

The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration

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Summary

1 Regeneration in forest canopy gaps is thought to lead invariably to the rapid recruitment and growth of trees and the redevelopment of the canopy. Our observations, however, suggest that an alternate successional pathway is also likely, whereby gap-phase regeneration is dominated by lianas and stalled in a low-canopy state for many years. We investigated gap-phase regeneration in an old-growth tropical forest on Barro Colorado Island (BCI) in Panama to test the following two hypotheses: (i) many gaps follow a pathway in which they remain at a low canopy height and are dominated by lianas and (ii) the paucity of trees in this pathway is a function of liana density.

2 We surveyed a total of 428 gaps of varying ages (*c.* 5, *c.* 10, and 13+ years old) and identified those which followed the conventional pathway of regeneration and others that remained stalled in a low-canopy state for many years and were dominated by either lianas or palms. Each of these pathways will likely have different successional trajectories that will favour the growth of a distinct suite of mature species and ultimately result in contrasting species composition.

3 The successional pathway of liana-dominated, stalled gaps is common throughout the forest. We estimate conservatively that 7.5% of the gaps that form each year will follow this pathway, probably due to the suppression of tree regeneration by lianas, and that many of these stalled gaps will persist for much longer than 13 years. Consequently, a high proportion of gaps in the forest at any given time will be stalled. Furthermore, liana tangles, which persist in the tropical forest understorey for extended periods of time, almost certainly originate in these gaps.

4 Liana abundance was positively correlated with pioneer tree abundance and diversity while negatively correlated with non-pioneer tree abundance and diversity. Thus, lianas appear to inhibit non-pioneer tree survival while indirectly enhancing that of pioneer trees.

5 Lianas are abundant in many types of tropical and temperate forests and a successional pathway involving liana-dominated, stalled gaps may therefore be frequent and widespread.

Key-words: Species diversity, forest succession, canopy dynamics, Barro Colorado Island, Panama.

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Introduction

Treefall gaps are thought to play a major role in the regeneration of many plant species in both tropical

and temperate forests (Ricklefs 1977; Strong 1977; Denslow 1980a, 1987; Runkle 1981; Canham & Marks 1985). Plant community composition may be dependent upon both the frequency of gap creation and the mode of gap-phase regeneration (Hartshorn 1978; Denslow 1980b, 1987; Brokaw 1985a; Lawton & Putz 1988; Phillips & Gentry 1994). Gap-phase

regeneration is typically thought to follow one primary pathway (*sensu* Pickett *et al.* 1987) that begins, following a treefall, with germination from the soil seed bank and the rapid growth of advance regeneration, i.e. the seedlings and saplings that were present in the understorey prior to gap formation (Whitmore 1975; Brokaw 1985a, 1987; Fraver *et al.* 1998). Tree densities within the gap increase initially but begin to decline within 3 to 6 years of gap formation as the trees increase in size (Brokaw 1985a, b; Hubbell & Foster 1986; Runkle & Yetter 1987). In tropical forest gaps, the height of the canopy can increase by as much as 5 to 7 m yr⁻¹, particularly when common pioneer trees (e.g. *Trema micrantha*, *Cecropia insignis* and *Zanthoxylum* spp.) are present (Putz 1983; Brokaw 1985a, 1987) and by several metres per year for non-pioneer trees (e.g. *Simarouba amara*, *Virola sebifera* and *Protium panamensis*; Brokaw 1985a).

Observations from Barro Colorado Island (BCI) have led us to suggest that many gaps may follow an alternative successional pathway, whereby they are dominated by lianas or palms and remain stalled in a low-canopy state for many years. This stalled-gap pathway may be common, and we suggest that it is predominantly caused by a suppression of tree regeneration by the dense tangles of lianas that clog gaps and thus lower tree density and diversity. Indeed, liana tangles have been observed in many forests (Fox 1968; Hegarty 1989; Balée & Campbell 1990; Yavitt *et al.* 1995), and some researchers have suggested that they originate in gaps (Hartshorn 1978; Putz 1984a). Moreover, Whitmore (1989) argued that large gaps could be invaded by woody climbers that could 'arrest the next growth cycle'. Although there is some evidence for these claims (Putz 1984a), the impact of such lianas and of palms on forest-wide, gap-phase regeneration remains largely unknown.

Cases of arrested succession (*sensu* Niering & Goodwin 1974), whereby a successional sequence can be interrupted or halted by the establishment of recalcitrant vegetation, have been documented in a number of systems (McClanahan 1986; Putz & Canham 1992; Lugo 1997; Sarmiento 1997). The occurrence, impact and ramifications of arrested succession within mature systems (e.g. treefall gaps within old-growth forests), however, have not been well studied (but see Chapman *et al.* 1999). We suggest that the ability of lianas to colonize and proliferate allow them to arrest regeneration in gaps for many years and cause the pattern of regeneration to proceed on an altered successional trajectory. Specifically, lianas may become abundant in gaps because: (i) more than 90% of adult lianas survive the treefall that leaves them in a gap (Putz 1984a); (ii) lianas are often abundant in the intact forest prior to gap formation (Putz 1984a; Putz & Chai 1987); (iii) lianas also recruit into the gap both from

seed rain and the soil seed bank (J. W. Dalling, unpublished data); (iv) they can encroach into the gap from the surrounding intact forest (Peñalosa 1984); and (v) lianas present in a gap can sprout prolifically, producing many new stems (Appanah & Putz 1984). Consequently, arrival immediately following gap creation and rapid proliferation thereafter may lead to lianas being significantly higher in density and diversity in gaps than in the intact forest.

