

# Morphological correlates of fire-induced tree mortality in a central Amazonian forest

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**Abstract:** Tree characteristics were recorded from 2829 standing trees in 24 0.25-ha *terra firme* forest plots in central Amazonia, 3 y after a surface fire had swept through the study area. Sixteen of the plots were within forest that burnt for the first time at the end of the 1997–98 El Niño (ENSO) event, and the remaining eight plots were within unburnt primary forest. In order to investigate the morphological correlates of tree mortality, we measured tree diameter at breast height (dbh) and bark thickness, and recorded burn height, bark roughness and the presence of latex, resin and buttress roots. Leaf litter depth was also recorded at the base of all trees in the unburnt forest. Using logistic regression models, tree mortality was best explained by the burn height, although dbh and the presence of buttresses were also important. Buttressed trees were associated with deeper leaf litter accumulation at their bases and higher char heights than trees without buttresses. Moreover, trees surviving the fire had significantly thicker bark than living trees in unburnt forest plots, indicating that thin-barked trees are more prone to selective mortality induced by heat stress. Latex did not appear to have had any significant effects on mortality, though resins were less abundant amongst the live trees in the burnt forest than in the unburnt controls. Levels of fire-mediated tree mortality in this study are compared with those in other Amazonian forest regions in light of historical factors affecting tree resistance to fires.

**Key Words:** Amazonia, bark properties, El Niño events, fire disturbance, surface fires, tropical forest

## INTRODUCTION

Fire events within Amazonian forests have been rare over the past 7000 y (Sanford *et al.* 1985, Turcq *et al.* 1998) and until recently the high rainfall, moist microclimate and ability of trees to utilize deep soil water in times of low rainfall (Nepstad *et al.* 1999) have ensured that tropical rain forests remained largely immune to fires. However, the synergistic effects of forest disturbance, such as logging and extended El Niño-mediated dry seasons, have alarmingly resulted in increasingly more frequent understorey fires (Goldammer 1999, Nepstad *et al.* 1999, Siegert *et al.* 2001). Such fires impact severely on the avian community (Barlow *et al.* 2002), cause the mortality of around 32–44% of trees  $\geq 10$  cm dbh (Cochrane & Schulze 1999, Haugaasen 2000, Holdsworth & Uhl 1997), and may switch the lowland Amazon forest from a carbon sink (Chambers *et al.* 2001) to a carbon source (J. Barlow, unpubl. data). Recent increases in El Niño frequency and severity (Dunbar 2000) and a new wave of forest disturbance and frontier expansion (Nepstad *et al.* 2001, Peres 2001) suggest that fire is likely to remain a dominant disturbance agent in large parts of Amazonia.

Given this scenario, a thorough understanding of tree

tolerance to fires is crucial. Differential susceptibility of trees to fires would be expected to lead to local extinction events affecting a nested subset of the original species pool thus altering forest composition. This could have potentially disastrous implications for both local people who are heavily reliant on forest resources and for the forest fauna as a whole, but particularly frugivorous species dependent on specific food species. While some authors have used standardized burn simulations in order to investigate the vulnerability of trees to fires (Pinard & Huffman 1997, Uhl & Kaufmann 1990) many of their predictions remain largely untested in the field. The objective of this study was therefore to explore the potential role of the morphological characteristics of trees in determining their susceptibility to an unprecedented ground fire resulting from the 1997–98 El Niño dry season.

Many factors may influence tree mortality induced by heat stress in Amazonian forests. Holdsworth & Uhl (1997) demonstrated that tree mortality was linked to the degree of fire damage received by each tree, whilst Pinard *et al.* (1999) found that trees that had died exhibited significantly higher char marks. While burn intensity is due to a combination of many factors, we hypothesized that the depth of the fuel layer around the base of trees could

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explain some of the variation. Tree size may be another important factor, and many studies within 18 mo of a fire have uncovered strong size-dependent mortality (Barlow *et al.* 2002, Cochrane & Schulze 1999, Peres 1999, Pinard *et al.* 1999). Although little is known about the role of buttress roots, both Uhl & Kauffman (1990) and Pinard & Huffman (1997) hypothesized that they might protect some areas of the cambium from fire damage and therefore aid the survival of trees.

Bark thickness is often used as an indication of the fire tolerance of trees in fire-adapted ecosystems (Gill 1995, Harmon 1984). Within Amazonian forests both Uhl & Kauffman (1990) and Pinard & Huffman (1997) found bark thickness to explain a high degree of the variance in peak cambial temperatures (77% and 63%, respectively) during experimental burns. Bark roughness may also be important as external bark characteristics can affect external bark temperatures (Uhl & Kauffman 1990), with thin exfoliating barks becoming hotter than fissured barks with greater surface areas. Other bark properties such as moisture content and specific gravity appear to have little influence on the thermal diffusivity of bark (Martin 1962, Pinard & Huffman 1997, Uhl & Kauffman 1990, Vines 1968) and were not examined here. However, we explicitly considered the presence of latex and resins because their functional role in mediating post-fire mortality remains poorly known. Tree species possessing latex and resins have been found to be more frequent in heavily disturbed forests (Hegde *et al.* 1998) and it may be that these traits may protect trees from heat stress or from post-fire pathogen infections and invertebrate infestations. Conversely, latex and resins may act to increase mortality by increasing bark flammability.

