Available online at www.elixirpublishers.com (Elixir International Journal)

Environment and Forestry

Elixir Environment and Forestry 183 (2024) 57094 - 57102

ISSN: 2229-712X

# Colonisation of Trees by Lianas in Tropical Forests in the Yoko Forest Reserve (Tshopo, DR Congo)

Mbula Mekando Innocent[1]*, Lisingo Wa Lisingo Janvier[2], Mumbanza Mundondo Francis[3], Makelele Ahanamungu Isaac[4] and Ewango Ekokinya Corneille[1]

[1]Faculty of Management of Renewable Natural Resources, University of Kisangani
[2]Faculty of Sciences, University of Kisangani
[3]Department of Environmental Sciences, University of Kinshasa
[4]Department of Biology, Official University of Bukavu

ARTICLE INFO

**Article history:**
Received: 9 November 2023;
Received in revised form:
20 December 2023;
Accepted: 8 January 2024;

**Keywords**
Colonisation,
Lianas,
Tropical forests,
Yoko.

## ABSTRACT

A study was carried out on the colonisation of trees by lianas in tropical forests in the Yoko forest reserve (Tshopo, DR Congo). Observations focused on the main parameters (structure and diversity) of the lianas in order to determine the relationship patterns that exist between the host tree and the liana at our site. Inventories of stems with a diameter at breast height (dbh) ≥ 10 cm for trees and (dbh) ≥ 1 cm for woody lianas hosted on supports were carried out in fifteen 40 m × 40 m plots (totalling 2.4 hectares) set up in the tropical forests of the Yoko forest reserve. Creeper attachment mechanisms were observed in the field and supplemented by basic literature, and the number of creepers climbing each tree trunk was counted- Overall, 57 liana species were inventoried, and 41 genera and 23 families were recorded. The liana species best represented in terms of IVI value are: Manniophyton fulvum (40.02%), Millettia duchesnei (21.04%), Strychnos camptoneura (17.57%), Dichapetalum mundense (14.97%), Landolphia parvifolia (13.91%) and Dalhousiea africana (12.37%). The most abundant families were Euphorbiaceae (20.6%), Dichapetalaceae (13.31%), Fabaceae (11.86%), Connaraceae (11.06%), Aponaceae (10.26%) and Rubiaceae (8.25%). A total of 1,247 individuals of lianas were inventoried in all fifteen plots, giving an average density of 519 stems/ha. They represent a basal area of 3.79 $m^2$/ha. Most of the lianas are voluble and climb their supports (49.88%), followed by sarmentose lianas (21.84%). A total of 1,177 trees were surveyed, 381 of which (32.3%) had lianas on their trunks. The proportion of infested trees differed according to diameter category, with medium and large trees having more lianas on their trunks and a higher total basal area of lianas than small trees. Trees with thorny, rough bark are more likely to support vines.Trees with thorny bark are positively associated with lianas with tendrils, and trees with rough bark are positively associated with lianas with hooks. Trees 40 cm and taller were positively associated with lianas with hook and sarment modes of attachment.

## Introduction

Creepers are abundant and diverse in tropical forests (Schnitzer *et al.*, 2002). They account for 25 to 40% of woody stems and more than 25% of woody species (Schnitzer *et al.*, 2011).

As well as making a significant contribution to maintaining the diversity of tropical forests (Bongers *et al.*, 2005), lianas influence the structure of tropical forest ecosystems (Kusumoto *et al.*, 2013) by playing a key role in the dynamics of these forests (Ledo *et al.*, 2016; Tymen *et al.*, 2016; Rahman *et al.*, 2020).

At various spatial and temporal scales, liana abundance and distribution are determined on the one hand by biotic processes or factors, including differences in intrinsic life cycle, forest structure and host tree availability, and on the other hand by abiotic factors, such as environmental variables and disturbances to forest ecosystems. Moreover, lianas are not generally distributed randomly in their carrier trees (Campbell *et al.*, 1993), and the characteristics of the trees ensure their resistance or susceptibility to colonisation. Several studies have reported that host tree characteristics are important in determining liana association (Putz, 1984). These include the possession of rapid diameter growth rates, flexible stems, long branchless shafts, variation in bark texture and variation in the rate at which bark is shed (Putz, 1980; Balfour *et al.*, 1993; Carsten *et al.*, 2002).

Although limited by their dependence on a support structure to access light, lianas have repeatedly developed climbing mechanisms and physiological traits, essential functional traits that structure their communities (Bell *et al.*, 1988; Hegarty *et al.*, 1991; Kasumoto *et al.*, 2013). The growth of lianas on canopy trees is a natural phenomenon, however, the term infestation or colonisation is frequently used to describe the load of lianas on trees. Creepers can

**Tele: +243 859272855**
**E-mail address: innoncent.mbula@unikis.ac.cd**

infest a host tree by climbing the trunk, growing with the tree and continuing to develop in the crown of the same host tree or by growing laterally into the tree crown from a neighbouring tree (Putz 1984; Campbell *et al*., 1993).

It is worth noting that, in recent years, several studies on lianas have been carried out due to the growing awareness of the role lianas play in tropical forest ecosystems (Schnitzer, 2005; Gerwing *et al*., 2006), however, there is little information on the functional diversity of lianas (Odell, 2018) and on the interaction of lianas with other life forms in African tropical forests (Mumbanza, 2021).

In view of the above, it is now imperative that we improve our understanding of lianas as an important component of tropical forests. To this end, we need to determine the tree-liana relationship in order to understand the ecology and management strategies of tropical forests.

The main objective of this work is to determine the relationship patterns between lianas and trees in tropical forests at the Yoko Forest Reserve. To achieve this, the following specific objectives were pursued:

- To assess the structure and diversity of lianas found in the target forests
- Determine the relationship between tree size and liana characteristics (density, for example);
- Demonstrate the relationship between tree characteristics (e.g. bark types) and lianas (e.g. attachment mechanisms).

## Materials and Methods

### Study site

The study was conducted around the Yoko forest reserve (N 00° 19′12″; E 25° 17′43″), located in the Ubundu territory, Tshopo province, DR Congo.