Liana proliferation in gaps may reduce growth and increase mortality of trees by pre-empting light, increasing below-ground competition, mechanically preventing trees from growing upward and providing cover for seed- and seedling-predators. In general, lianas appear to reduce tree growth and survivorship in both gap (Putz 1984a) and non-gap (Nicholson 1958; Lowe & Walker 1977; Clark & Clark 1990) areas throughout the forest. For example, Putz (1984a) found a negative relationship between liana basal area and tree diameter growth in gaps. Because lianas are abundant in many tropical forests (Gentry 1982, 1991; Gentry & Dodson 1987; Clark & Clark 1990; Appanah *et al.* 1992), the potential for lianas to alter gap-phase regeneration could be frequent and widespread, but data on the prevalence or duration of stalled gaps remain scarce.

In this study, we tested two related hypotheses that challenge the traditional view that all treefall gaps follow a pathway of rapid canopy height regeneration and tree domination. Instead, we propose that: (i) many gaps remain at a low-canopy height and are dominated by lianas, and (ii) the paucity of trees in such gaps is a function of liana density. We addressed these hypotheses by surveying a total of 428 gaps of three different ages in an old-growth tropical forest on BCI.

Methods

STUDY SITE

We conducted this study in a 50-ha old-growth forest plot on Barro Colorado Island (BCI) in central Panama (Hubbell & Foster 1983, 1986; Condit *et al.* 1992a, b; Hubbell *et al.* 1999). This 1600 ha island was isolated from the mainland in 1914 following the creation of Gatun Lake (McCullough 1977; Leigh *et al.* 1996) and is covered by a seasonally moist, lowland tropical forest that receives an annual rainfall of approximately 2600 mm, 90% of which typically falls between May and December (Leigh & Wright 1990; Dietrich *et al.* 1996; Foster & Brokaw 1996). For detailed information on the 50-ha forest-dynamics plot and on the formation, geology, climate, flora and fauna of BCI, see Croat (1978), Hubbell & Foster (1983, 1986), Gentry (1990) and Leigh *et al.* (1996).

GAP IDENTIFICATION AND DEFINITION

We identified gaps using canopy-height data that have been collected annually since 1983, using a range pole or range finder at the intersection of every 5 × 5 m subplot located throughout the 50-ha plot (> 20 000 points yr⁻¹). Canopy heights were classified as: 0–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m or > 30 m (for data collection methodologies see Hubbell & Foster 1986; Welden *et al.* 1991; Condit *et al.* 1992b; Dalling *et al.* 1998; Hubbell *et al.* 1999).

We defined a gap as an area of 25–75 m² that had a sustained canopy height of at least 20 m for two consecutive years before dropping to a height of 5 m or less during the following year (taken to be the year of gap formation; our methods follow those of Hubbell & Foster 1986; Welden *et al.* 1991; Dalling *et al.* 1998; Hubbell *et al.* 1999). Relatively small gaps compose the majority (up to 83% by number, Dalling *et al.* 1998) of all gaps in both mature and secondary forests (Sanford *et al.* 1986; Barton *et al.* 1989; Yavitt *et al.* 1995; Brokaw 1996; Hubbell *et al.* 1999). In addition, small gaps (25–100 m²) represented approximately two-thirds of the total gap area on BCI (Hubbell *et al.* 1999). We identified those gaps that had been created during three arbitrarily selected time periods: 1990–91 (*c.* 5-year-old gaps, *n* = 82), 1985–86 (*c.* 10-year-old gaps, *n* = 173), and prior to and including 1983 (gaps of 13+ years old, *n* = 173; defined as areas that were at a low-canopy height (< 5 m) for the first two consecutive years, 1983 and 1984, for which data were available). We visited and verified all 459 sites that met these criteria and excluded 31, most of which occurred over streams and trails, leaving 428 for analysis. For clarity, we regard the point where the canopy height measurement was recorded as the gap centre. We acknowledge, however, that we did not know the exact location of the gap centre, but the sampling scheme ensured that we encompassed both the centre and edge, even though we could not pinpoint the exact location of either of these zones.

GAP CLASSIFICATION AND FURTHER SELECTION

In March 1996, we visually assessed the vegetation cover in the canopy of all 428 gaps to determine the predominant canopy growth-form (*i.e.* that which covered at least 50% of the uppermost canopy in the area above the gap centre) and accordingly classified gaps as either liana-dominated, palm-dominated, or tree-dominated. We further classified those gaps that had failed to regenerate above 10 m by 1995 as 'low-canopy' gaps compared with 'high-canopy' gaps, where heights were typically much greater. Thus, we had two different types of gap based on canopy height, which were dominated by

one of three different growth forms and which dated from one of three periods. Our choice of only 10 m for the low–high-canopy boundary was constrained by the relatively wide bounds in the canopy-height data, and we therefore probably underestimated the proportion of gaps that were in a low-canopy state.

