

# Impact of Tree Deciduousness and Bark Type on Liana Abundance in Three Successional Stages of Tropical Dry Forest

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Participants: Stephen Ironside, Scott Drucker, David Reyes

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## Abstract

Lianas are an important aspect of forest structure and successional dynamics, and fewer studies have been done on lianas in tropical dry forests. Biotic factors, particularly host characteristics, can be more decisive in liana success in a given area. Previous studies, mostly conducted in wet forests, have shown that liana abundance declined with forest successional age. We contended that liana abundance would increase as our three plots of dry forest—early secondary, late secondary, and old growth—age, and that both host bark type and deciduousness would be important factors in this increase. We found that liana abundance increased as the forest aged and that lianas were more successful on smooth-barked and deciduous trees.

## Introduction

As a tropical forest moves through different stages of succession after disturbance, a rapid recovery of species richness and diversity can be seen (Ruiz et al. 2005). Lianas (woody climbers) play an important role in the recovery of forests after both natural and anthropogenic disturbances; they compose a large percentage of species inhabiting gaps and are often some of the first species to appear after such a disturbance (Schnitzer 2000), and play an important role in maintaining species diversity, regenerating forests, and ecosystem processes as a whole (Schnitzer and Bongers 2002). Lianas rely on other plants for their structural support and are highly adapted for disturbed areas (Gerwing and Farias 2000; Putz 1983; Schnitzer 2000). They compose a large component of the canopy in tropical forests, and typically contribute to about one-

third of the entire leaf area (Schnitzer and Bongers 2002) as well as between 10% and 45% of woody stem diversity (Schnitzer 2005). Lianas transport water effectively due to their efficient vascular systems and deep roots (Schnitzer 2005), and are therefore strong competitors with trees for water, especially in seasonally dry forests (Schnitzer 2005; Swain and Grace 2007; Van der Heijden and Phillips 2008). Lianas have been shown to be detrimental to tree fitness in a variety of ways; they suppress tree growth and increase tree mortality rates (Van der Heijden et al. 2008) and increase the size and rates of creation of treefall gaps (Nabe-Nielsen 2001).

Studies from tropical wet forests have shown that the abundance of lianas declines as the forests age (DeWalt et al. 2000; Letcher and Chazdon, in press), though there are few studies on the mechanisms driving this decline. Although lianas are common in tropical forests worldwide, there is relatively little known about their biology or ecology (Carsten et al. 2002). Numerous studies of neotropical dry forests have tended to treat the dry forests in a general sense, focusing on how they relate to tropical wet or moist forests (Gentry 1995) instead of recognizing that they constitute a large, diverse set of plant communities that occur in a stressful climate with little rainfall for part of the year (Medina 1995). Although dry forests compose 42% of tropical forests worldwide (Chazdon et al. 2007), these ecosystems have been diminished to less than 0.1% of their original expanse on Central America's Pacific side, and are considered the most endangered ecosystem in the lowland tropics (Gillespie et al. 2000).

Previous studies have shown that lianas prefer slow-growing trees with inflexible trunks, high-density wood, short leaves, and rough bark (Van der Heijden et al. 2008). Lianas have been found to be more abundant in areas with a pronounced dry season and low annual rainfall (Gentry 1991; Schnitzer 2005), though Van der Heijden and Phillips said that neither annual rainfall nor its seasonality relate to liana density in neotropical forests (2008). It has also been shown that liana success may be due to biotic factors, particularly regarding host characteristics, rather than abiotic factors such as the amount of water or nutrients (Balfour and Bond 1993). The purpose of this study is to quantify liana abundance in three successional stages of tropical dry forest with regards to two factors as they affect liana establishment on hosts: host bark type and deciduousness. We contend that, contrary to prior studies in wet forests (DeWalt et al. 2000; Letcher and

Chazdon, in press), liana abundance in a dry forest will increase as the forest ages, lianas will prefer smooth-barked trees as hosts (Balfour and Bond 1993; Campbell and Newbery 1993; Carsten et al. 2002), and that the deciduousness of trees also affects liana density.

