



Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon

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Abstract

The abundance of lianas (woody vines) and the detrimental impact that they have on tropical rain forest trees is widely recognized. Lianas are particularly abundant in disturbed areas of the forest, such as logging gaps, and pre-harvest liana cutting has been widely recommended throughout the tropics to reduce the impact of lianas during and following tree harvest. The effectiveness of forest-wide liana cutting, however, is currently unresolved, particularly for reducing liana abundance in logging gaps. Furthermore, our understanding of the dynamics and rate of liana colonization in gaps is limited. We tested: (1) the speed at which lianas recruit into logging gaps and their dynamics afterwards; and (2) whether pre-harvest liana cutting actually reduces the abundance of lianas in post-harvest logging gaps. To test hypothesis 1, we compared liana recruitment in new, 1 and 6-year-old logging gaps. For hypothesis 2, we compared liana abundance and tree infestation by lianas in 1-year-old logging gaps in which all lianas had been cut 9 months prior to tree felling vs. 1-year old logging gaps in which lianas were not cut. Lianas recruited heavily into logging gaps within 1 year, mostly by means of stem sprouts, and many of these new stems were apparently able to persist for longer than 6 years. Lianas were significantly more abundant in the root/bole zone of gaps than in the canopy zone, mostly due to the vigorous regeneration of stem sprouts. Canopy openness was highest in gaps one year after logging, possibly due to the smothering effect of the lianas on developing trees. Although liana abundance increased significantly over the 6-year gap chronosequence, direct liana infestation of trees remained the same. Pre-logging liana cutting, however, significantly reduced the number of lianas and also the number of liana-infested trees in logging gaps. Consequently, liana cutting appears to be an effective method to reduce the abundance of lianas and thus minimize their detrimental effects on regenerating trees in logging gaps.

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Keywords: Lianas; Climbing plants; Climber cutting; Trees; Forest management; Tropical forest; Cameroon

1. Introduction

The detrimental impact of climbing plants on trees is a widely recognized phenomenon in both natural and managed tropical forests. Climbing plants, particularly lianas (woody vines), compete intensely with

trees for both above- and below-ground resources and therefore can significantly decrease tree fecundity, growth rate, and survivorship in closed-canopy forest, treefall gaps, and open fields (Putz, 1984; Stevens, 1987; Clark and Clark, 1990; Dillenburg et al., 1993; Schnitzer and Bongers, 2002). Lianas are particularly abundant in disturbed forests and in disturbed areas of natural forests, such as treefall gaps, where they can recruit rapidly and abundantly, and subsequently

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suppress tree regeneration for many years (Putz, 1984; Babweteera et al., 2000; Schnitzer et al., 2000; Tabanez and Viana, 2000; Schnitzer and Carson, 2000, 2001). For example, Schnitzer et al. (2000) demonstrated that high liana abundance in natural treefall gaps in Panama could suppress tree regeneration for more than 13 years. During tree extraction in managed and logged forests, lianas can substantially increase the damage and mortality of neighboring trees (collateral damage) and increase the size of logging gaps by binding the trees together, thus pulling down multiple trees in addition to the one being harvested (Appanah and Putz, 1984; Putz, 1985; but see Parren and Bongers, 2001). Lianas also impact tree regeneration detrimentally following tree extraction by suppressing the growth and regeneration of valuable timber trees, as well as causing bending of the tree trunks and thus reducing their value as timber (Putz, 1985; Pinard and Putz, 1994; Vidal et al., 1997). Furthermore, the effects of lianas on trees are likely to become more intensified in the near future, because lianas appear to be increasing in abundance in response to global climate change (Phillips et al., 2002).

To minimize the effects of lianas on tree regeneration in managed forests, pre-harvest climber cutting has been used as a silvicultural tool throughout the tropics, costing many millions of dollars annually worldwide (Guigonis, 1978; Appanah and Putz, 1984; d'Oliveira and Braz, 1995; Pinard et al., 1995; Pinard and Putz, 1996; Amaral et al., 1998; Sist et al., 1998; Perez-Salicrup et al., 2001). Pre-harvest climber cutting can reduce the amount of collateral tree damage and thus post-felling canopy gap sizes, and it is commonly assumed that pre-harvest liana cutting results in a long-term reduction of the number of climbers in the forest after timber extraction (Appanah and Putz, 1984; Putz et al., 1984; Putz, 1985; Vidal et al., 1997; Gerwing, 2001; Parren and Bongers, 2001; Gerwing and Vidal, 2002). However, pre-harvest climber cutting may be a double-edged sword, sometimes resulting in a net increase in liana stems. Climbers may respond to cutting by rapidly producing many new stems, which can eventually dominate logging gaps and logged forests (Gerwing and Vidal, 2002). Even stems as small as 1 m in length can resprout vigorously, giving rise to many young, vegetatively-derived stems (Appanah and Putz, 1984), particularly in the high light environment of a gap (Putz, 1984, 1991; Schnitzer

et al., 2000). For example, in a study in a forest in Cameroon, Parren and Bongers (2001) followed the fate of 184 experimentally cut liana stems and found that although 70% of the stems died after 22 months ($n = 184$), the 56 surviving individuals vigorously produced many new vegetative offshoots, ultimately resulting in a net increase in the number of living stem sprouts after 2 years ($n = 208$). Even if climber cutting is initially successful in reducing the number of lianas, the additional number of vegetatively-produced liana stems in logging gaps may actually increase the total number of liana stems following climber cutting (Putz et al., 1984), potentially reducing the vitality of the remaining trees in the gap. Consequently, lianas may have an equally detrimental effect on the remaining trees in logging gaps, regardless of pre-harvest cutting.