The Yoko forest reserve is bounded to the north by the town of Kisangani and disturbed forests, to the south and east by the Biaro river, and to the west by priority road 410 (Kisangani-Ubundu road), along which it extends from kilometre points 21 to 38. It is irrigated by the Yoko river, which divides it into two blocks: the northern block with 3,370 ha and the southern block with 3,605 ha, giving a total area of 6,975 ha at an average altitude of 400 m. The figure below shows the location of the study area in relation to the city of Kisangani.

As the Yoko forest reserve is located close to the city of Kisangani, we attribute the latter's climatic characteristics to it. According to climatological data for the years 2013-2022 for the city of Kisangani, the average annual rainfall is 1,731 mm and the average annual air temperature is 25.18°C, with little seasonal variability. The region's climate is therefore described as an Af-type tropical rainforest climate according to the revised Köppen-Geiger classification (Peel *et al*., 2007). The figure below shows the umbrothermal curve for the town of Kisangani

In addition, the Yoko Forest Reserve has a ferralitic soil, mainly composed of quartz sand mixed with a little kaolinitic clay and hydrated iron oxides (Van Ranst *et al*., 2010).

Two main types of vegetation cover the Kisangani forest region: dense moist forests on dry land, which include evergreen forests and semi-deciduous forests, and forests on hydro-morphic soils (Lebrun *et al*., 1954). Within these forests and as a result of human activities such as slash-and-burn agriculture, logging, cutting and charcoal-making, gathering, hunting, fishing and livestock rearing, there are secondary or reconstituting formations and agricultural complexes (Boyemba, 2011).

## Methods

### Sampling

In the forests of the Yoko forest reserve, we used machetes and compasses to set up permanent square sample plots measuring 40 m x 40 m in fifteen replicates. To facilitate the woody species inventories, each 40 m x 40 m plot was divided into 4 sub-plots of 20 m × 20 m.

### Data collection

We carried out an inventory of trees according to a standard international protocol for tropical forest inventories (Malhi *et al*., 2002) and we also carried out an inventory of lianas according to the protocol established by Gerwing *et al*. (2006) and supplemented by Schnitzer *et al*. (2008). In each subplot considered as a sampling unit (n = 60), all tree stems with a diameter ≥ 10 cm were identified and measured using a circumferential tape, while all liana stems (woody lianas on supports) with a diameter ≥ 1 cm were identified and measured using callipers and circumferential tape, generally at a distance of 1.3 m along the stem from the last rooting position. Herbaceous lianas, hemi-epiphytes, rattans and climbing Poaceae, Araceae, Arecaceae and Cyclanthaceae were excluded from the sampling. In general, trees and lianas were identified in the field by combining their biological characteristics (Lejoly *et al*., 2010). We counted the number of lianas climbing each tree trunk. The family nomenclature used is based on Angiosperm Phylogeny Group (APG III, 2009), while the species nomenclature follows Lebrun *et al*, (1991-1997).

Climbing mechanisms were assessed in the field and using the available literature. Thus, the climbing mechanisms of all liana species were classified into the following categories: (1) sarmentose lianas (attach themselves by the arrangement of their lateral branches or by sudden bends in their stems), (2) hook lianas (the stems are supported by short, curved and/or thickened branches), (3) vines with adhesive roots (they are anchored by adventitious roots applied to the support), (4) vines with tendrils (they are wrapped around the support by tendrils), (5) voluble vines (they wrap themselves around the branches of the support).

We also attributed bark texture to each tree species, either by direct observations in the field and/or by using data available in the literature (Vivien *et al*., 1985; Vivien *et al*., 2011). With the exception of palms (Calamus sp, Elaeis guineensis and Raphia laurentii) which have no bark as such, but which show traces of leaf insertion, the texture of tree bark has been classified into four categories following Campbell *et al*, (1993): (1) smooth, (2) slightly rough (the surface being any combination of small dimples, scales or shallow cracks), (3) rough (the surface being large scales or cracks), and (4) trees with thorns.

In each 20 × 20 m2 subplot, trees were classified as small stems (10 cm ≥ Dhp < 20 cm), medium (20 cm ≥ Dhp < 40 cm) and large stems (Dhp ≥ 40 cm) (MECNT, 2007); and lianas as small (1cm≥ Dhp ≤ 3 cm), medium (3 cm > Dhp ≤ 6 cm) or large (Dhp > 6 cm) (Vivek *et al*., 2015).

### Data analysis methods

### Floristic characterisation index

Importance values were determined for each species recorded on the subplot on the basis of a formula from Curtis *et al*, (1951) and Cottam *et al*, (1956) which use the summation of density, dominance and relative frequency.

### Creeper infestation

The host-tree load is calculated as the total number of climbing lianas divided by the total number of trees colonised per site, and the colonising liana load is calculated in exactly the same way (Kuzee *et al*., 2005). The climbing liana infestation rate is the ratio of the total number of liana-bearing tree stems divided by the total number of trees in the site (Pérez-Salicrup *et al*., 2001).

### Statistical processing of the data

We used the chi-square test of independence to explore the relationships between, on the one hand, the diameter classes of the trees (10-19.9 cm, 20-39.9 cm and > 40 cm) and the presence/absence or attachment mechanisms of the lianas on the trees and, on the other hand, the type of bark on the trees (Spiny, Smooth, Slightly rough, Rough) and the presence/absence or attachment mechanisms of the lianas on the trees. We also explored the pattern of distribution of the number of creepers per tree by comparing the observed frequency distribution of trees infested with different numbers of creepers with the expected Poisson distribution, using the chi-squared goodness-of-fit test (Sokal *et al*., 1995), and calculated the ratio of variance to mean (also called the coefficient of dispersion). If this ratio is equal to one, it indicates that the counts come from a Poisson distribution. If this ratio is greater than one, this would correspond to an agglomerated distribution, while a ratio of less than one would suggest a regular distribution of individuals in the population (Krebs, 1999; Pretzsch, 2010).

We set up two generalised linear mixed-effects models to determine the effect of tree diameter on the number of lianas and the presence/absence of lianas on trees, respectively.

Model 1: NumberLianas ~ log(DHP) + (1 | Families/Genera/Species) + (1 | Plots)

Model 2: PresAbsLianas ~ log(DHP) + (1 | Families/Genera/Species) + (1 | Plots)

In each model, we included the plots in which the trees were located as a random effect to control for any spatial autocorrelation. We also included phylogeny in these models as another random effect to control for possible interdependence between tree species (Mumbanza, 2021).