## Methods

*Study Site.* —This study was carried out during the dry season at the Organization for Tropical Studies' Palo Verde Biological Station in Palo Verde National Park, Guanacaste, Costa Rica, from 27 February 2009 to 1 March 2009. Three plots of forest—early secondary, late secondary, and old-growth—were located approximately three kilometers from the Palo Verde OTS station (Figure 1) using the undergraduate thesis work of Vladimir Jimenez (1999) as well as GPS receivers and ArcGIS v.9.3 software (ESRI 2008). The methodology used by Jimenez (1999) to classify the forests around Palo Verde is contestable, as he based his classifications on aerial photographs of the region and did not personally explore the area in order to better determine the ages of forests there. Although Van der Heijden and Phillips found that liana density is unrelated to soil fertility or other soil gradients (2008), we used ArcGIS to confirm consistency among the soil types of the three plots, and all were determined to be antisols.

*Field Methods.* — Six transects of 2 x 50m were laid out in each forest plot using a fifty meter measuring tape at a minimum of twenty meters from the access road to avoid edge effects. The diameters of all trees  $\geq 2.5$ cm and all lianas  $\geq 0.5$ cm inside the two meter width of the transects were recorded. The diameters of all trees were measured at breast height (DBH, 1.3m) with a diameter tape and all lianas were measured with calipers at 1.3 m from the rooting point. If a tree or liana branched off below the 1.3m mark, each stem was counted as one individual. Both measurements were taken to the nearest 0.1cm. However, only trees and lianas that rooted within the plot were recorded, as in Putz (1984b). Also, lianas that had sent down adventitious roots in the plot but had obvious rooting points outside of the plot were omitted, as in Letcher and Chazdon (in press). The number of lianas per tree as well as the DBH and bark type of the tree was recorded. Bark type of each tree was qualitatively measured using a bark index where trees were divided into having smooth bark, scaled and rough bark, or defended bark. Defended bark included ant-defended (Schupp and Feener 1991) trees as well as

prickles/spines and peeling bark. Each tree was categorized as deciduous, non-deciduous, or semi-deciduous based on current tree foliage levels. Spherical densiometer readings were taken every ten meters in each transect to assess current canopy coverage.

*Statistical Methods.* — Contingency Table Analyses were used to determine differences among liana density and forest age, deciduousness of trees and forest type, the success of lianas regarding the deciduousness of their hosts, the amount of trees having each respective bark type per plot, as well as the lianas' success on each type of host bark. A post-hoc Wilcoxon Sign-Rank test was used to determine where the differences among lianas and bark types lay, and another Wilcoxon Sign-Rank test was used to determine where the significance between liana presence/absence and the deciduousness of trees lay. A Oneway ANOVA was conducted on the spherical densiometer readings versus forest age. All statistical analyses were conducted using JMP v. 5.1.2 software (SAS Institute 2004).

## Results

We counted a total of 281 trees and 360 lianas across the three plots. The number of lianas increased significantly as the forest aged, while the number of trees did not (Figure 2; Contingency Table Analysis,  $\chi^2 = 9.09$ ,  $df=2$ ,  $p= 0.0106$ ). As the forest plots aged, there were significantly more deciduous trees and less non-deciduous trees (Figure 3; Contingency Table Analysis,  $\chi^2=19.53$ ,  $df=4$ ,  $p= 0.0006$ ). A significant difference among the number of lianas present/absent on deciduous vs. non-deciduous trees was found in that there were more lianas present on deciduous trees (Figure 4; Contingency Table Analysis,  $\chi^2 = 6.19$ ,  $df=2$ ,  $p= 0.0453$ ), and post-hoc Wilcoxon Sign-Rank tests showed that the differences were significant in that there were more lianas present on deciduous trees ( $p < 0.0001$ ) and more lianas absent on non-deciduous trees ( $p < 0.0001$ ). There was a significantly larger number of smooth-barked trees in the late secondary and old-growth plots, while defended bark trees had higher numbers in the early secondary plot (Figure 5; Contingency Table Analysis,  $\chi^2=19.69$ ,  $df=4$ ,  $p= 0.0006$ ). A significance among the number of lianas present/absent on each bark type was also found (Figure 6; Contingency Table Analysis,  $\chi^2 = 32.01$ ,  $df=2$ ,  $p < 0.0001$ ); we conducted a post-hoc

Wilcoxon Sign-Rank test, determining that the significance lay within the smooth bark type ( $p < 0.0001$ ). We ran a Oneway ANOVA on the spherical densiometer data ( $p = 0.0635$ ), and though there was no significant difference among the three plots, the data trended towards there being less light as the forest aged.

## Discussion

Contradictory to previous studies in wet forests (DeWalt et al. 2000; Letcher and Chazdon, in press) in which liana abundance increased with forest succession, our study shows that the number of lianas in the tropical dry forest increases significantly with succession, although the number of trees did not (Figure 2). We attribute this, in part, to the bark type and deciduousness of liana hosts.

