Welwi. ex Ficalho	Moraceae	Tree	Early	++++
Ficus sp.	Moraceae	Tree	Early	++
Ficus sur Forssk.	Moraceae	Tree	Early	+
Flabellaria paniculata Cav.	Malpighiaceae	Liana	Early	+
Friesodielsia gracilis (Hook. f.) Steenis	Annonaceae	Liana	-	+
Funtumia africana (Benth.) Stapf	Apocynaceae	Tree	Early	+
Funtumia elastica (Preuss) Stapf	Apocynaceae	Tree	Early	++++
Garcinia kola Heckel	Clusiaceae	Tree	Late	+
Glyphaea brevis (Spreng.) Monachino	Tiliaceae	Shrub	Late	+
Grewia carpinifolia Juss.	Tiliaceae	Liana	Early	+++
Hippocratea sp.	Celastraceae	Liana	Early	+++
Hylodendron gabunense Taub.	Fabaceae	Tree	Early	+
Jateorhiza macrantha (Hook. f.) Exell & Mendonca	Menispermaceae	Liana	Early	++++
Keetia vulgae Oliv.	Rubiaceae	Tree	-	+
Landolphia dulcis (Sabine) Pichon	Apocynaceae	Liana	Late	++
Lannea welwitschii (Hiern) Engl.	Anarcadiaceae	Tree	Early	+++