We quantified liana and tree abundance and diversity in 26 liana-dominated, low-canopy gaps that were randomly selected from all of those that were both liana-dominated and low-canopy for the three time periods. Few of these gaps had regenerated above 6–7 m (S. A. Schnitzer, personal observation). We paired each gap (*n* = 9, 9 and 8, respectively, for the 13+, 10 and 5-year-old gaps) with the closest high-canopy gap that was formed in the same year and was of the same approximate size. Gap pairs were separated by an average distance of 53.2 m (median = 37.5 m), with none more than 210 m apart. We made paired comparisons to account for the forest-wide variation in liana and tree abundance, diversity and species composition, so that we could examine the relationship between liana density and the suppression of trees during gap-phase regeneration.

SAMPLING LIANAS WITHIN GAPS

We divided each of the 52 selected gaps into four equal-sized quadrants. We then subsampled the density, diversity and size (diameter) of lianas within non-overlapping 1 × 5 m transects that radiated from the centre to the edge of the gap at a randomly chosen compass direction within each of the four quadrants. We measured the diameter of all liana stems (≥ 1), including multiple stems of the individuals, that crossed the plane of the transect parallel to the ground at a height of 130 cm. Stems with a smaller diameter were included in the census but were assigned a diameter of 0.5 cm. We pooled the transect data for each gap to get an estimate of liana density and diversity per 25–75 m² gap area. All lianas and trees were identified and verified in the field and by herbarium specimens by Eduardo Sierra, a professional botanist with more than 12 years of taxonomic experience on BCI.

Lianas in gaps can resprout vigorously and each individual plant can produce many stems that contribute to a liana tangle (Appanah & Putz 1984; Putz 1984a). We therefore determined both the number of liana individuals and the total number of liana stems in each gap. We defined an *individual* as an independent liana (genet) that was not connected above-ground or obviously connected below-ground to any other stem included in the census (methods follow those of Putz 1984a). We defined a *stem* as any vegetative offshoot (ramet) of an individual already included in the census. We acknowledge, however, that currently or previously existing under-ground connections prevented us from always dis-

tinguishing a true genetic individual, but we assumed that the effect of lianas is proportional to their abundance, regardless of whether the stems are truly independent.

SAMPLING TREES WITHIN GAPS

We measured the diameter of all trees ≥ 1 cm d.b.h. within each of the 52 gaps. We classified each tree as a member of either the pioneer or non-pioneer (shade-tolerant) guild according to Dalling *et al.* (1998). Pioneers are described as species that establish and regenerate, typically from seed, only in gaps, while non-pioneers can establish and persist both in gaps and in the intact forest (Swaine & Whitmore 1988; Whitmore 1989; Dalling *et al.* 1998).

STATISTICAL ANALYSES

We estimated the change in the proportion of liana-dominated, low-canopy gaps of the three ages: 5 years ($n=82$), 10 years ($n=173$), and 13+ years ($n=173$). We compared liana density and basal area between the liana-dominated low canopy and paired high-canopy gaps using a paired one-way analysis of variance (ANOVA) in SYSTAT (SAS Institute 1995; Wilkinson *et al.* 1992; Sokal & Rohlf 1995). In our ANOVA model, we used the difference between each of the gap pairs as replicates, and compared the mean of those differences to zero. We included the interaction of gap type and year in the model. In addition, we used a Fisher's exact test to examine the frequency with which liana-dominated gaps had higher liana individual and total stem density and

basal area than the paired high-canopy gaps (Sokal & Rohlf 1995; Weir 1996).

To examine the relationship between lianas and trees in gaps, we regressed the pioneer and non-pioneer tree density and species richness on the density and basal area of liana individuals (genets) for the 26 low-canopy gaps, the 26 high-canopy gaps, and all 52 gap sites combined. We used regression rather than correlation analysis because we argue for a cause and effect relationship, even though the data are correlative (see Conclusions). The separate analyses allowed us to determine whether there is evidence for an alternate successional pathway of regeneration in the liana-dominated, low-canopy gaps. The combined analysis allowed us to examine the relationship between trees and lianas along a gradient of liana density. We used liana individual density because it is a more conservative measure than the total stem density and would not give undue weight to small stems, although it does in fact yield very similar regression results. Results using liana density were always similar to those using basal area and only the former regressions are therefore presented.

Results

HYPOTHESIS 1: MANY TREEFALL GAPS FOLLOW A PATHWAY IN WHICH THEY REMAIN AT A LOW CANOPY HEIGHT AND ARE DOMINATED BY LIANAS

Recalcitrant low-canopy gaps were indeed common within the 50-ha plot on BCI. Approximately 29%, 12% and 43%, respectively, of the 13+, 10 and 5-year-old gaps remained at a low-canopy height (Fig. 1). Except for 5-years-old sites, where palms