Lianas have been previously found to have higher success rates on rough and flaky bark (Carsten et al. 2002) and to have difficulties climbing trees with smooth bark as those trees lack attachment sites for their climbing structures (Putz and Smithsonian Tropical Research Institute 1980), although this was disproven (Boom and Mori 1982). We came to different conclusions. Lianas in all plots were much more successful on trees with smooth bark as opposed to either scaly/rough or defended bark (Figure 6). As the forest plots aged, the number of smooth-barked trees increased, as did the abundance of lianas (Figure 5, 2). The number of defended bark trees was highest in the early secondary plot (Figure 5), which consisted mostly of Acacia (Schupp and Feener 1991), and there was an extremely low number of lianas in this plot (Figure 2).

The deciduousness of host trees also affected the presence or absence of lianas. The number of deciduous trees increased as the forest aged, and the number of non-deciduous trees decreased (Figure 3). More lianas were present on deciduous trees, and more lianas were absent on non-deciduous trees (Figure 4). Lianas grow twice as fast as trees during wet seasons in wet forests, and up to seven times faster than trees in the same forest in the dry season (Schnitzer 2005). This could point to a factor contributing to a higher abundance of lianas in the old growth forest: the lianas in this forest have had more dry seasons to grow and reproduce than their counterparts in the younger forests. This may be limited to tropical dry forest ecology, however, since in the wet forest the availability of water is usually not a main issue. Although no statistical tests were run,

tree size could also have been a contributing factor, since if the deciduous trees were larger than the non-deciduous trees, lianas might have preferred them more because there would be more light for them during the dry season.

Although our spherical densiometer readings turned out not to be statistically significant, the data did trend towards there being less light as the forest aged. As lianas are helophytes, they should succeed better in areas where there is more light. We would have expected opposite results during these readings—that light availability increased with forest age. While there were more deciduous trees as the forest aged and less non-deciduous trees, the data was not analysed to see if the non-deciduous trees were, on average, larger than the deciduous trees. This could have affected overall canopy coverage during the dry season, and influenced even more the rate at which lianas were absent from non-deciduous trees in the old growth forest. However, it has also been suggested that trellis availability is more important than either light or water availability to liana growth (Putz 1984a), and perhaps the increase in the number of trees, particularly smooth-barked ones, helped to increase liana abundance more than the decreasing light helped to decrease this abundance.

We have shown that, indeed, a liana's ability to successfully climb towards the canopy depends on biotic factors mainly concerning the forest structure and its structural requirements (Putz and Chai 1987; Chittibabu and Parthasarathy 2001). Though data on liana success on different host barks varies, it has been shown that this characteristic does significantly affect liana abundance in some form. In the dry forest, lianas thrived on deciduous trees, and increased with forest age even though overall light availability decreased. More studies on liana abundance and host characteristics are needed, particularly in dry forest ecosystems.