We used R 4.0.3 (R core Team, 2020) to carry out all these analyses. We used the R package ggstatsplot (Patil, 2021) to perform the independence and chi-square goodness-of-fit tests and the R package lme4 (Bates *et al*., 2015) to perform the generalized linear mixed-effects analyses. For the latter analyses, we assessed the validity of the models using the R package DHARMa (Hartig, 2018).

To decide on the significance of a test, we referred to the value of the statistic (p-value) provided by the R software at the end of each analysis:

- if p-value ≥ 5%: non-significant difference;
- if p-value<5%, <1% and <0.1%: significant difference (*), very significant difference (**) and highly significant difference (***), respectively.

## Results

### Floristic and structural characteristics

Overall, 57 liana species were inventoried (57 species in the small liana category, 28 species in the medium liana category and 16 species in the large liana category), with 41 genera and 23 families recorded. There are 6 species with IVI values above 10%, in ascending order: Manniophyton fulvum (40.02%), Millettia duchesnei (21.04%), Strychnos camptoneura (17.57%), Dichapetalum mundense (14.97%), Landolphia parvifolia (13.91%) and Dalhousiea africana (12.37%). The most abundant families are Euphorbiaceae (20.6%), Dichapetalaceae (13.31%), Fabaceae (11.86%), Connaraceae (11.06%), Aponaceae (10.26%) and Rubiaceae (8.25%). The results of this study indicate that a total of 1,247 liana individuals were inventoried in all fifteen plots, giving an average density of 519 stems/ha. They represent a basal area of 3.79 m2/ha. It should also be noted that the first class, with a diameter of 1 to 3 cm, contains the largest number of liana stems, with 1,056 stems (representing 84.68%). Five types of liana attachment mechanism were encountered: hook, adhesive root, voluble, tendril and sarmentose liana. Most lianas are voluble and climb their supports (49.88%), followed by sarmentose lianas (21.84%), hook lianas (14.83%), tendril lianas (13.04%) and lianas with adhesive roots (0.41%). We also inventoried a total of 1,177 trees, 381 of which had vines on their trunks (32.3%). The number of lianas on trees in tropical forests in the Yoko forest reserve has a variance/mean ratio of 3.05.

### Structural clustering in host-tree liana interaction

The results of this study show (Figure 3) that there is a highly significant positive association between tree diameter and the presence of lianas on trees (p-value < 0.0001***), and between tree diameter and the number of lianas on trees (p-value < 0.0001***).

Furthermore, the chi-square test of independence indicates that there is less chance of encountering trees bearing lianas in the 10-19.9 cm diameter category (Figure 4).

### Functional grouping in the tree host - liana interaction

The chi-square test of independence indicates that there is a link between tree bark type and the presence (absence) of lianas on the trees ($\chi2 = 37.48$; ddl = 3; p-value < 0.0001***). Trees with smooth (Li) and slightly rough (Lru) bark were less likely to have lianas than trees with spiny (Ep) and rough (Ru) bark (Figure 5).

In addition, there was also a link between tree bark type and the attachment mechanisms of lianas infesting the trees ($\chi2 = 38.35$; ddl = 9; p-value <0.0001***). Pearson's residual values show that trees with thorny bark (Ep) are positively associated with lianas with the tendril (Vr) attachment mode. Similarly, trees with rough bark (Ru) are positively associated with lianas in the hook attachment mode (Cr), while trees with slightly rough bark (Lru) are negatively associated with lianas in the hook attachment mode (Cr). In addition, the chi-square test of independence still indicates that there is a link between tree size and the attachment mechanisms of the lianas that infest these trees ($\chi2 = 24.33$; ddl = 6; p-value = 0.0004**). Pearson's residual values show that trees 40 cm in height and above are positively associated with lianas with hooked (Cr) and sarmentose (Sr) attachment modes, whereas trees between 20 and 39.9 cm in height are negatively associated with lianas with sarmentose (Sr) attachment mode (Figure 6).

## Discussions

### Floristic and structural characteristics

The results of this study in terms of species richness (57 species), density (519 stems/ha) and basal area (0.75 $m^2$/ha) are inferior to those of other studies carried out in Africa or elsewhere (Gentry, 1991; DeWalt *et al*., 2000; Laurance *et al*., 2001; Schnitzer *et al*., 2002). Patterns of liana recruitment, growth and mortality and the ability of tree species to avoid or accept liana infestation have played a role in variation in structure and floristic richness. Fast-growing tree species were found to be less affected by lianas (van der Heijden *et al*., 2008; Visser *et al*., 2018a; Visser *et al*., 2018b). However, the ability to grow rapidly does not act in isolation to confer a certain level of protection on trees against creeper infestation. In fact, this tree characteristic is often associated with several others, such as larger leaves and branchless trunks (van der Heijden *et al*., 2008) or the characteristics of its bark (Perez-Salicrup *et al*., 2000;

Campanello *et al*., 2007; Addo-Fordjour *et al*., 2012; Wright *et al*., 2015). Consequently, it is probably the combined effect of these morphological and functional characteristics that underlies the low floristic richness of the lianas in this study.

The Dichapetalum genus of the Dichapetalaceae family is the most numerous in terms of species. It is represented by 6 species. Furthermore, the species composition and dominance of the families found in this study are more or less the same as those found in most of the African tropical forests studied (Jongkind *et al*., 2005, Swaine *et al*., 2005; Kuzee *et al*., 2005; Ewango, 2010; Mumbanza, 2021). The most important species and families (Euphorbiaceae, Fabaceae, Combretaceae, Dichapetalaceae, Connaraceae and Apocynaceae) are widely distributed in the Upper Guinea region (Jongkind et al., 2005, Swaine et al., 2005; Addo-Fordjour et al., 2008; Mumbanza, 2021), suggesting that all the lowland forests of West and Central Africa have a similar composition, suggesting that all lowland forests in West and Central Africa have a similar taxonomic composition in their liana communities (Ewango, 2010).