Plant species	Family	Habit	Successional status	Frequency
Lecaniodiscus cupanioides Planch. ex Benth.	Sapindaceae	Tree	Late	++++++
Leptoderris micrantha Dunn	Fabaceae	Liana	Early	+++
Leptoderris sp.	Fabaceae	Liana	Early	+
Lonchocarpus cyanescens (Schum. & Thonn.) Benth.	Fabaceae	Liana	Early	+
Maesopsis eminii Engl.	Rhamnaceae	Tree	Early	+
Malacantha alnifolia (Bak.) Pierre	Sapotaceae	Shrub	Early	+
Mallotus mildbraedii Chev.	Euphorbiaceae	Tree	-	+
Mallotus oppositifolus (Geisel.) Mull. Arg	Euphorbiaceae	Tree	Late	+
Mallotus subulata Mull. Arg	Euphorbiaceae	Tree	-	+
Manihot glaziovii Mull. Arg	Euphorbiaceae	Tree	Early	++
Margaritaria discoidea (Baill.) G.L. Webster	Euphorbiaceae	Tree	Early	+
Mezoneuron benthamianum Baill.	Fabaceae	Liana	Early	+++++
Microdesmis puberula Hook. f. ex planch.	Pandaceae	Shrub	Late	+++++
Milletia thonningii (Schum. & Thonn.) Bak.	Fabaceae	Tree	-	+
Mondia whitei (Hook. f.) Skeels	Apocynaceae	Liana	Late	++
Monodora tenuifolia Benth.	Annonaceae	Tree	Late	++
Morinda lucida Benth.	Moraceae	Tree	-	+
Morus mesozygia Stapf	Moraceae	Tree	Early	+
Motandra guineensis (Thonning) A. DC.	Apocynaceae	Liana	Late	++++++
Myrianthus arboreus P. Beauv.	Moraceae	Tree	Late	++++
Napoleona imperialis P. Beauv.	Lecythidaceae	Tree	-	+
Napoleona vogelii Hook. & Planch	Lecythidaceae	Tree	Late	+
Neuropeltis acuminata (P. Beauv.) Benth.	Convolvulaceae	Liana	Late	+
Newbouldia laevis (P. Beauv.) Seemann. ex Bureau	Bignoniaceae	Tree	Early	+
Olax subcorpioides Oliv.	Olacaceae	Tree	Late	+++
Oncinotis gracilis Stapf	Apocynaceae	Liana	Early	++++
Oncoba sp.	Flacourtiaceae	Liana	-	+
Pergularia daemia (Forsk.) Chiov.	Apocynaceae	Liana	Early	+
Periploca nigrescens Afzel.	Periplocaceae	Liana	Early	+++
Pierreodendron africanum (Hook. f.) Little	Simaroubaceae	Tree	Early	+
Piptadenastrum africanum (Hook. f.) Brenan	Fabaceae	Tree	Early	+
Pterocarpus sp.	Fabaceae	Tree	-	++
Pycnanthus angolensis (Welw.) Warb.	Myristicaceae	Tree	Early	++++
Pyrenacantha staudtii (Engl.) Engl.	Icacinaceae	Liana	Early	++
Rauvolfia vomitoria Afzel.	Apocynaceae	Shrub	Early	++
Ricinodendron heudelotii (Baill.) Pierre ex Pax.	Euphorbiaceae	Tree	Late	++++
Rytigynia sp.	Rubiaceae	Liana	Early	+
Salacia sp.	Celastraceae	Liana	Early	+
Secamone sp.	Asclepiadaceae	Liana	Early	++
Senegalia ataxacantha DC.	Fabaceae	Liana	Early	+++++
Sherbournia bignoniifolia (Welw.) Hua	Rubiaceae	Liana	Early	+
Simicratea welwitschii (Oliv.) N. Halle	Celastraceae	Liana	Early	+++
Smilax anceps Willd.	Smilacaceae	Liana	Early	++++
Spondias mombin Linn.	Anarcadiaceae	Tree	-	+
Sterculia tragacantha Lindl.	Sterculiaceae	Tree	Early	+++
Strombosia pustulata Oliv.	Olacaceae	Tree	Late	+
Tacazzea apiculata Oliv.	Apocynaceae	Liana	Late	+
Tabernaemontana pachysiphon Stapf	Apocynaceae	Tree	Late	++
Terminalia superba Engl. & Diels	Combretaceae	Tree	Early	+
Tetracera alnifolia Willd.	Dilienaceae	Liana	Late	++
Tetrapleura tetraptera (Schum. & Thonn.) Taub.	Fabaceae	Tree	Late	+
Trichilia heudelotii Planch. ex Oliv.	Meliaceae	Tree	Early	++
Trichilia prieuriana	Meliaceae	Tree	Early	+++++
Trichilia sp.	Meliaceae	Tree	Early	+
Triclisia subcordata Oliv.	Menispermaceae	Liana	Early	++
Trilepisium madagascariensis DC	Moraceae	Tree	Early	+++
Triplochiton scleroxylon K. Schum.	Sterculiaceae	Tree	-	++
Unidentified	Unidentified	Liana	-	+++
Voacanga africana Stapf	Apocynaceae	Tree	Early	++
Zanthoxylum sp Linn.	Rutaceae	Tree	Early	+

Table 2: Liana species, host preference and colonization probability of dominant host species in a regenerating secondary forest in Nigeria.

Liana species	Host preference	Colonization (χ^2)
Baissea campanulata	-	-
Chasmanthera dependens	*Celtis zenkeri*	4.309*
	Ficus mucuso	4.816*
	Milletia thonningii	5.314*
Combretum sp.	*Albizia zygea*	4.699*
	Cola millenii	5.355*
	Celtis zenkeri	3.995*
	Ficus mucuso	9.517*
	Funtumia elastica	6.356**
	Lecaniodiscus cupanioides	3.889*
	Manihot glaziovii	8.082**
	Milletia thonningii	6.515**
	Pycnanthus angolensis	6.134**
	Ricinodendron heudelotii	5.287*
	Sterculia tragacantha	7.726**
	Trichilia heudelotii	8.454**
Mezoneuron benthamianum	-	-
Motandra guineensis	*Cola millenii*	5.306*
	Celtis zenkeri	9.065**
	Sterculia tragacantha	7.267**
Oncinotis gracilis	-	-
Periploca nigrescens	-	-
Senegalia ataxacantha	-	-
Smilax anceps	-	-

Key: * values are significant at $p<0.05$; ** values are significant at $p<0.01$

Table 3: Liana colonization of host species based on girth size class category in a regenerating secondary forest in Nigeria.