To date, the exact process and speed by which lianas recruit into gaps is poorly understood. In addition, the long-term effectiveness of pre-harvest climber cutting in reducing the number of lianas that recolonize logging gaps has also not been resolved (Parren and Bongers, 2001; Perez-Salicrup et al., 2001; Schnitzer and Bongers, 2002). We used a 6-year chronosequence of logging gaps to determine the effectiveness of pre-harvest climber cutting and the speed of liana recruitment in a forest concession in Cameroon. We tested the hypotheses that: (1) lianas recruit into logging gaps very early after gap creation, mostly through stem sprouting while the gap is still open; and (2) pre-harvest liana cutting will significantly reduce liana stem abundance, including stem spouts, in logging gaps. We further investigated the mechanism by which lianas recruit into gaps by examining whether the speed of liana recruitment differs in different zones of the gap (crown, root and bole). Knowing the speed and process by which lianas recruit into gaps and the specific zones of the gap that they invade is essential for understanding how lianas affect regeneration in gaps and for formulating effective liana management plans.

2. Methods

2.1. Study site

We initiated this study in 1996, in and around a 500 ha area within a 2000 km² forest logging concession 100 km east of Kribi, Cameroon (3°N, 10°E).

The 500 ha study area was located within a relatively flat, homogeneous area of the forest, although the topography of the entire forest ranges from undulating to rolling with some relatively small, isolated hills (Waterloo et al., 1997). The forest is evergreen, with a 25–40 m closed-canopy and emergent trees surpassing 60 m in height (Parren and Bongers, 2001). The mean annual rainfall in this area is approximately 2000 mm, with two distinct dry seasons that last from May until August and from December until March (Waterloo et al., 1997). Climbers were abundant in the forest, with 408 stems (>2 cm in diameter) per ha, comparable to other tropical forests (e.g., Gentry, 1991a; Mascaro et al., 2003), particularly for large lianas greater than 5 cm in diameter (~113 stems/ha; Appanah and Putz, 1984; Vidal et al., 1997; Parren and Bongers, 2001). Logging tends to be relatively selective and light in this forest; on average only one tree over 60 cm in diameter is harvested per hectare per year (Parren and De Graaf, 1994; Jonkers and Van Leersum, 2000).

2.2. Establishing a chronosequence of logging gaps

We established a chronosequence of logging gaps in areas of the forest that had been previously logged without pre-harvest liana cutting. We located six new (year 0) and six 1-year-old (year 1) gaps by following the progress of the logging company and marking new gap sites within several weeks of timber harvest. We used logging records to accurately determine six logging gaps that were approximately 6 years old. These gaps gave a chronosequence of 6 years in which we could examine liana infestation into logging gaps in which there had been no pre-harvest liana cutting. We selected gaps that were approximately the same size (mean gap size = $810 \text{ m}^2 \pm 314$ (S.D.)), according to the Runkle method for gap size determination (Runkle, 1981, 1982; Van der Meer et al., 1994). The 6-year-old gaps were located about 6 km from the 0- and 1-year old gaps in the same expanse of forest, which had similar tree and liana abundance (Parren, unpublished data).

We divided each of the gaps into the crown and the root/bole zone (Fig. 1). Using logging records, we could accurately locate tagged stumps of the felled trees and knowing the tree heights, we were able to

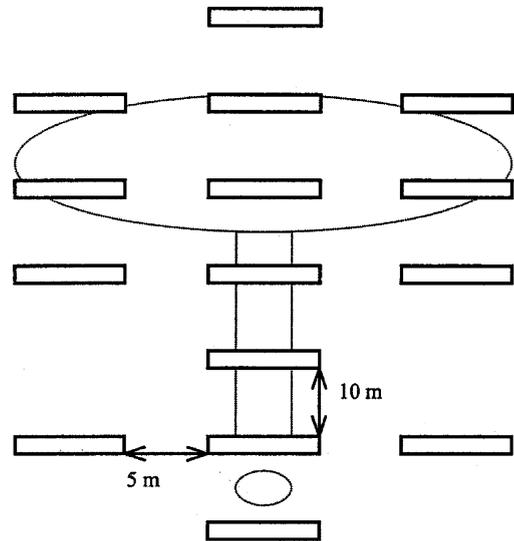


Fig. 1. Sampling design for each treefall gap. Each rectangular box represents a $1 \text{ m} \times 5 \text{ m}$ subplot in which we sampled all lianas and trees >1 cm dbh and taller than 1 m. We sub-sampled all liana ramets >1 mm dbh in the leftmost $1 \text{ m} \times 1 \text{ m}$ section of each $1 \text{ m} \times 5 \text{ m}$ subplot. We divided the gap into two zones: the root/bole zone consisted of the bottom seven subplots and the canopy zone consisted of the top seven subplots.

accurately determine the locations of the root/bole and crown zones. We combined the root and the bole zones because it was not always possible to distinguish between these two zones, whereas the distinction between the canopy and bole zones was, in nearly all cases, clear. In each of these two zones, we established up to eight $1 \text{ m} \times 5 \text{ m}$ subplots, in which we censused all trees and lianas >1 m in height. The grid layout was designed to accurately estimate the entire gap area affected by the treefall (Fig. 1).