The number of individuals decreases with increasing diameter classes in our forests. For a total of 1247 liana individuals, 84.68% were represented by small lianas, 12.75% by medium lianas and 2.56% by large lianas. With the greatest number of individuals, the smallest diameter class contributed 40.7% (1.54 $m^2$/ha) to the total basal area and the medium class 32.2% (1.21 $m^2$/ha). Large lianas, with 32 individuals, added 27.0% (1.02 $m^2$/ha) to the basal area of lianas in our research site. The small class therefore contributed the maximum basal area of lianas. These results are similar to those of other studies carried out in Africa and elsewhere in the world (Dewalt *et al*., 2000; Letcher *et al*., 2009; Ewango, 2010; Barry *et al*., 2015; Mumbanza *et al*., 2020). We attribute this trend to the fact that lianas allocate more energy to growth in height and leaf production than to growth in diameter.

In this study, most lianas are voluble, accounting for 49.88%. This trend has been found in several studies carried out in Africa and elsewhere (Gentry 1991; Senbeta *et al*., 2005; Kuzee *et al*., 2005; Addo-Fordjour *et al*., 2008; Ewango, 2010; Thomas *et al*., 2015; Vivek *et al*., 2015; Wright *et al*., 2015). This highlights the potential role played by environmental filtering in the formation of liana communities (Mumbanza, 2021). These results suggest that lianas rapidly colonise the forest after agricultural abandonment, and can maintain their competitive ability by adjusting their functional strategies during succession.

The infestation rate found in our study seems very low compared with those found in some studies in the Neotropics, where lianas are more numerous (Pérez-Salicrup *et al*., 2001; Alvira *et al*., 2004; Malizia *et al*., 2006). This could be explained by the difference between the environmental conditions and the methods used. In the neotropics, climate change is influencing liana abundance, which has not yet been proven in Africa's tropical forests (Ewango, 2010). It should be remembered here that we limited ourselves to assessing the infestation of tree trunks by lianas ≥ 1 cm in diameter, generally measured at 1.30 m from the ground.

In our study, the number of lianas per host tree varied from 1 to 38. However, trees with only one creeper stem on their trunks accounted for 23.42%. The presence of more than 20 liana stems per tree was rare (4.3%) and two trees in all our forests had 38 liana stems. Furthermore, in this study, the numbers of lianas on trees had a variance/mean ratio greater than one (i.e. 3.05), suggesting a clustered distribution of lianas in the tropical forests at Yoko Forest Reserve. This observed aggregation of lianas on trees indicates a contagion phenomenon where the presence of a liana individual on a tree leads to a greater probability of having another liana individual infesting the same tree. This may be the result of a facilitation process whereby the new colonising lianas use the stem of the first established liana to climb the tree canopy (Campanello *et al*., 2007). This may also be a result of the structure of the forests and the characteristics of the lianas and a limitation on their dispersal, as many liana species develop mechanisms for clinging to their support (Putz, 1984) and can reproduce vegetatively and have seeds dispersed by animals in the region (Mumbanza *et al*., 2020). These results are similar to those found in other tropical forests (Putz, 1984; Clarck *et al*., 1990; Pérez-Salicrup *et al*., 2005).

### Structural clustering in the host tree - liana interaction

The proportion of infested trees differed according to diameter category, with medium and large trees supporting more lianas on their trunks and a higher total basal area of lianas than small trees in the Yoko forest reserve. These results corroborate those found by Ewango (2010). In fact, he indicated that large trees were particularly important for liana abundance and medium-sized trees had a significant positive effect, unlike small trees, which had no effect on lianas in the mixed forests of Ituri in DR Congo. This suggests that there is an increase in the infestation load of lianas on trees as tree size increases. This trend has already been demonstrated by other studies (Clark *et al*., 1990), and can be explained by the fact that, on the one hand, large trees can offer more surface area and exposure time for liana colonisation, and on the other hand, large trees are generally taller, able to reach the upper layers of the canopy where lianas can develop better because light is fully available (Mumbanza *et al*., 2020).

### Functional grouping in the tree host - liana interaction

On the one hand, our results corroborate those of several studies which have shown that lianas whose branches grow around the stems of trees can climb larger trees, and lianas with hooks can climb trees of different diameters (Hegarty 1991; Pinard *et al*., 1994). On the other hand, our results are similar to those of other studies that have found that trees do not carry lianas because of the texture of their bark, since trees with smooth bark escape liana infestation (Putz, 1984; Campbell *et al*., 1993; Schnitzer *et al*., 2000; Carsten *et al*., 2002; Alvira *et al*., 2004; Campanello *et al*., 2007) and rough-barked trees provide anchor points for liana climbing and therefore facilitate liana infestation.

## Conclusion

This study focused on liana colonisation of trees in tropical forests in the Yoko Forest Reserve (Tshopo, DR Congo). The main objective was to determine the relationship patterns between lianas and trees at our site.

The results obtained indicate that:

- Overall, 57 liana species were inventoried, and 41 genera and 23 families were recorded. A total of 1,247 individuals of lianas were inventoried in all fifteen plots, representing an average density of 519 stems/ha. They represent a basal area of 3.79 $m^2$/ha. Most of the lianas are voluble and climb their supports (49.88%). A total of 1,177 trees were surveyed, 381 of which had lianas on their trunks (32.3%).
- There was a highly significant positive association between tree diameter and the presence of lianas on the trees (p-value < 0.0001***) and between tree diameter and the number of lianas on the trees (p-value < 0.0001***). There was also a link between the type of bark on the trees and the presence (absence) of lianas on the trees (p-value < 0.0001***).

- There was also a link between tree bark type and the attachment mechanisms of lianas infesting the trees (p-value <0.0001***). Similarly, there was a link between the size of the trees and the attachment mechanisms of the lianas infesting these trees (p-value = 0.0004**).

We therefore find that lianas are grouped within the (structural) identities of their host trees in the forests of the Yoko Forest Reserve. This implies that the colonisation of trees by lianas in the Yoko Forest Reserve varies not only according to structural attributes, but also according to the functional identities of the lianas.