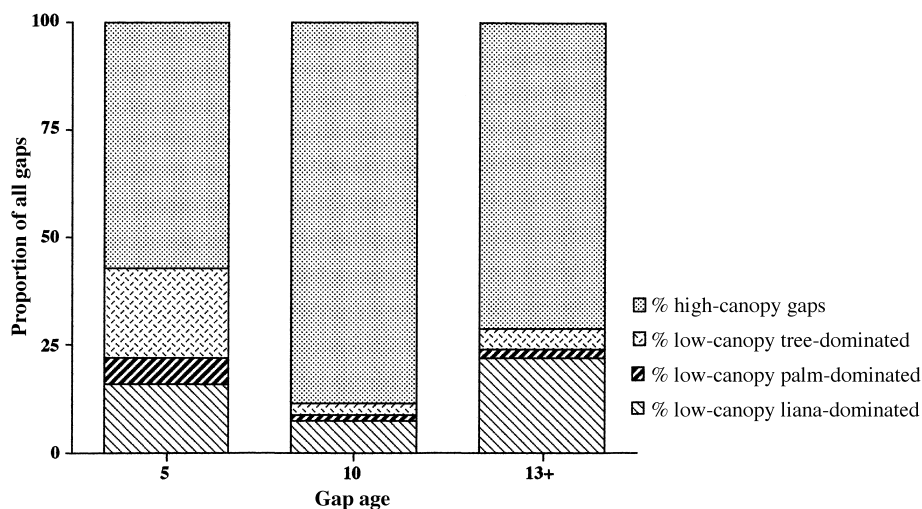


Fig. 1 The proportion of 25–75 m² gaps of different types in 1996 in a 50-ha plot on Barro Colorado Island, Panama. The gaps were either 5 years old ($n=82$), 10 years old ($n=173$), or 13+ years old ($n=173$). Gaps in which the canopy had regenerated to > 10 m in height were classed as high canopy.

and trees dominated a significant proportion of the low-canopy gaps, liana-domination was the most common condition of these gaps, and this category composed 22%, 7.5% and 16% of all of the gaps formed during the 13+, 10 and 5-year-old periods, respectively (Fig. 1). Note that our definition for the gaps aged 13+ years old probably resulted in an inflated percentage of these gaps being classed as dominated by lianas. Because we did not have canopy height information prior to 1983, it was impossible to determine the exact year of gap creation. Consequently, we may have included a disproportionately high number of recalcitrant liana-dominated gaps that had formed in the years prior to 1983, while missing those gaps that were formed in the same years but had regenerated naturally and were thus no longer identifiable as a gap. If this is the case, the accumulation of gaps formed over many years in our oldest category would suggest that gaps can remain in a low-canopy state dominated by lianas for much longer than the 13 years examined in this study. Alternatively, the high percentage of low-canopy gaps of 13+ years old could be due to particularly favourable conditions for liana colonization in 1983–84. Domination and suppression by lianas would then be nearly three times as frequent in such favourable years as at other times. Consequently, our 7.5% estimate of the proportion of gaps dominated by lianas (based on the 10-year-old gaps) may be extremely conservative.

Our classification of liana-dominated gaps based on visual cover estimates was confirmed by higher liana density and basal area (Fig. 2). Liana-dominated gaps had three times greater mean liana individual (genet) density and almost four times greater total stem (ramet) density per 20 m² subsampled area than in high-canopy gaps (Fig. 2a, b). Liana-dominated gaps were nearly always significantly greater than their paired high-canopy gaps in liana individual density (24 of 26), total stem density (25 of 26), liana individual basal area (26 of 26) and total stem basal area (26 of 26; $P < 0.0001$ for each of the four comparisons, Fisher's exact test). We did not detect a significant effect of gap age on liana density between the gap types ($F_{1,2} = 0.73$, $P = 0.40$), suggesting that when lianas colonize gaps they do so relatively early and then persist for many years.

HYPOTHESIS 2: THE PAUCITY OF TREES IN THE LIANA-DOMINATED PATHWAY IS A FUNCTION OF LIANA DENSITY

Non-pioneers were the predominant tree type, comprising approximately 90% of the trees per gap (mean non-pioneers = 46.2 ± 3.0 SE; mean pioneers = 5.3 ± 0.8 SE; $n = 52$) in all of the gaps combined. The relative proportions of non-pioneer to pioneer trees were nearly identical in both the liana-dominated, low-canopy and the high-canopy gaps. In the

liana-dominated, low-canopy gaps, liana density showed a significant negative relationship with the density of these non-pioneer trees but not with their species richness (Fig. 3a). There was no relationship, however, between liana density and non-pioneer species richness in the liana dominated, low-canopy gaps (Fig. 3a). On the other hand, in the high-canopy gaps, there was a positive relationship between liana density and the density and species richness of non-pioneer trees when liana abundance was low, but the slopes levelled-off or became negative as liana abundance increased (Fig. 3b). When we pooled the low-canopy and high-canopy gaps to provide an extended gradient of liana density, there was a curvilinear relationship between liana density and both the density and species richness of non-pioneer trees (Fig. 3c). This suggests that lianas