Liana	Girth size category	LR test	*p*-value	*df*	OR for infestation
Baissea campanulata	Girth size	1.279	0.53	2	
	Small	0.651	0.42	1	0.744
	Big	0.985	0.32	1	0.52
Chasmanthera dependens	Girth size	17.169	<0.0001	2	
	Small	16.892	<0.0001	1	0.313
	Big	2.19	0.14	1	0.54
Combretum sp.	Girth size	37.361	<0.0001	2	
	Small	34.306	<0.0001	1	0.245
	Big	1.435	0.23	1	0.667
Mezoneuron benthanianum	Girth size	6.942	0.03	2	
	Small	5.412	0.02	1	0.335
	Big	0.016	0.90	1	1.074
Motandra guineensis	Girth size	26.285	<0.0001	2	
	Small	24.742	<0.0001	1	0.316
	Big	6.475	0.01	1	0.42
Oncinotis gracilis	Girth size	13.816	0.001	2	
	Small	10.547	0.001	1	0.151
	Big	0.193	0.66	1	0.769
Periploca nigrescens	Girth size	12.361	0.002	2	
	Small	11.366	0.001	1	0.239
	Big	2.114	0.15	1	0.39
Senegalia ataxacantha	Girth size	5.151	0.08	2	
	Small	4.145	0.04	1	0.495
	Big	2.424	0.12	1	0.366
Smilax anceps	Girth size	4.123	0.13	2	
	Small	3.368	0.07	1	0.409
	Big	0.002	0.97	1	1.026

LR – Likelihood ratio of infestation; OR – Odds-ratio of infestation

Table 4: Liana colonization of host species based on successional status class category in a regenerating secondary forest in Nigeria.

Liana	Host successional status category	LR test	*p*-value	*df*	OR for infestation
Baissea campanulata	Successional status	0.356	0.84	2	
	Early	0.20	0.66	1	1.603
	Late	0.287	0.59	1	1.772
Chasmanthera dependens	Successional status	0.164	0.92	2	
	Early	0.129	0.72	1	1.462
	Late	0.148	0.70	1	1.512
Combretum sp.	Successional status	12.131	0.002	2	
	Early	4.787	0.03	1	0.315
	Late	10.814	0.001	1	0.152
Mezoneuron benthanianum	Successional status	3.589	0.17	2	
	Early	0.682	0.41	1	0.650
	Late	2.158	0.14	1	0.453
Motandra guineensis	Successional status	6.584	0.04	2	
	Early	2.708	0.10	1	0.324
	Late	6.448	0.01	1	0.126
Oncinotis gracilis	Successional status	3.740	0.15	2	
	Early	0.635	0.43	1	1.513
	Late	0.002	0.96	1	1.025
Periploca nigrescens	Successional status	1.438	0.49	2	
	Early	1.766	0.18	1	0.34
	Late	1.423	0.23	1	0.363
Senegalia ataxacantha	Successional status	1.903	0.39	2	
	Early	0.00001	0.99	1	9.9E7
	Late	0.00001	0.99	1	8.4E7
Smilax anceps	Successional status	0.891	0.64	2	
	Early	0.07	0.79	1	1.324
	Late	0.01	0.92	1	0.896