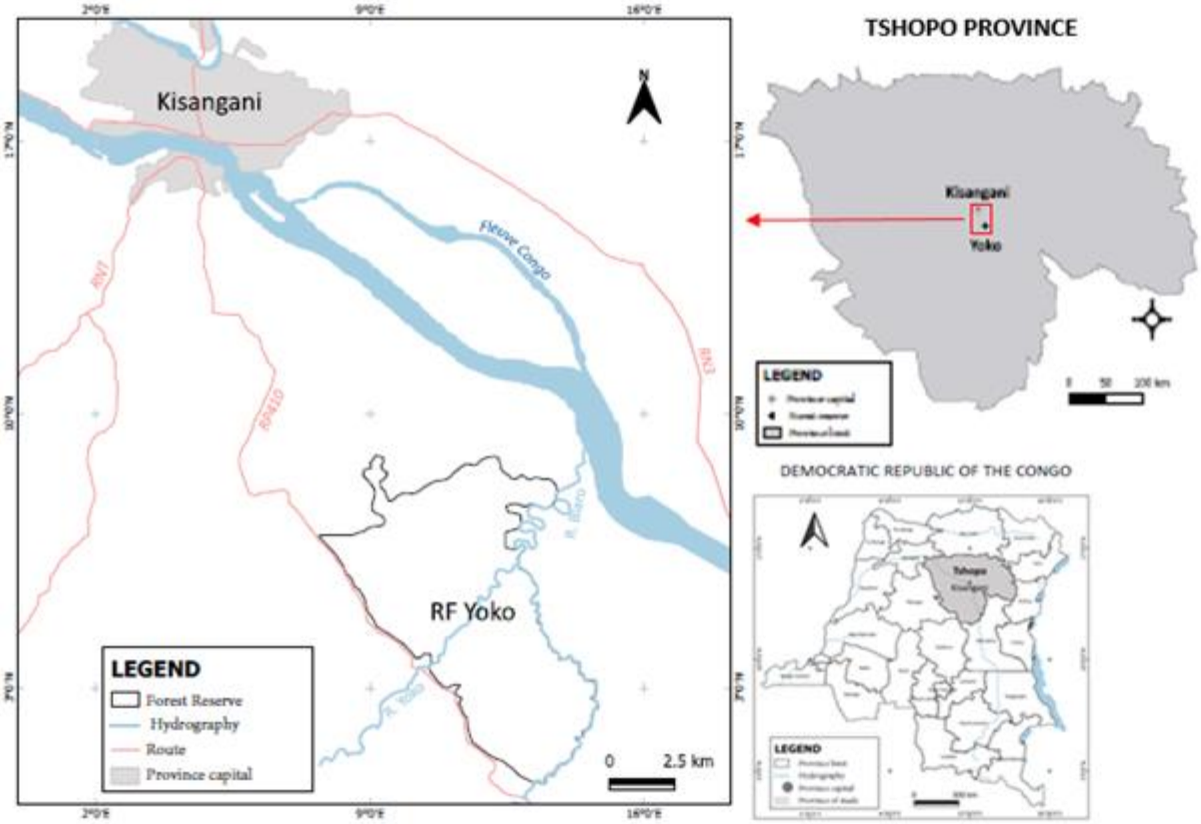


**Figure 1. Location of the study area in relation to the town of Kisangani (Tshopo Province, DR Congo)**

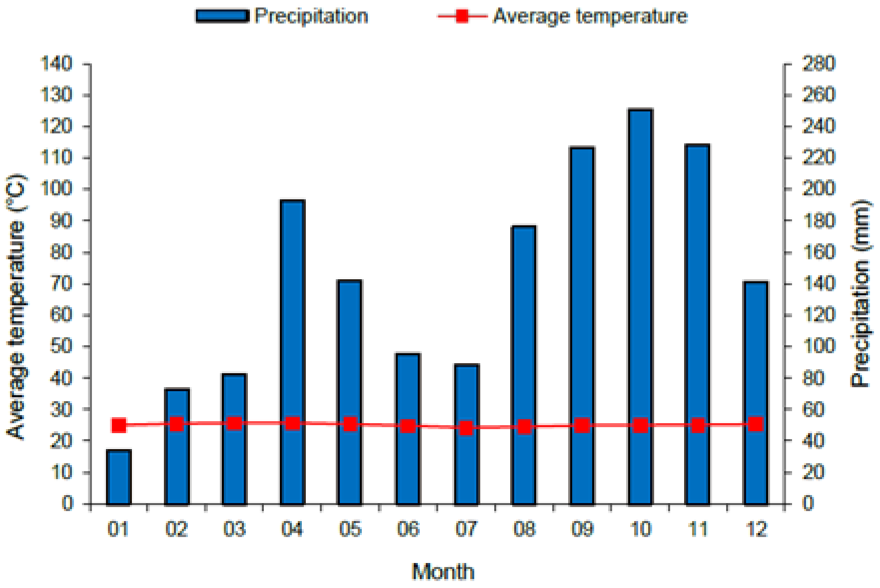


**Figure 2. Umbrothermal curve for the city of Kisangani (Yoko site), monthly averages for the years 2013-2022 (data source: Bangboka station)**