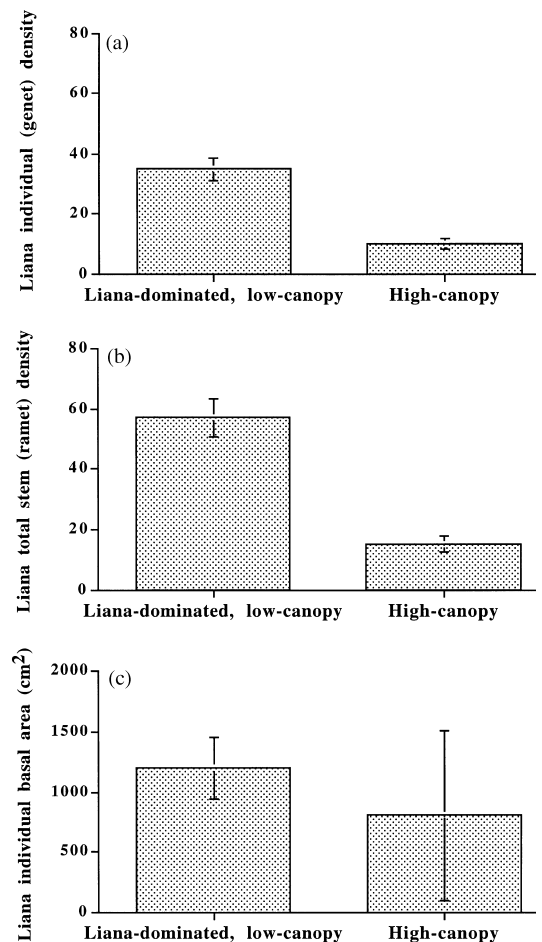


Fig. 2 Mean liana density for (a) individuals, (b) total stems, and (c) mean basal area of the liana-dominated, low-canopy and the paired high-canopy gaps per 20 m² area subsampled within the gap. Error bars represent one standard error of the mean; however, paired analyses were used to analyse the data. The liana-dominated gaps had significantly higher individual liana density ($F_{1,24} = 13.15$, $P = 0.001$), total liana stem density ($P < 0.0001$, d.f. = 25), and basal area ($F_{1,24} = 7.37$, $P = 0.012$).

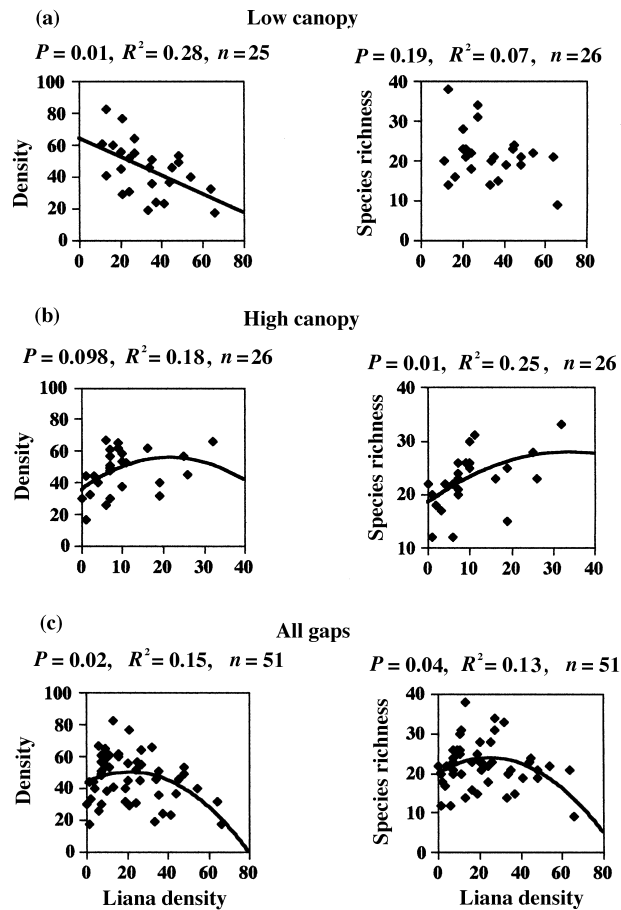


Fig. 3 Non-pioneer tree density and species richness per gap regressed on liana density per 20 m² subsampled area for (a) liana-dominated, low-canopy gaps, (b) high-canopy gaps, and (c) all gaps combined. We included all non-pioneer trees ≥ 1 cm d.b.h. within the 75 m² gap area. Outliers identified using a Mahalanobis outlier analysis (SAS Institute 1995) were excluded.

begin to affect non-pioneer trees negatively at densities of 20–30 lianas 20 m⁻² (see Fig. 3b, c).

Surprisingly, the relationship between liana density and the density and species richness of pioneer trees were positively correlated in both the liana-dominated, low canopy (Fig. 4a) and the tree-dominated, high-canopy gaps (Fig. 4b). In addition, we found a significant positive, linear relationship between liana density and both pioneer density and species richness along the entire gradient of liana density (all gaps combined; Fig. 4c).

Discussion

THE FREQUENCY OF STALLED GAPS AND THE ORIGIN OF LIANA TANGLES IN TROPICAL FORESTS

We estimate that the presence of lianas stalls tree recruitment in about 7.5% of all gaps per year. Moreover, stalled gaps will tend to accumulate throughout the forest as lianas continue to suppress gaps over time (note the high number of stalled gaps

in the 13+ gap category; Fig. 1). We are not suggesting that the number of liana-dominated, stalled gaps increases indefinitely; rather, that there is a steady-state in which the recruitment of new stalled gaps is balanced by the release of old ones. We suggest that this steady-state is approximately 22% for gaps older than 13 years (Fig. 1).

Patches of dense tangles of lianas have been observed in many forests (Putz 1980, 1985; Hegarty 1989; Balée & Campbell 1990; Phillips & Gentry 1994; Yavitt *et al.* 1995), and some have suggested that these liana tangles are formed shortly after gap creation (Hartshorn 1978; Putz 1984a). Data in support of this contention, however, remain scarce (but see Putz 1984a), but in a companion study, we have found that lianas were significantly higher in abundance and diversity in gaps than in the intact forest (Schnitzer & Carson, 2001). We propose that liana diversity in tropical forests is maintained by the formation of canopy gaps, and this study demonstrates that a significant proportion of gaps become engulfed by lianas. Overall, it appears that liana tan-