2.3. Pre-harvest liana cutting gap selection

Within the 500 ha study area, we established six square 1 ha plots surrounded by a 100 m buffer zone. Nine months prior to logging, we cut all lianas in these plots and in the surrounding buffer zones. We used gaps from the six 1-year old gaps from the chronosequence study in which the lianas were not cut, to serve as control plots. The 1-year-old liana-cut and uncut gaps were logged at approximately the same time to control for temporal differences in liana and tree recruitment, and each treatment was located in nearby

adjacent areas of the forest. Prior to cutting, liana abundance did not differ between the blocks (Parren, unpublished data). One year following tree harvest, we located six similar-sized logging gaps in each of the liana-cut and control plots. The mean gap size was $658 \text{ m}^2 \pm 200$ (S.D.), and mean gap sizes did not significantly differ among the liana-cut and control plots (669 and 641 m^2 , respectively). We partitioned the gaps into root/bole and canopy zones using the same methodology that we had used for the chronosequence gaps described above (Fig. 1).

2.4. Gap censuses

One year following tree harvest (21 months after liana cutting), we censused the lianas and trees within each of the $1 \text{ m} \times 5 \text{ m}$ subplots of the liana-cut and control gaps as well as the chronosequence gaps. We measured the abundance as well as the diameter 130 cm from the roots (dbh) of all liana individuals and trees $>1 \text{ cm}$ dbh that broke the plane of the $1 \text{ m} \times 5 \text{ m}$ subplots 1 m above the ground, as well as the height for the trees meeting these criteria. We considered a liana to be a distinct individual (genet) if it was independently rooted and was not obviously attached to any other liana stem (methods follow Schnitzer and Carson, 2001; Burnham, 2002; Mascaro et al., 2003). We acknowledge, however, that we were not always able to distinguish liana ramets from genets because of current or previous underground connections between stems (see Schnitzer and Carson, 2001; Gerwing and Vidal, 2002; Mascaro et al., 2003). We also counted all liana stem sprouts $>1 \text{ mm}$ diameter (ramets), including all multiple stems of each individual. Because of the large number of liana sprouts, we restricted our sampling of these small stems to the leftmost $1 \text{ m} \times 1 \text{ m}$ section of each $1 \text{ m} \times 5 \text{ m}$ subplot (looking up the tree from the root zone; Fig. 1), but we present the stem sprout data in units of 5 m^2 so that they are comparable to the liana genet data. For each of the above-mentioned variables, we averaged the number of subplots per zone and used the gap as our unit of replication ($n = 6$). For each tree, we visually estimated the level of infestation of lianas into the tree's crown. For liana infestation of the tree's crown, we used the following scale: 1 = no lianas in tree; 2 = lianas on stem only; 3 = at least one liana in the crown, but no lianas connecting crown with any other trees; 4 = at least one, but typically

more, lianas in crown and lianas connecting crown with other trees; and 5 = lianas completely covering tree crown (methods modified from Clark and Clark, 1990). To estimate canopy openness, we visually assessed the amount of open sky above the center of each of the $1 \text{ m} \times 5 \text{ m}$ subplots in the gap, 2 m above the ground. We assigned canopy openness as one of the four categories: 1 = 0–10%; 2 = 11–50%; 3 = 51–90%; and 4 = 91–100% openness. We used relatively broad liana infestation and canopy openness classes in order to minimize our estimation error.

2.5. Data analyses

We analyzed recruitment of lianas and trees into the 6-year chronosequence of logging gaps and the response of lianas and trees to pre-harvest liana cutting using two-way analysis of variance (ANOVA; SAS Institute, 2000). For the chronosequence analysis, we included the gap age (0, 1, and 6) and zone (crown vs. root/bole) as the independent variables; and liana abundance ($>1 \text{ cm}$ dbh), number of liana stem sprouts, tree abundance, tree dbh, tree height, tree infestation, and canopy openness as the dependent variables. We divided the trees into either saplings (1–4 cm dbh) and trees ($>4 \text{ cm}$ dbh); however, we concentrated our analyses on the saplings in order to capture the dynamics of gap-phase regeneration following logging (Schnitzer and Carson, 2001). For the pre-harvest liana cutting experiment, we used an ANOVA similar to the model used for the chronosequence analysis but we substituted the liana cutting treatment (liana-cut vs. control) for gap age. We analyzed the data to ensure that they conformed to the assumptions of ANOVA and log-transformed the number of lianas and canopy openness so that their distribution were normal. Because the large tree data were not normally distributed even with log-transformations, we analyzed them using Kruskal–Wallis non-parametric analyses, which do not assume a normal distribution (Sokal and Rohlf, 1995).