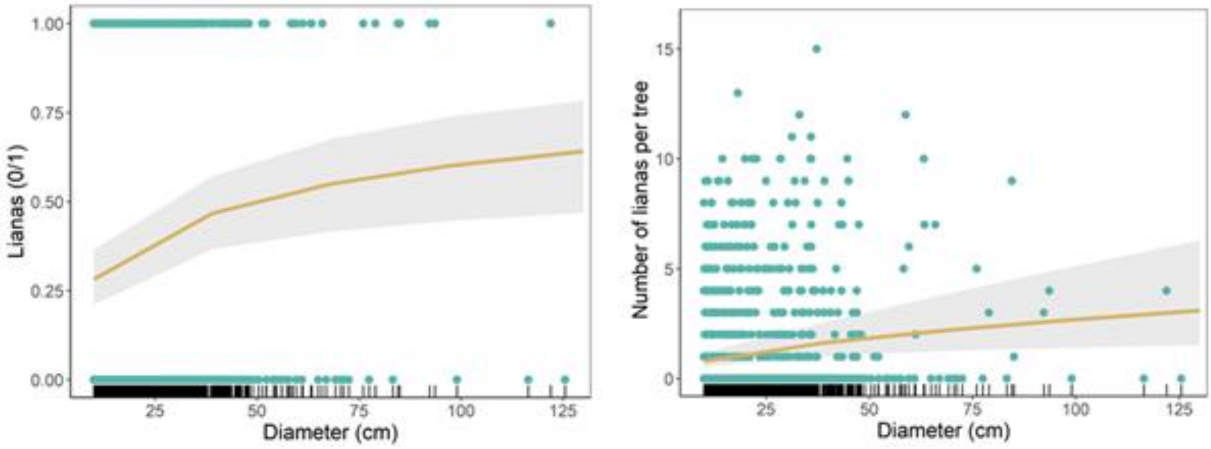
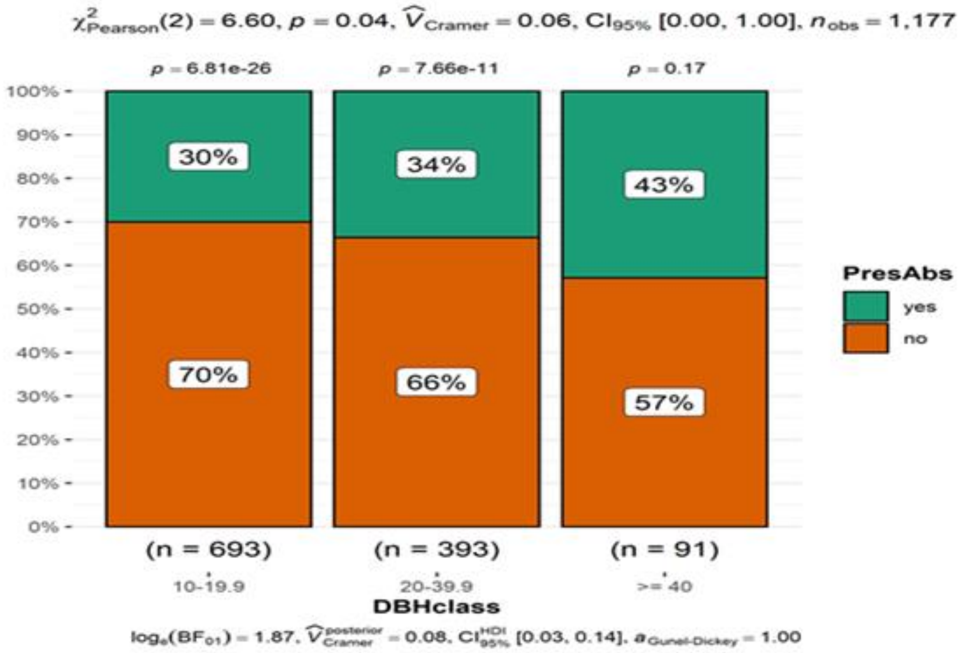


**Figure 3. Adjusted model of the presence or absence of lianas per tree as a function of tree diameter (left) and adjusted model of the evolution of the number of lianas per tree as a function of tree diameter (right) at our site. Each yellow regression line represents the posterior mean of the 'tree diameter' fixed effect, the grey ribbon around it represents the posterior 95% interval, and the green points represent the individual data**



**. Figure 4.Number of trees with and without lianas in three different categories of DHP in our site**

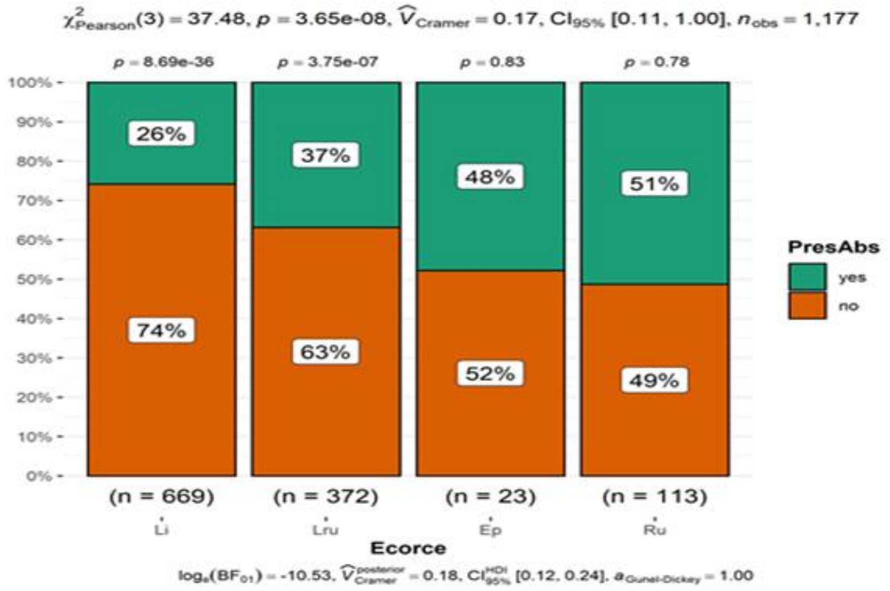


**Figure 5. Number of trees with and without lianas according to tree bark type at our site (Li=smooth, Lru=slightly rough, Ep=spiny and Ru=rough)**

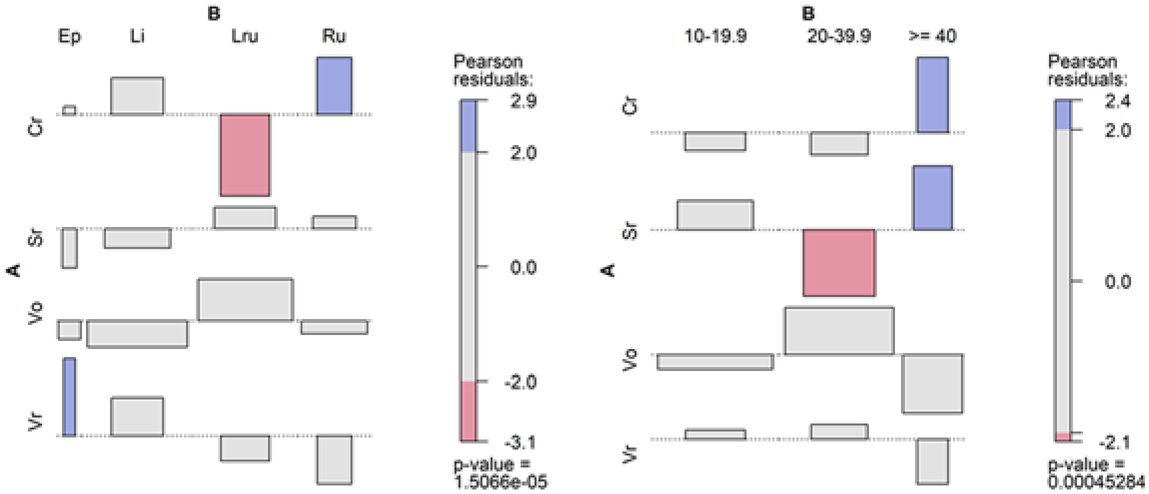


**Figure 6. Association between host tree bark types (spiny (Ep), smooth (Li), slightly rough (Lru) and rough (Ru)) and liana attachment mechanisms (hooks (Cr), sarmentose (Sr), voluble (Vo) and tendrils (Vr)) (left) and association between tree size (grouped by three categories) and vine attachment mechanisms (hooks (Cr), sarmentose (Sr), voluble (Vo) and tendrils (Vr)) (right) in our site**

## References

Addo-Fordjour, P., Rahmad, Z. B., & Shahrul, A. 2012. Effects of human disturbance on liana community diversity and structure in a tropical rainforest, Malaysia: implication for conservation. Journal of Plant Ecology, 5, 391-399.