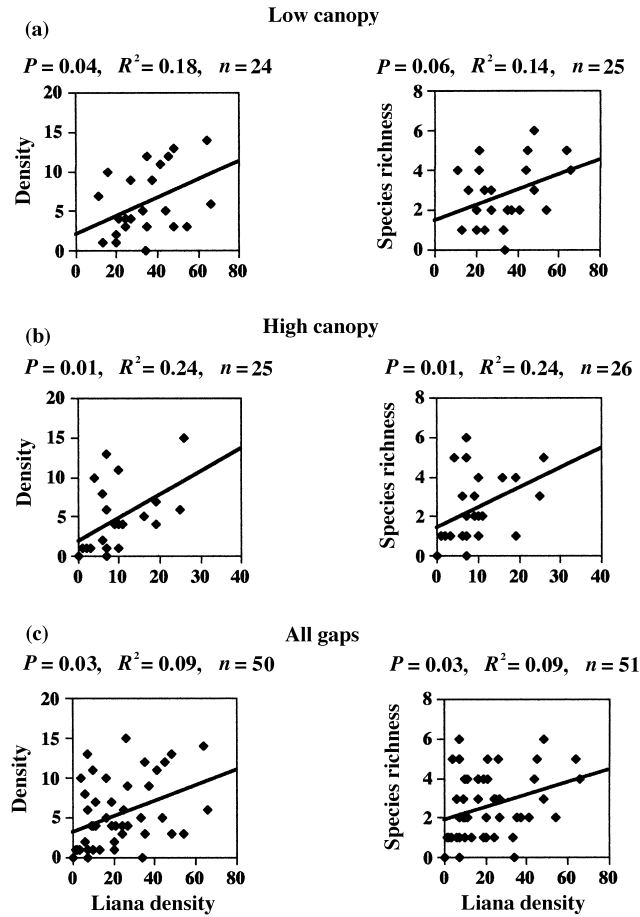


Fig. 4 Pioneer tree density and species richness per gap regressed on liana density per 20 m² subsampled area for (a) liana-dominated, low-canopy gaps, (b) high-canopy gaps, and (c) all gaps combined. Outliers identified using a Mahalanobis outlier analysis (SAS Institute 1995) were excluded.

gles arise when a treefall pulls down adult lianas into a gap and these adults sprout new stems and spread copiously. In addition, lianas colonize the gap from seed and from advance regeneration and also encroach into the gap from the edge (Appanah & Putz 1984; Peñalosa 1984; Putz 1984a; Putz & Chai 1987; Schnitzer & Carson, 2001). In the high light environment of a gap, lianas that fail to find a trellis often show rapid lateral growth rather than vertical growth (Putz 1984a), winding around the forest floor (Peñalosa 1984) and potentially contributing to the liana tangle. Once a liana tangle forms, it continues to expand, thereby blocking and delaying conventional gap-phase regeneration of trees by pre-empting light and imposing mechanical interference. At some subsequent point, trees escape vertically through the tangle and close the canopy above leaving an impenetrable thicket of lianas in the understory. These liana tangles are typically observed in many patches of closed canopy tropical forest and we have found similar tangles of *Vitis* spp. in temperate forests (Long & Carson, unpublished data).

In addition to delaying canopy regeneration, lianas appeared to sharply reduce the abundance of non-pioneer trees in stalled gaps (Fig. 3a). They can therefore essentially stall the entire gap because non-pioneers composed approximately 90% of the number of trees in the gaps. Although our data are correlative, we suggest that this could be a cause and effect relationship, with lianas reducing the abundance of non-pioneer trees either through resource competition (e.g. light pre-emption or underground competition) or by physically barring trees from growing vertically. Furthermore, our data are consistent with numerous studies that demonstrate that lianas, even in relatively low abundance, tend to decrease the growth of non-pioneer trees and increase their mortality (Ogawa *et al.* 1965; Lowe & Walker 1977; Putz 1983, 1984a; Putz *et al.* 1984; Whigham 1984; Clark & Clark 1990). We also demonstrate that the species composition of a gap, as well as many other characteristics (e.g. light availability and diversity) is likely to depend upon whether or not a gap gets clogged by a high density of lianas, with this situation usually occurring within

the first 5 years after gap creation (note that there was no significant difference in liana density among the different aged gaps).

A MODEL OF GAP-PHASE REGENERATION THAT INCLUDES MULTIPLE SUCCESSIONAL PATHWAYS

A successional sequence can be interrupted or arrested by a variety of causes, including the pre-emption of resources, competition, soil degradation, the lack of input, dispersal or survival of seeds, and human interference (McClanahan 1986; Putz & Canham 1992; Lugo 1997; Sarmiento 1997; Chapman *et al.* 1999). We suggest that not only can succession in gaps be arrested for many years, but that the eventual regeneration will proceed on different successional trajectories depending upon the arresting agent. We propose three possible successional pathways of gap-phase regeneration characterized by canopy height and contrasting species composition (Fig. 5). Specifically, the 'classic' pathway of tree domination, with a characteristic tall

canopy can be replaced by pathways of either liana or palm domination, with characteristic low canopies. Although this 'classic' pathway does describe the most common mode of gap-phase regeneration in the forest on BCI (Fig. 1), its predominance has perhaps obscured two distinct alternative successional pathways, one of which was common at this site.