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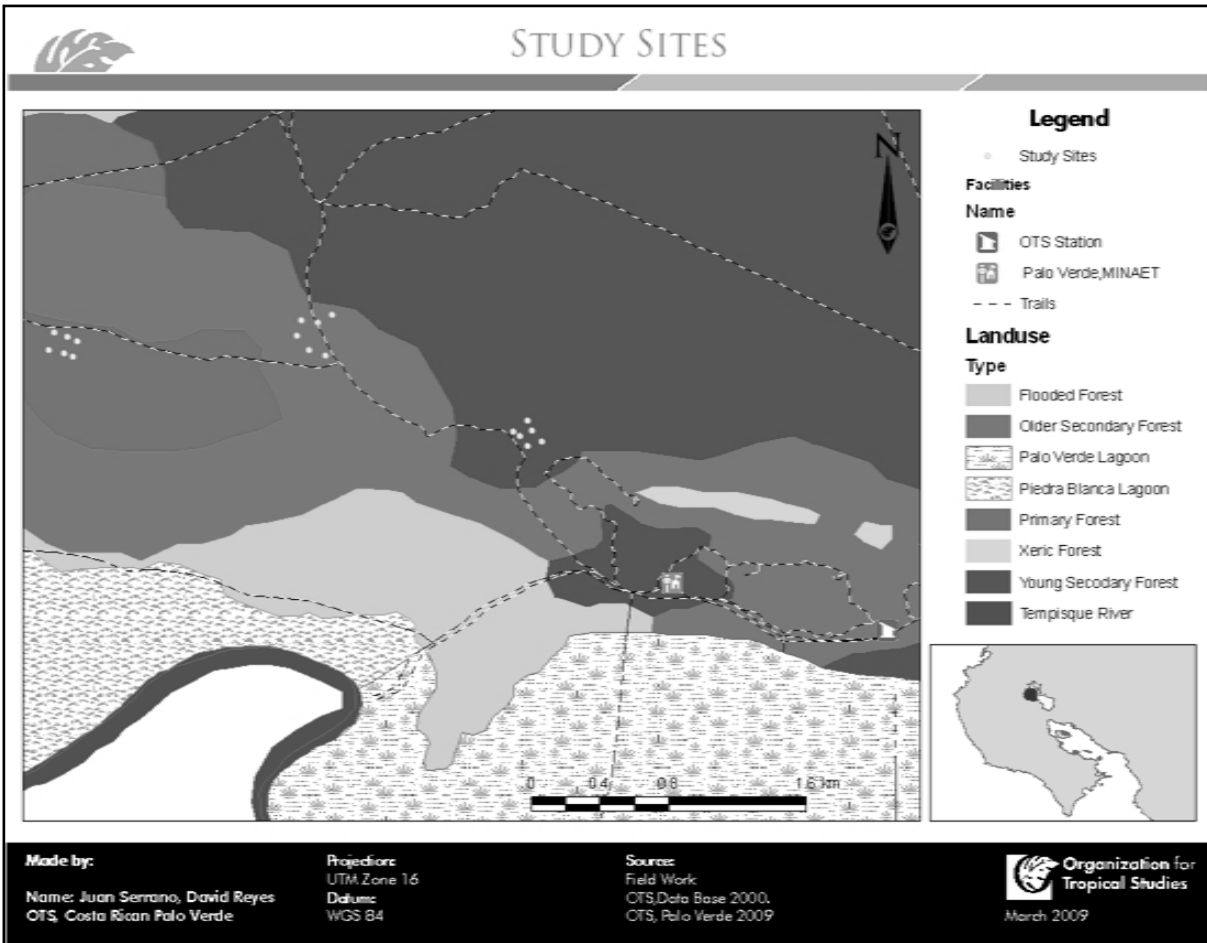


Figure 1: GPS points showing the locations of the 18 transects used in the study divided evenly into the three successional stages of tropical dry forest at Palo Verde National Park.

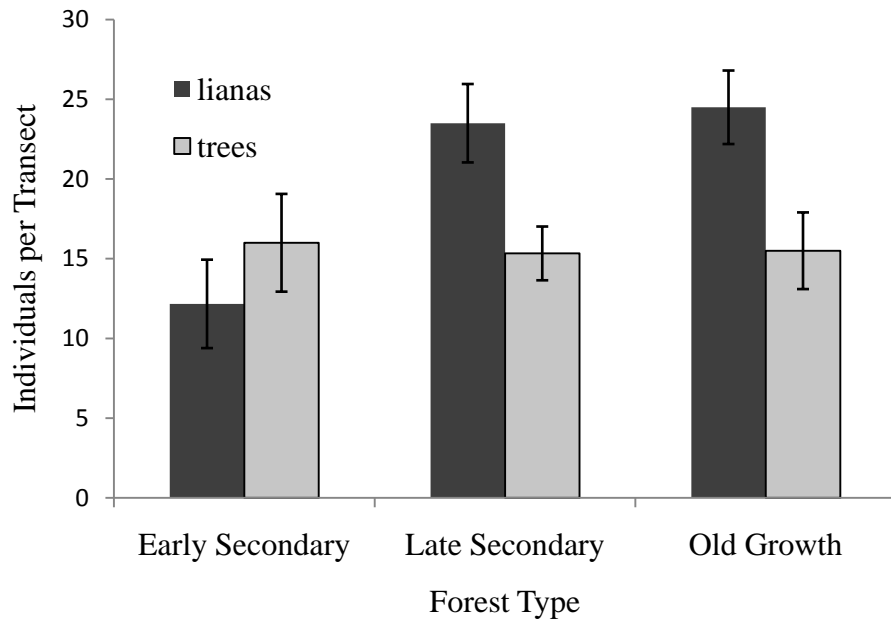


Figure 2: Liana abundance increased significantly as the forest aged, while tree abundance did not. Error bars show  $\pm 1$  SE.