Addo-Fordjour, P., Anning, A.K., Atakora, E.A., & Agyei, P.S. 2008. Diversity and distribution of climbing plants in a semi-deciduous rain forest, knust Botanic Garden, Ghana. International Journal of Botany, 4, 186-195.

Alvira, D., Putz, F.E., & Fredericksen, T.S. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. Forest Ecology and Management, 190, 73-86.

Angiosperm Phylogeny Group III, 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society, 161, 105 – 121.

Balfour, D.A., & Bond, W.J. 1993. Factors limiting climber distribution and abundance in a southern African forest. Journal of Ecology, 6, 93 – 99.

Barry, K.E., Schnitzer, S.A., Van Breugel, M., & Hall, J.S. 2015. Rapid liana colonization and community development along a secondary forest chronosequence. Biotropica, 47(6), 672– 680.

Bates, D., Kliegl, R., Vassishth, S., & Baayen, R.H. 2015. Parsimonious mixed models. Academia, Arxiv :1506.04967v1(stat.ME)

Bell, D.J., Forseth, I.N., & Teramura, A.H. 1988. Field water relations of three temperate vines. Oecologia, 74, 537–545.

Bongers, F., Parren, M.P.E., Swaine, M.D., & Traoré, D. 2005. Forest climbing plants of West Africa: Introduction. Pp. 5 – 18. In: Bongers, F., Parren, M.P.E., & Traore´, D. (eds). Forest Climbing Plants of West Africa: Diversity, Ecology and Management. CAB International, Wallingford, Oxfordshire, UK.

Boyemba, F.B. 2011. Ecologie de Pericopsis elata (Harms) Van Meeuwen (Fabaceae), arbre de forêt tropicale africaine à répartition agrégée. Thèse de doctorat, Université Libre de Bruxelles, Belgique, 181 p.

Campanello, P. I., Garibaldi, J. F., Gatti, M. G., & Goldstein, G. 2007. Lianas in a subtropical Atlantic Forest: Host preference and tree growth. Forest Ecology and Management, 242, 250-259.

Campbell, E.J.F., & Newbery, D.M. 1993. Ecological relations¬hips between lianas and trees in lowland rain forest in Sabah, East Malaysia. Journal of Tropical Ecology, 9, 469 – 490.

Carsten, L.D., Juola, F.A., Male, T.D., & Cherry, S. 2002. Host associations of lianas in a south-east Queensland rain forest. Journal of Tropical Ecology, 18, 107-120.

Clark, D.B., & Clark, D.A. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican wet forest. Journal of Tropical Ecology, 6, 321 – 331.

Cottam, G., & Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. Ecology, 37, 451 – 460.

Curtis, J.T., & McIntosh, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology, 32, 476 – 496.

Dewalt, S.J., Schnitzer, S.A., & Denslow, J.S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. Journal of Tropical Ecology, 16(1): 1 – 19.

Ewango, C.E.N. 2010. The liana assemblage of a Congolian rainforest: diversity, structure and dynamics. PhD. Thesis. Wageningen University, Netherlands, p149.

Gentry, A.H. 1991. The distribution and evolution of climbing plants. Pp 3-49. In Putz, F.E. & Mooney, H.A (eds). The Biology of Vines. Cambridge University Press.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E., & Thomas, D.W. 2006. A standard protocol for lianacensuses. Biotropica, 38, 256 – 261.

Harper, J., & Hawksworth, D. 1995. Preface. Pp. 5-12. In: Hawksworth, D. (ed.). Biodiversity: measurement and estimation. London: Chapman & Hall.

Hartig, F. 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.0.
https://CRAN.R-project. org/package=DHARMa

Hegarty, E.E., & Caballé, G. 1991. Distribution and abundance of vines in forest communities. Pp 313–335. In Putz F.E.& Mooney H.A. (eds) The biology of vines. Cambridge University Press, Cambridge, UK.

Jongkind, C.C.H., & Hawthorne, W.D. 2005. A botanical synopsis of the lianes and other forest climbers. Forest climbing plants of West Africa: diversity, ecology and management, Pp 19-39.

Krebs, C. J. 1999. Ecological methodology. 2nd edition. New York, USA: Addison Wesley Longman.

Kusumoto, B., Enoki, T., & Kubota, Y. 2013. Determinant factors influencing the spatial distributions of subtropical lianas are correlated with components of functional trait spectra. Ecological Research, 28, 9 – 19.

Kuzee, M. E., & Bongers, F. 2005. Climber abundance, diversity and colonisation in degraded forests of different ages in Côte d'Ivoire. Pp. 73 – 92. In: Bongers, F., Parren, M.P.E., &Traoré, D. (eds). Forest climbing plants of West Africa: diversity, ecology, and management. CABI Publishing, Wallingford, Oxfordshire, UK.

Laurance, W., Pérez-Salicrup, D., Delamônica, P., Fearnside, P., D'angelo, S., Jerozolinski, A., … Lovejoy, T. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology, 82, 105-116.

Lebrun, J-P., & Gilbert, G. 1954. Une classification écologique des forêts du Congo – Belge. INEAC, séries Scientifiques (63), Bruxelles, 89 p.

Lebrun, J-P., & Stork, A.L. (1991–1997). Enumération des plantes à fleurs d'Afrique tropicale. Vols 1 – 4. Genève, Suisse: Conservatoire et Jardin botaniques de la Ville de Genève.