3. Results

3.1. The speed of liana recruitment into logging gaps

Liana abundance was initially low in logging gaps, but lianas recruited rapidly within 1 year, mostly as

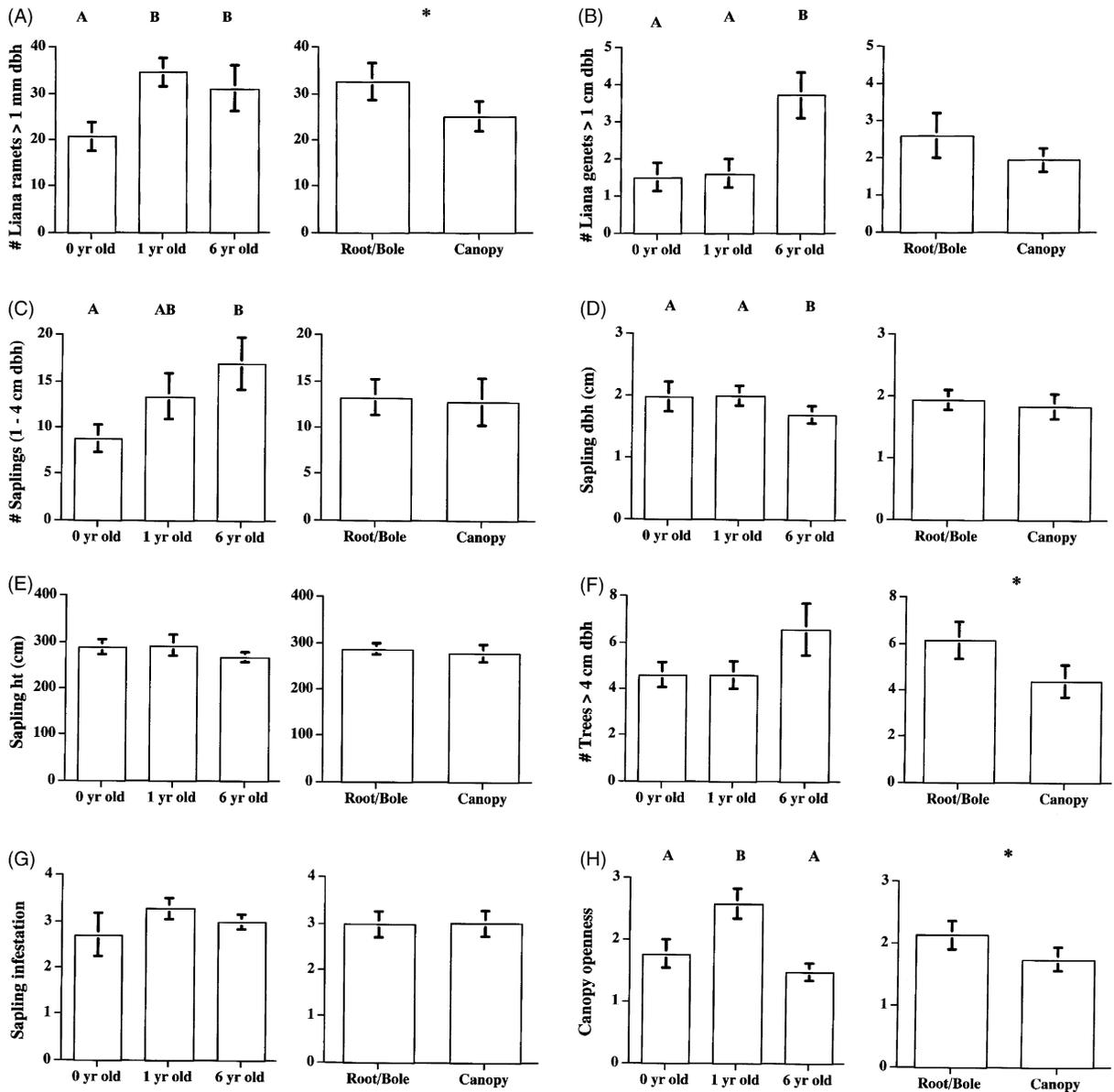


Fig. 2. Mean liana and tree recruitment per 5 m² area into new (0 year old), 1-, and 6-year-old single-tree timber extraction gaps (column 1) and the zone of the gap (root/bole and canopy) into which the lianas recruited (column 2). We classified trees as either saplings (1–4 cm dbh) or trees (>4 cm dbh). We divided lianas into two groups: (1) liana stem sprouts (ramets) >1 mm dbh; and (2) liana individuals (genets) >1 cm dbh. Different letters denote significant differences among the different aged logging gaps. Asterisks denote significant differences between the gap zones. Errors bars represent ±1 S.E. Data for the number of large lianas (>1 cm dbh) and sapling canopy openness were log-transformed to normalize the data; non-transformed data are presented.

ramets via stem sprouting, and they remained in high abundance throughout the 6-year study period. Within several weeks of timber extraction (year 0), there was an average of 20.7 liana stem sprouts >1 mm dbh per