Lianas are the dominant life-form in a second successional pathway of gap-phase regeneration (Fig. 5), which is characterized by a recalcitrant low canopy, a relatively low abundance of non-pioneer trees and a relatively high abundance of pioneer trees. This pathway will likely follow a long-term trajectory whereby lianas remain dominant and diverse, but with some pioneers present. Although some gaps that were initially dominated by lianas escaped this fate, 7.5% of the 173 10-year-old gaps remained stalled, and the proportion of these gaps likely increased over time (Fig. 1).

Lianas are common in both tropical and temperate forests (Smith & McCay 1979; Gentry 1982, 1991; Smith 1984; Whigham 1984; Gentry &

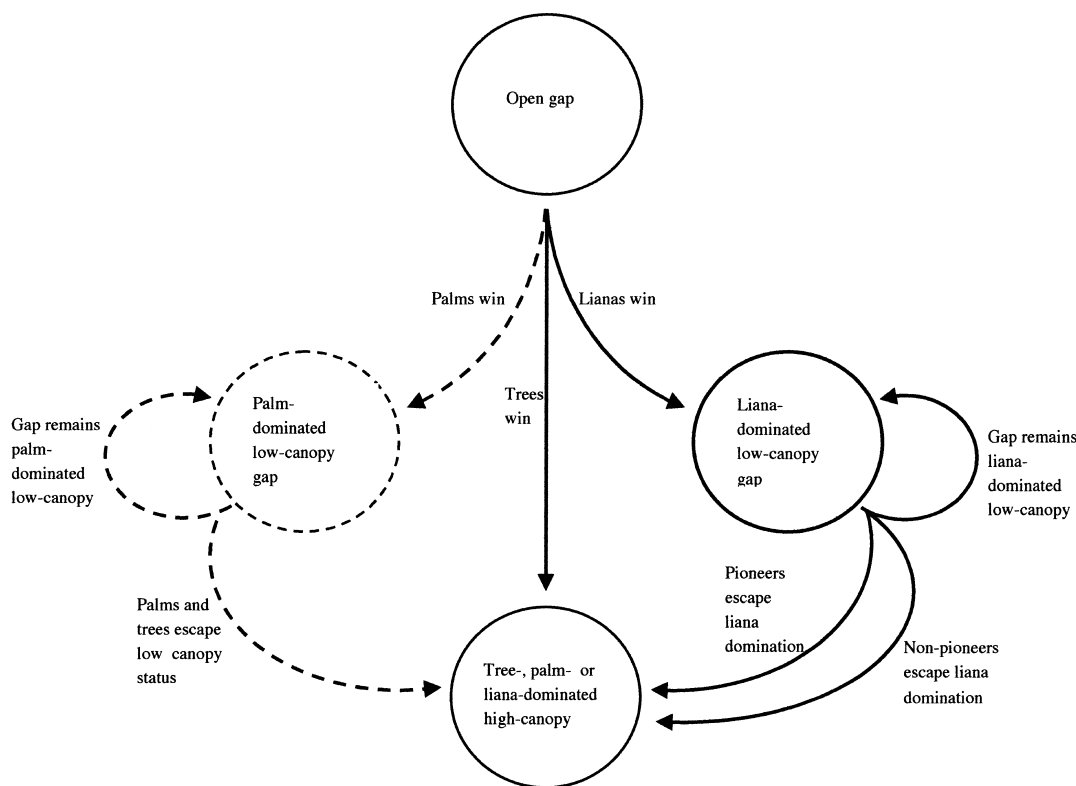


Fig. 5 A proposed model of forest gap-phase regeneration in which treefall gaps can regenerate via one of three pathways. In the conventional pathway, the gap is dominated by trees and rapidly regenerates a high canopy. This was the most abundant pathway on Barro Colorado Island, composing 71% of all gaps of 13 years and older. Alternatively, gaps could be stalled in a low-canopy state, dominated by either lianas or palms. Lianas dominated the majority of these low-canopy gaps, and 22% of all gaps 13+ years old followed this pathway. Liana-dominated, low-canopy gaps are characterized by a relatively low density of non-pioneer trees and a relatively high density of pioneer trees. We depicted the palm-dominated pathway with dashed lines because we have little evidence that this pathway is common (only 2.3% of all gaps followed a palm-dominated, low-canopy pathway). The relatively low percentage of palm-dominated gaps, however, is likely to be a function of the relative paucity of palms on BCI, and we suggest that this pathway may be important in the many tropical wet forests that have a relatively high abundance of palms.

Dodson 1987; Clark & Clark 1990; Schnitzer & Carson unpublished data) and the liana-dominated pathway may therefore be common in many forests throughout the world. For example, wild grape vines (*Vitis* spp.) appear to stall gaps in temperate forests by reducing tree growth rates and increasing mortality (Smith & McCay 1979; Smith 1984). Furthermore, Long and Carson (unpublished data) found a significant negative relationship between *Vitis* spp. density and tree density in gaps in an old-growth temperate forest fragment in north-west Pennsylvania ($F_{1,12} = 5.6$, $P = 0.04$, $R^2 = 0.32$). The presence of this liana-dominated pathway may have important ramifications at the ecosystem level, leading to over-estimations of above-ground biomass in forests. Indeed, Laurance *et al.* (1997) found a large increase in lianas within 100 m of disturbed forest edge that could not replace the loss of tree biomass in those sites, even after 17 years. While the continued absence of trees may have been due to the increased disturbance as a result of high wind turbulence (Laurance *et al.* 1997), the large increase in liana density probably played a role in stalling tree regeneration. Additionally, Phillips & Gentry (1994) suggested that the relative abundances of both lianas and gap-dependent tree species are increasing in forests on a global scale because of increasing forest productivity and gap formation. If this trend continues, then it is likely that lianas will have an increasing impact on gap-phase regeneration and that the liana-dominated pathway will become more common.