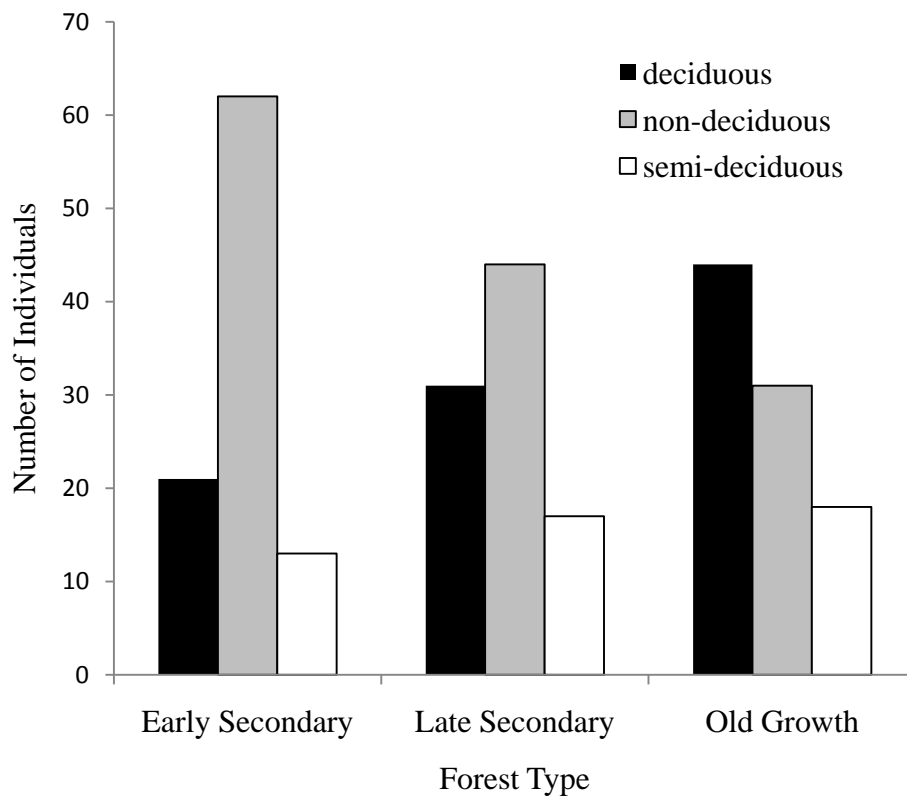


Figure 3: Deciduous tree abundance increased as the forest aged, while non-deciduous tree abundance decreased. There was no significant difference regarding semi-deciduous trees.

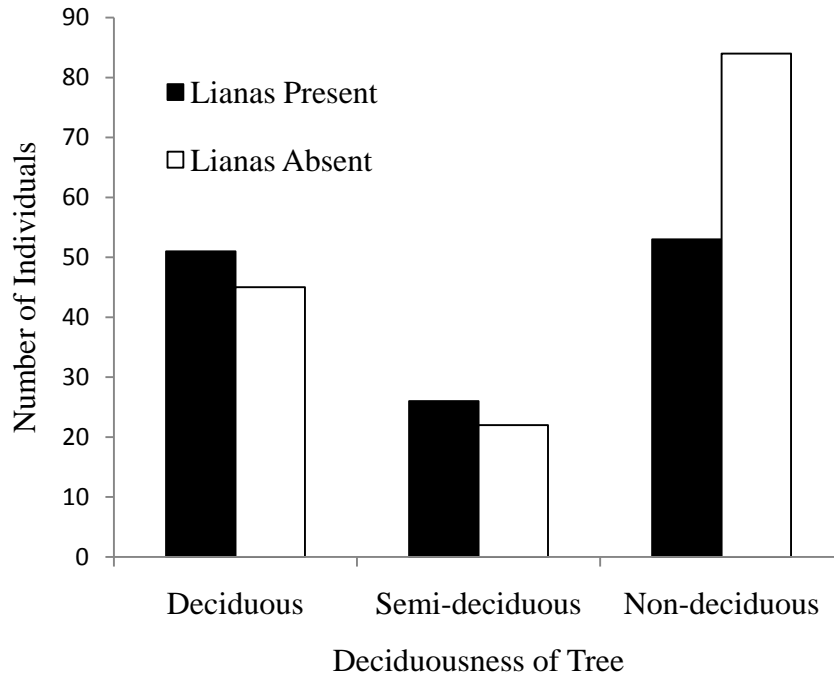


Figure 4: There were significantly more lianas absent from non-deciduous trees than there were absent on deciduous trees