5 m² subplot throughout all zones of the gap (Fig. 2a). By year 1, however, the number of liana stem sprouts was significantly higher, averaging 34.7 ($P = 0.003$; Table 1 and Fig. 2a) and remained essentially

Table 1
ANOVA for the chronosequence plots (0, 1, and 6 years after tree felling) and for the pre-harvest liana cutting vs. control plots^a

Source	Treatment			Zone		
	ss	F	P	ss	F	P
Chronosequence plots						
Number of liana stem sprouts	1265.79	7.28	0.003	497.85	5.73	0.02 ^b
Number of lianas (>1 cm dbh) ^c	7.98	7.72	0.002	0.20	0.39	0.54
Number of saplings (1–4 cm dbh)	410.72	6.28	0.005	1.78	0.05	0.82
Sapling dbh	0.70	3.32	0.05	0.12	1.14	0.29
Sapling height	0.46	1.66	0.30	0.07	0.38	0.54
Sapling infestation	2.02	0.19	0.19	0.01	0.01	0.48
Canopy openness ^c	1.95	13.01	<0.0001	0.33	4.44	0.04 ^b
Liana-cut vs. control plots						
Number of liana stem sprouts	796.95	13.55	0.002	534.40	9.10	0.007 ^b
Number of lianas (>1 cm dbh)	534.40	9.10	0.03	0.16	0.24	0.63
Number of saplings (1–4 cm dbh)	3.76	0.14	0.71	49.59	1.83	0.19
Sapling dbh	0.27	2.00	0.17	0.08	0.60	0.45
Sapling height	2.18	8.86	0.008	0.15	0.63	0.44
Sapling infestation	9.68	29.97	<0.0001	1.15	3.56	0.07
Canopy openness	2.91	8.64	0.008	0.05	0.15	0.70

^a An interaction term was used in the model but was not shown here because it was not significant for all cases except canopy openness for the liana-cut vs. control plots ($P = 0.05$). The number of degrees of freedom was 2 for the tests among the chronosequence plots and 1 for the tests between the liana-cut and control plots.

^b In each case the mean number of trees and lianas was greater in the root/bole zone than in the crown zone.

^c Log-transformed to normalize data.

unchanged by year 6 (31.1). The number of larger lianas (genets >1 cm dbh) remained the same between years 0 and 1 (1.5 and 1.6 stems per 5 m², respectively), but increased significantly to 3.7 by year 6 ($P = 0.002$; Table 1 and Fig. 2b). These findings suggest that liana stem sprouts recruit into gaps within the first year and that many of these stems are able to persist and grow into the 1 cm dbh size-class by year 6, at which point many of them may become indistinguishable from genets. Although most of the regeneration that we observed was from ramets, lianas probably also recruited into the gaps from seed; however, we cannot quantify the proportion of liana ramets and genets.

3.2. Liana colonization in relation to gap zone

Both liana ramet and genet abundance were significantly greater in the root/bole zone than the crown zone. There were 32.5 ± 1.8 (S.E.) liana stem sprouts per 5 m² in the root/bole zone compared to 25.1 ± 2.5 in the crown zone ($P = 0.02$; Fig. 2a and Table 1). For individual liana stems (genets >1 cm dbh), there was

an average of 2.6 ± 0.3 per 5 m² in the root/bole zone and 2.0 ± 0.4 in the crown zone (Fig. 2b); these differences, however, were not statistically significant ($P = 0.54$; Table 1). The lack of a significant interaction between liana colonization and gap zone suggests that lianas were consistently more abundant in the root/bole zone than the crown zone.

3.3. Sapling and tree colonization in logging gaps

Mean sapling abundance increased significantly in logging gaps by year 6, suggesting that relatively small, sapling-sized trees continued to recruit into the gaps after the first year (Fig. 2c and Table 1). Mean sapling diameter, however, decreased between years 1 and 6 (Fig. 2d), possibly because many of the larger saplings grew out of the 1–4 cm size-class and were replaced by smaller ones. Indeed, larger trees (>4 cm dbh) increased slightly, but not significantly by year 6 ($P = 0.10$; Fig. 2f and Table 2).

There were no differences in the mean height of saplings or the amount of liana infestation among the different aged gaps (Fig. 2e and g), even though liana

Table 2

Kruskal–Wallis analyses for the number and the level of liana infestation of big trees (>4 cm dbh) in chronosequence plots (0, 1, and 6 years after tree felling) and for the pre-harvest liana cutting vs. control plots^a

Source	Treatment		Zone	
	χ^2	<i>P</i>	χ^2	<i>P</i>
Chronosequence plots				
Number of trees (>4 cm dbh)	4.66	0.10	4.33	0.04 ^b
Tree infestation	5.30	0.07	3.28	0.07
Liana-cut vs. control plots				
Number of trees (>4 cm dbh)	0.001	0.97	4.09	0.04 ^b
Tree infestation	8.25	0.004	0.62	0.43

^a The number of degrees of freedom was 2 for the tests among the chronosequence plots and 1 for the tests between the liana-cut and control plots.