LR – Likelihood ratio of infestation; OR – Odds-ratio of infestation

Previous studies in the Biological Gardens of the Obafemi Awolowo University, Ile-Ife had documented the dynamics, abundance and relationship of climbers with host species in the forest, whereas this study examined the colonization probability of lianas in the forest. *M. guineensis* had been reported in previous studies to be the most abundant liana species in the forest (Muoghalu and Okeesan, 2005; Uwalaka and Muoghalu, 2017; Uwalaka *et al*., 2020). This study showed that this liana not only preferentially infested some host species but was also the only liana in the forest that preferred host species with both large and small girth sizes. This could explain why it is increasing in abundance in the forest because as the host girth sizes increase and other lianas are being shed, *M. guineensis* which has the ability to colonize the large trees increases in abundance. Moreover, the ability of *M. guineensis* to dominate both regenerating and old-growth forests had been documented by Wheeler *et al.* (2016). This means that lianas such as *M. guineensis* that colonize trees with large trunks are likely to persist throughout forest succession (Barry *et al.*, 2015). Using successional status as a factor, the infestation of lianas was more related to the presence of late-successional host species because most of the dominant liana species (*S. ataxacantha, Combretum* sp. and *M. guineensis*) had more preference for late-successional host tree species.

Since the late-successional host species are characteristic of forests undergoing repairs, their heavy infestation will likely lead to inhibition of forest regeneration, although they might survive the infestation by outliving the lianas (Ingwell *et al*., 2010). The abundance of more early-successional host species than the late-successional host species in the forest played a key role in the infestation of host species in the forest by a few other lianas (e.g. *C. dependens, Combretum* sp. and *M. guineensis*). This is expected since forest clearance promotes the emergence of lianas which use the available early-successional tree species as support to reach top strata to capture adequate sunlight. The preference of early-successional host species by lianas could alter the successional process currently going on in the forest as a result of the mechanical stress they will cause the host species, which might in turn lead to their mortality (Schnitzer and Bongers, 2002; Schnitzer and Carson, 2010). With past studies suggesting that lianas prefer slow-growing late-successional tree species but hardly have any effect on the early-successional pioneer tree species (Schnitzer *et al*., 2000; Laurance *et al*., 2001), the findings of this study further agree with the assertion of Barry *et al.* (2015) who opined that early-successional trees are more prone to liana infestation since lianas have the ability to alter successional dynamics. This shows that there were

different preferences for colonization of host species by lianas studied in the forest. It had further been suggested that gaps do not favour a high abundance of late-successional species (Schnitzer and Carson, 2001). The forest could most likely still be at its early stage of recovery and the occurrence of the few late-successional host species could be an indication that there would be a replacement dynamics whereby the few existing late-successional host species would develop to replace the presently more diverse early-successional host species. This is in agreement with the assertion of Meng *et al.* (2011) that late-successional species that are present during the earlier stage of succession can potentially replace early-successional species as succession progresses. This, they opined, is critical for forest management since it gives forest managers clues on which forest species to protect during succession. Therefore, it is likely that as the forest closes and passes through different seral stages, liana abundance and infestation would also increase since mature forests are made up of more late-successional woody species (Chokkalingam and De Jong, 2001). The lianas showed no association with the successional dynamics of host species. This could be because the lianas are host-specific (Pe´rez-Salicrup *et al.*, 2001) which favoured the presence of lianas as a result of the presence of more early-successional host species than the late-successional host species. Even though the early-successional trees hosted more lianas than the late-successional trees, they still had fewer liana infestation compared to the late-successional trees.

Therefore, the conservation of late-successional tree species in the forest is very important, given the rising concern for biodiversity conservation in mitigating climate change. The importance of late-successional tree species in this respect cannot be overemphasized since they are known to live longer, acquire more biomass and sequester more carbon than the early-successional tree species (Lang and Knight, 1983; Guariguata and Ostertag, 2001; Sheil, 2001). It is more likely that the host species in the study area are still in the initial floristic composition stage judging from the representation of the late- and early-successional host species in the floristic inventory.

Late-successional host species are gradually replacing the early-successional hosts in the forest. This makes it more necessary to monitor the regeneration process in the forest closely. Furthermore, it would likely take the secondary forest a long time to reach its next seral stage because all the dominant lianas are early-successional species that would impede the regeneration of the tree species in the forest unless special silvicultural steps such as liana removal from tree species are put in place.

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