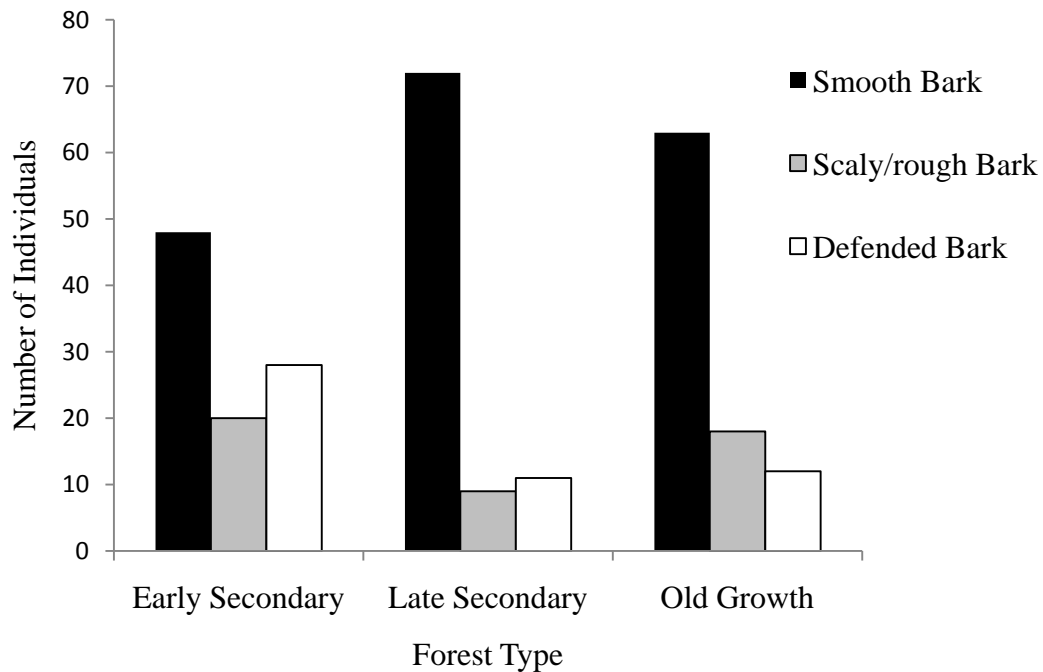


Figure 5: Number of trees with each type of bark among forest ages. Defended bark is prevalent in the early secondary plot, while smooth bark increases for the late secondary and old growth plots.

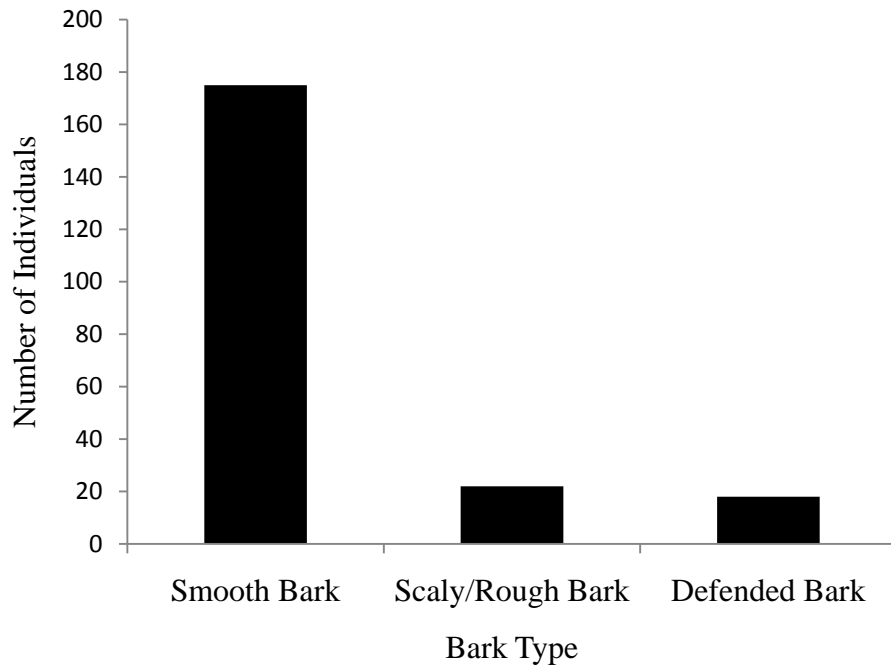


Figure 6: There were significantly more lianas on smooth bark type trees than on scaly/rough or defended bark.