^b In each case the mean number of trees and lianas was greater in the root/bole zone than in the crown zone.

abundance had increased significantly (Fig. 2a and b). Canopy openness, however, was significantly higher in year 1 than in years 0 or 6; the latter 2 years were not significantly different from each other (Fig. 2h and Table 1). Canopy openness also differed significantly between the treefall zones, with an average openness index of 2.1 ± 0.1 (S.E.) in the root/bole compared to 1.8 ± 0.2 (S.E.) the canopy zone ($P = 0.04$; Table 1). The higher light levels in the root/bole zone may have enhanced the recruitment of trees into the larger size-class, with large trees being significantly more abundant in the root/bole zone compared to the crown zone ($P = 0.04$; Fig. 2f and Table 2).

3.4. The effects of liana cutting in logging gaps

Pre-harvest liana cutting reduced the number of lianas in logging gaps 1 year after timber extraction. The average number of liana stem sprouts (>1 mm dbh) and liana individuals (>1 cm dbh) were both significantly lower in the liana-cut than the control gaps (Fig. 3a and b and Table 1). For liana stem sprouts, there were 36.7 ± 2.4 (S.E.) per 5 m^2 in the control plots, while only 24.3 ± 2.4 (S.E.) in the liana-cut plots. Lianas >1 cm dbh were twice as abundant in the control gaps compared to the liana-cut gaps (1.6 ± 0.3 (S.E.) vs. 0.8 ± 0.3 (S.E.), respectively). Similar the chronosequence gaps, liana stem sprouts were significantly more abundant in the root/bole zone

than in the canopy zone, but liana genets did not differ between the gap zones.

These findings demonstrate that even though lianas sprout vigorously after cutting, pre-harvest liana cutting still significantly reduced the number of liana stems, including multiple stem sprouts, in logging gaps. Correspondingly, the average amount of liana infestation on both saplings and trees was significantly lower in the liana-cut compared to the control gaps (Fig. 3f and g and Tables 1 and 2). Surprisingly, both the average sapling height and the amount of canopy openness were significantly lower in the liana-cut plots (Fig. 3e and h and Table 1). The abundance and diameter of saplings and trees and the height of trees, however, did not differ significantly between the liana-cut and the control gaps (Fig. 3c and d and Tables 1 and 2).

4. Discussion

4.1. How lianas colonize logging gaps

Lianas recruited into logging gaps in high abundance within 1 year of gap formation. The majority of these lianas were ramets, sprouting from fallen liana stems. These liana ramets appeared to persist in the gaps for many years, eventually reaching the 1 cm dbh size-class within 6 years. Our findings are consistent with those of other studies of liana invasion in both natural and logging gaps (Putz, 1984; Babweteera et al., 2000; Schnitzer et al., 2000; Tabanez and Viana, 2000; Gerwing and Vidal, 2002); although Kennard (1998) suggested that climber infestation is mainly a colonizing process, rather than being predominated by stump sprouts of surviving lianas. For example, in natural treefall gaps, Putz (1984) found that lianas were very abundant in young gaps and decreased only after many years. Schnitzer et al. (2000) also reported that lianas recruited en masse into natural treefall gaps, reaching very high abundance and often completely suppressing tree regeneration within 5 years of gap formation. In Brazil, Thompson et al. (1998) monitored small trees and lianas over a period of 4 years in different gap sizes and concluded that liana densities in large gaps were twice those of interior forest. In a selectively logged forest in Uganda, Babweteera et al. (2000) also found that lianas recruited rapidly and