Ledo, A., Illian, J.B., Schnitzer, S.A., Wright, S.J., Dalling, J.W., & Burslem, D.F.R.P. 2016. Prediction of fine-scale distribution of above-ground biomass in a tropical moistforest. Journal of Ecology, 104, 1819 – 1828.

Lejoly, J., Ndjele, M-B., & Geerinck, D. 2010. Catalogue - flore des plantes vasculaires des districts de Kisangani et de la Tshopo (RD Congo). Taxonomania, 30, 1 – 308.

Letcher, S.G., & Chazdon, R.L. 2009. Lianas and self-supporting plants during tropical forest succession. Forest Ecology and Management, 257, 2150 – 2156.

Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T., Wright, J., Almeida, S.,…Vinceti, B. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). Journal of Vegetation Science, 13(3): 439 – 450.

Malizia, A., & Grau, H. R. 2006. Liana–host tree associations in a subtropical montane forest of north-western Argentina. Journal of Tropical Ecology, 22, 331-339.

MECNT, 2007. Direction Inventaire et Aménagement Forestiers (DIAF). Guide opérationnel : Normes d'inventaire d'aménagement forestier, RDC, 16p.

Mumbanza, M.F. 2021. The role of lianas for the structure and function of tropical rainforests of the Congo basin. PhD Thesis, Ghent University, Belgium, p. 301.

Mumbanza, F.M., Bauters, M., Kearsley, E., Boeckx, P., Lubini, C.A., & Verbeeck, H. 2020. Liana communities exhibit different species composition, diversity and community structure across forest types in the Congo Basin. Biotropica, 00, 1 – 13.

Odell, E. 2018. Lianas, trees and insect herbivory. Thisis, Griffith University, Queensland-Australia. https://hdl.handle.net/10072/380989

Patil, I. 2021. Visualizations with statistical details: The 'ggstatsplot' approach. Journal of Open Source Software, 6(61), 3167. https://doi.org/10.21105/joss.03167

Peel, M.C., Finlayson, B.L., & McMahon, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences, 11, 1633 – 1644.

Pérez-Salicrup, D., Sork, V.L., & Putz, F.E. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica, 33, 34-47.

Pérez-Salicrup, D. R., & de Meijere, W. 2005. Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas, Mexico. Biotropica, 37(1), 153-156.

Pinard M.A., & Putz F.E. 1994. Vine infestation of large remmant trees in logged forest in Sabah, Malaysia: Biomechanical facilitation in vine succession. J. Trop. Forest. Sci. 6: 302-309.

Pretzsch, H. 2010. Forest dynamics, growth and yield. Berlin–Heidelberg, Germany: Springer-Verlag. http://dx.doi.org/10.1007/978-3-540-88307-4

Putz, F.E. 1980. Lianas vs. trees. Biotropica, 12, 224-225.

Putz, F.E. 1984. How trees avoid and shed lianas. Biotropica, 16, 19 – 23.

Putz, F. E., & Holbrook, N. 1991. Biomechanical studies of vines. In F. E Putz & A. H. Mooney (Eds.), The biology of vines (pp. 73-98). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511897658.005

R Core Team. 2020. The R project for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-proje ct.org

Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. Am. Nat., 166, 262 – 276.

Schnitzer, S.A., & Bongers, F. 2002. The Ecology of Lianas and Their Role in Forests. Trends in Ecology and Evolution, 17 (5), 223 – 230.

Schnitzer, S.A., & Bongers, F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology Letters, 14, 397 – 406.

Schnitzer, S. A., Rutishauser, S., & Aguilar, S. 2008. Supplemental protocol for liana censuses. Forest Ecology and Management, 255(3), 1044 – 1049.

Senbeta, F., Schmitt, C. B., Denich, M., Demissew, S., Velk, P.L., Preisinger, H., ... Teketay, D. 2005. The diversity and distribution of lianas in the Afromontane rain forests of Ethiopia. Diversity and Distributions, 11, 443-452.

Swaine, M. D., Hawthorne, W., Bongers, F., & Aceves, M. 2005. Climbing plants in Ghanaian forests. In F. Bongers, M. P. E. & D. Traoré (Eds.), Forest climbing plants of West Africa: diversity, ecology and management (pp. 93-108). Wallingford, UK: CABI Publishing.

Thomas, D., Burnham, R.J., Chuong, D., Kenfack, D., & Sainge, M.N. 2015. Liana abundance and diversity in Cameroon's Korup National Park. Pp. 13 – 22. In: Schnitzer, S.A., Bongers, F., Burnham, R.J., &Putz, F.E. (eds). The ecology of lianas. Wiley-Blackwell, Oxford, UK.

Van der Heijden, G.V., & Phillips, O. 2008. What controls liana success in Neotropical forests. Global Ecology and Biogeography, 17, 372-383.

Van Ranst, E., Baert, G., Ngongo, M., & Mafuka, P. 2010. Carte pédologique de Yangambi (planchette 2 : Yangambi, échelle 1 : 50.000). Ghent, Belgium: Ugent, Hogent.

Visser, M.D., Schnitzer, S.A., Muller-Landau, H.C., Jongejans, E., De Kroon, H., Comita, L.S., Hubbell, S.P., Wright, S.P., & Zuidema, P. 2018a. Tree species vary widely in their tolerance for liana infestation: a case study of differential host response to generalist parasites. Journal of Ecology, 106, 781 – 794.

Visser, M. D., Muller-Landau, H., Schnitzer, S.A., Kroon, H., Jongejans, E., & Wright, S. 2018b. A host–parasite model explains variation in liana infestation among co-occurring tree species. Journal of Ecology, 106, 2435-2445.

Vivek, P., & Parthasarathy, N. 2015.Liana community and functional trait analysis in tropical dry evergreen forest of India. Journal of Plant Ecology, 8(5), 501–512.

Vivien, J., & Faure, J.J. 1985. Arbres des forêts denses d’Afrique centrale. Saint Berthevin, 945p.

Vivien, J., & Faure, J.J. 2011. Arbres des forêts denses d’Afrique centrale. Agence de coopération culturelle et technique, Paris, 565p.

Wright, S.J., Sun, I.F., Pickering, M., Fletcher, C.D., & Chen, Y.Y. 2015. Long-term changes in liana loads and tree dynamics in a Malaysian forest. Ecology, 96, 2748 – 2757.