We propose that there might be a third successional pathway of gap-phase regeneration leading to palm-dominated, low-canopy gaps (Fig. 5). Although palms suppressed canopy height regeneration in only a small proportion of the 10-year-old gaps (1.2%; Fig. 1), this is may be because palms are not particularly abundant on BCI, and a palm-dominated pathway might well be more common in wetter forests like La Selva Biological Station in Costa Rica, where palm density and diversity are much higher (Lieberman *et al.* 1985; Clark 1994).

The palm-dominated pathway is likely to lead to a different species composition from either of the other two pathways. Palms grow slowly in the understorey and are often fully established before the gap is formed. Palms can suppress woody seedling regeneration by casting a very dark shadow as well as dropping heavy fronds that are slow to decay and can damage and smother young seedlings (Denslow *et al.* 1991). Indeed, there is often a paucity of seedlings under the canopy of many palms in the intact forest on BCI (S. A. Schnitzer, personal observation). In addition, lianas are rarely associated with palms (Putz 1984a; Hegarty 1989), which may be a result of the species composition specific to the palm-dominated pathway (but see Putz 1984b and Hegarty 1989 for alternative expla-

nations for the relationship between lianas and palms). Consequently, it is likely that only very shade-tolerant and resilient tree and palm species will regenerate in the palm-dominated pathway. We acknowledge that there are likely to be other pathways of gap-phase regeneration caused by plants like *Heliconia* and bamboo (F. E. Putz, personal communication), which are common in some forests; however, we did not find evidence of these other pathways in this study. Overall, our data demonstrate that multiple successional pathways occur in tropical forests following gap formation and, with the exception of the palm-dominated pathway, these pathways are also known to occur in temperate regions.

DO LIANAS PROMOTE PIONEER TREE ABUNDANCE AND DIVERSITY?

We suggest two likely, but not mutually exclusive, explanations for the positive relationship between liana density and pioneer tree density and diversity. First, many lianas may share life-history traits with pioneer trees and both are therefore likely to be found in gaps. We are not arguing that lianas are pioneer species (*sensu* Swaine & Whitmore 1988) because many lianas are common as advance regeneration (Putz 1984a; Putz & Chai 1987; Schnitzer & Carson unpublished data) and they make-up only a small percentage (2.2%) of the soil seed bank (Dalling & Denslow 1998). Rather, many liana species, like pioneers, are high light demanding, are capable of rapid growth and produce large seed crops (Lowe & Walker 1977; Putz 1984a, b; Whitmore 1989; Phillips & Gentry 1994); and gaps may thus provide opportunities for extensive colonization, establishment and rapid growth for both groups.

A second explanation is that a high abundance of lianas may promote pioneer tree density and diversity in gaps by reducing the competition from non-pioneer trees. Non-pioneer trees can rapidly increase canopy height and closure. High liana abundance in gaps can extend the life of a gap, in terms of light availability, by slowing rates of gap closure in the low- and mid-canopy layers (10–30 m) just above the liana tangle. Pioneers can emerge from a liana tangle into the open, high light, subcanopy zone of the gap because of their rapid growth rate, large leaves, and monopodial growth form (Lowe & Walker 1977; Putz 1984a, 1984b, 1985; Putz *et al.* 1984). Indeed, Putz (1984a) found that young pioneer trees often emerged from liana tangles between 10 and 20 years after gap formation. Further, Clark & Clark (1990) found that lianas were virtually absent in the crowns of 142 pioneer trees of *Cecropia obtusifolia* and *Cecropia insignis*, but were common (*c.* 80%) in the crowns of seven non-pioneer tree species. Although attendant ants may be

involved in removing climbers in these *Cecropia* species (Janzen 1973), Putz & Holbrook (1988) reported that, even in the absence of ants, *Cecropia peltata* had a lower incidence of liana infestation than other common pioneer species. Consequently, high liana abundance may indirectly promote the abundance and diversity of pioneer trees in tropical forests.

The negative relationship between the abundance of lianas and non-pioneer trees suggests that lianas reduce tree survivorship rather than recruitment. In general, non-pioneer trees are present primarily as advance regeneration prior to gap formation and they typically do not recruit into the gap (Swaine & Whitmore 1988; Uhl *et al.* 1988; Whitmore 1989; Schnitzer & Carson, 2001). Therefore, an effect of lianas on non-pioneer recruitment is unlikely. On the other hand, pioneer trees only recruit into a gap and are rarely, if ever, present as advance regeneration (Swaine & Whitmore 1988; Whitmore 1989). The positive relationship between liana density and pioneer tree density and diversity suggests that lianas do not reduce net recruitment in gaps, but rather the stalling of gap-phase regeneration is due to decreasing tree survivorship.

Conclusions

Lianas appear to stall and alter conventional gap-phase regeneration by promoting pioneer tree density and diversity while reducing non-pioneer tree density. These altered, liana-dominated gaps can persist in the forest for many years and become common throughout the forest; they are likely to develop a species composition that contrasts sharply with that of conventional, tree-dominated gaps. Our model of gap-phase regeneration includes the multiple successional pathways that can occur and may be common in many tropical and temperate forests.

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