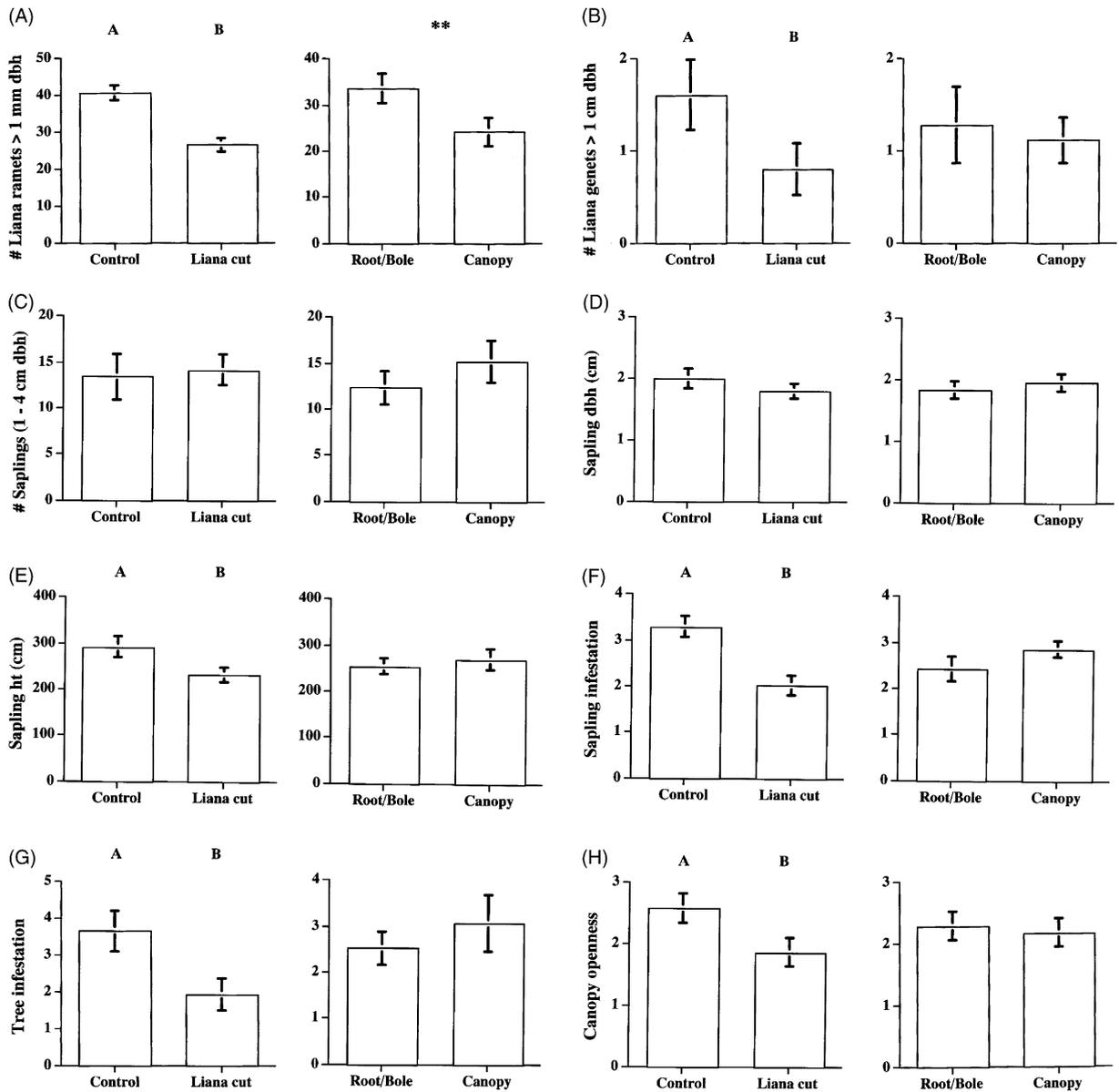


Fig. 3. Liana and tree recruitment in 1-year old, single-tree timber extraction gaps in which lianas were either left uncut (Control) or all lianas were cut 9 months prior to timber extraction (column 1) and the zone of the gap into which the lianas recruited (column 2). We classified trees as either saplings (1–4 cm dbh) or trees (>4 cm dbh). We divided lianas into two groups: (1) liana stem sprouts (ramets) >1 mm dbh; and (2) liana individuals (genets) >1 cm dbh. Different letters denote significant differences among the control and liana-cut logging gaps. Asterisks denote significant differences between the gap zones. Errors bars represent ± 1 S.E.

abundantly into large logging gaps (>400 m²). Similarly, lianas recruit in extremely high abundance into such large-scale disturbances as abandoned pastures and areas affected by hurricanes (Horvitz et al., 1998; DeWalt et al., 2000).

Interestingly, we found the majority of liana stems, particularly ramets, in the root/bole zone of the gap (~33 stems per 5 m²; Table 1). This zone may have had the most ramets because stem sprouts can originate along the entire length of a fallen liana stem. If the

liana is rooted at the base of the fallen tree, which many of the lianas were, then most of the stem sprouts will also be at the base and along the bole of the fallen tree. In addition, the root/bole zone may have had the most light and least amount of competition for below-ground resources. However, there were still a substantial number of stem sprouts in the canopy zone (~ 25 stems per 5 m^2), demonstrating that lianas can recruit into both zones in high abundance.

4.2. Pre-harvest liana cutting as a method for reducing liana load on trees

Our findings demonstrate that pre-harvest liana cutting significantly reduces liana abundance in post-logging gaps (see also Gerwing and Vidal, 2002), which resulted in significantly lower rates of liana infestation of trees. The detrimental effects of lianas on trees are well established in the literature (Nicholson, 1958; Putz, 1984; Stevens, 1987; Dillenburg et al., 1993; Schnitzer et al., 2000; Pérez-Salicrup and Barker, 2000; Schnitzer and Bongers, 2002), and thus we expect that in the long run, trees with high liana infestation will have less vigorous growth and reproduction. After 1 year, however, canopy openness was significantly higher and saplings were taller in the control plots, which had substantially more lianas (Fig. 3e and h). The positive relationship between liana abundance and canopy openness was probably due to the ability of lianas to keep the gap open for long periods of time. Schnitzer et al. (2000) reported that lianas favor the growth of some trees, primarily pioneers, at the expense of shade-tolerant trees, possibly by keeping gaps open for many years, thus giving the pioneers a chance to grow into the canopy (see also Putz, 1984). In this current study, the large number of lianas may have also inhibited canopy closure (Fig. 3h) and thus both the lianas and saplings grew slightly more in the higher-light environment. We suspect, however, that this benefit of increased light during the first year will be short-lived, and that the saplings with lower liana infestation will eventually surpass the height and vigor of trees that have more lianas in their crowns. If competition with lianas for below-ground, rather than above-ground resources in gaps is the mechanism that ultimately limits sapling growth, as has been suggested by a number of recent studies (Dillenburg et al., 1993; Pérez-Salicrup and Barker,

2000; Schnitzer et al., in review), then sapling growth should also decrease as the surrounding lianas increase in abundance and size.

4.3. Managing lianas in tropical forests

The decision to cut climbers in managed forests is complex, with a number of factors to consider. Treefall gaps, whether they are natural or anthropogenic in origin, appear to provide the optimal regeneration site for lianas (Putz, 1984; Babweteera et al., 2000; Schnitzer et al., 2000; Schnitzer and Carson, 2001). Consequently, managing lianas in gaps may be the key to controlling liana abundance in logged forests. Although it is likely that no reasonable management plan will be able to completely eradicate lianas from managed forests because of the ability of lianas to resprout copiously from cut and fallen stems, our findings suggest that pre-harvest climber cutting reduces the number of regenerating stem sprouts, which ultimately should lead to more rapid canopy tree regeneration. Pre-harvest climber cutting also provides a number of other beneficial results, including reducing the collateral damage to other trees and reducing the size of logging gaps (Appanah and Putz, 1984; Putz, 1984, 1985; Pinard and Putz, 1994; Vidal et al., 1997; but see Parren and Bongers, 2001). A potentially important long-term result of logging and liana cutting (which is sometimes followed by fire) may be a change in the composition of the liana community, favoring those species that can readily resprout in response to disturbance, while putting at a disadvantage those species that rely primarily on sexual reproduction (Bell, 2001; Bond and Midgley, 2001; Del Tredici, 2001; Gerwing and Vidal, 2002). For instance, Parren and Bongers (2001) reported that some species of liana resprouted readily after cutting, while others were much more vulnerable (see also Vidal et al., 1997). To date, however, the potential changes in liana communities in response to cutting have received very little attention (Gerwing and Vidal, 2002).

Post-harvest liana cutting may also be beneficial for controlling liana regeneration in logging gaps. Although Putz (1985) argued that there was very little benefit of post-harvest liana cutting and that it is very difficult to kill the multiple stems of recumbent lianas, a combination of selective pre- and post-harvest

climber cutting might be the best option for controlling liana regeneration after logging. The costs vs. benefits of post-harvest climber cutting, of course, must be assessed for specific regions in the tropics (e.g., Perez-Salicrup et al., 2001). Some of the considerations of this analysis most certainly will include: the cost of labor, the amount of effort for post-harvest climber cutting, and, most importantly, the effectiveness of post-harvest climber cutting in controlling liana resprouting and regeneration from seed.

Knowing the zone of the gap into which lianas recruit provides additional information on how lianas invade logging gaps and thus will be instrumental in devising management plans on how to control liana regeneration after logging. For example, if lianas recruit exclusively into the crown zone, then pre-harvest liana cutting may be necessary both around the bole of the target tree, where many of the lianas in the canopy originate, as well as in a larger area of forest around the target tree. The rationale for this latter treatment is that large lianas in the canopy of a tree may actually be rooted quite far from the base of that tree (Putz, 1984), and thus if the above-ground portion is cut and subsequently dies, then it cannot sprout from its recumbent stem after the tree is felled. Conversely, if lianas recruit exclusively into the root and bole zones, then pre-harvest liana cutting around the base of the target tree may be the most efficient method for limiting liana regeneration and therefore cutting in a larger area would not be necessary.

We found that liana sprouts consistently recruited into the root/bole zone in much higher abundance than in the crown zone (Fig. 2a), supporting the management strategy of cutting the lianas found around the base of the tree. However, lianas were still abundant in the crown zone, albeit in somewhat lower density, suggesting that both management strategies have some merit. Overall, we suggest that cutting lianas located in the area beneath the canopy of the target tree may be the best overall strategy for reducing liana infestation in logging gaps and promoting tree regeneration. This strategy will certainly remove most of the lianas in the canopy of the regenerating trees as well as greatly reduce below-ground competition, which may be important for liana-tree competition (Dillenburg et al., 1993; Pérez-Salicrup and Barker, 2000; Schnitzer et al., in review).

5. Conclusions

Lianas recruit rapidly into logging gaps in high abundance within the first year of gap formation. Recruitment was mostly from stem sprouts, many of which apparently became independently rooted individuals that were indistinguishable from genets within 6 years. Most of the liana recruitment was into the root/bole zone of logging gaps, but lianas were still in fairly high abundance in the canopy zone. Our findings demonstrate that pre-harvest liana cutting significantly reduced the number of lianas that regenerated in logging gaps, resulting in saplings that were infested with fewer lianas and were significantly taller than in the gaps where lianas were not cut prior to logging. Based on our findings and those of other studies, we recommend pre-harvest liana cutting in the area beneath the canopy of the target tree for controlling liana regeneration and promoting tree regeneration in logging gaps.

Acknowledgements

This study is a contribution to the Tropenbos Cameroon Programme. We thank the Tropenbos Foundation and IRAD, Cameroon, for their support, and Wijma for being able to work in their logging concession. S. Mutsaers, M. Elad, S. Okie and J. Ango collected a large part of the field data. We thank A. Ercoli, D. Pérez-Salicrup, F. Sterck, and one anonymous reviewer for helpful comments on this manuscript.

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