## STUDY SITE

This study was carried out in the Rio Arapiuns region of western Pará, central Brazilian Amazonia (02°39'S, 55°36'W). Most forest plots were located within the Tapajós–Arapiuns Extractive Reserve, and were distributed around four villages: Pasqual and Mentai on the Rio Arapiuns, and São José and Cachoeira do Maró on the Rio Maró (one of the two major tributaries of the Arapiuns). Four burnt forest plots were sampled around each village, and eight unburnt plots were sampled in the vicinities of São José and Cachoeira do Maró. The extensive burn coverage in the Rio Arapiuns meant that it was not possible to examine control plots in the vicinity of Mentai and Pasqual.

Much of this forest had been subjected to a surface fire in the period between December 1997 and January 1998 coinciding with a prolonged dry season resulting from the 1997–98 El Niño southern oscillation (ENSO) event. Although characterized by low flame heights (usually 10–25 cm), such surface fires were sufficiently intense to burn

the leaf litter and scorch the forest understorey to a height of approximately 2.5 m, but generally caused little structural damage to midstorey and canopy trees which in the short term remained largely foliated (Peres 1999). Interviews with local people confirmed that this was the only time these plots had burnt within living memory. Further details on the study area can be found in Barlow *et al.* (2002).

## METHODS

A total of 24 0.25-ha (10 × 250 m) forest plots were examined between September 2000 and June 2001. Sixteen plots lay within burnt forest, and were sampled in August–September 2000 in order to minimize any time-dependent variation in the effects of fire disturbance. The remaining eight plots were sampled in unburnt forest. To avoid edge-dependent mortality (Laurance 2000), plots were placed at least 200 m from the forest edge, and at least 500 m from the clearly distinguishable fireline separating burnt and unburnt forest. We examined all trees ≥ 10 cm dbh (diameter at breast height, or above the tallest buttress) that lay within each 0.25-ha plot, excluding those with more than half of their basal trunk outside the plot.

Trees were classed as dead if they were leafless and with a complete ring of dead cambium at breast height. The variables measured for each tree depended on their status (i.e. alive or dead) and whether they were within burnt or unburnt forest. However, the dbh of all trees was measured and each tree was assigned according to the trunk characteristic of its base (either unbuttressed, buttressed or stilted). Species with strongly canulated (channelled) trunks (e.g. such as *Minquartia guianensis* Aubl.) were included in the buttressed category.

Whilst bark thickness was recorded on both living and dead trees in all forest plots, only data from live trees are used here as we were unable to determine the original thickness of the desiccated bark on dead trees. Palms (Arecaceae) were also excluded as their phloem and xylem tissues run throughout their stems (Gill 1995). For each tree the bark thickness was recorded from small samples (c. 10 cm<sup>2</sup>) taken at 1 m in height. Following Pinard & Huffman (1997), the maximum thickness was measured whenever variation was detected in the sample. Bark texture was also graded as either rough (strongly fissured, or very scaly/flaky), medium (lightly fissured or scaly/flaky) or smooth. On all living trees, the occurrence of either latex or resin was recorded from the incision made to sample the bark thickness. Both colour and abundance were noted, the latter being classed into four groupings: absent, present but not free flowing, weakly flowing and strongly flowing.

The visible char height of the fires was noted on the trunk of all trees examined in the 16 burnt forest plots. Char heights were then categorized as following: 0 = no

visible fire marks; 1 = burnt at base to 30 cm; 2 = burnt from 30 cm to breast height (1.3 m); and 3 = burnt above breast height. Two additional variables were recorded in the unburnt forest. The fuel depth at the base of trees, defined as the vertical distance from the bottom of the litter layer to the highest dead leaf or twig within 5 cm of the trunk, was measured using methods similar to those of Uhl & Kaufman (1990). This was recorded at the base of all trees measured in six of the unburnt forest plots, and for the first 50 m of the remaining two unburnt forest plots. In addition, bark thickness at 30 cm height was also recorded for all live trees in the first 50 m of each unburnt forest plot.

At all plots both fallen wood and canopy cover were also recorded, though only the former is considered here. For each piece of fallen wood  $\geq 10$  cm in diameter, the length (only sections lying within the  $10 \times 250$  m plot) and diameter (either at 1.3 m from basal tree trunks where the base was within the plot, or at the nearest point within the plot to the base) were recorded. Fallen trees with their bases within the 0.25-ha plots were noted, and were similarly scored according to the type of basal tree trunk as either unbuttressed, buttressed or stilted. Because of the small sample of stilted trees, only unbuttressed and buttressed trees are considered hereafter.

## DATA ANALYSIS

We sampled burnt and unburnt forest plots 3 y after the fires, and much of the analysis is based on the assumption that the pre-burn forest structure and composition were similar across plots. Although this is difficult to ascertain due to the intervening time and the drastic changes in forest structure caused by the fires (Haugaasen 2000, Peres 1999), ANOVA and  $\chi^2$  were used to check the pre-burn structural similarity of two variables (dbh and occurrence of buttress roots) in the unburnt forest, the burnt forest plots close to the unburnt forest and the eight burnt plots far from the unburnt forest. Where it was not possible to check for pre-burn similarity (i.e. for characteristics such as latex, resin, and bark thickness and bark roughness) we restricted comparisons between burnt and unburnt forest to the 16 plots in the Rio Maró, minimizing the potential influence of spatial changes in floristics. Because of the high variation in burn intensity within burnt forest (Cochrane & Schulze 1999), we pooled data from all forest plots and carried out all analyses at the level of individual trees.

As we were unable to accurately measure some of the tree properties investigated in dead trees (i.e. bark thickness, bark roughness and the presence of latex and resin), it was only possible to look for effects within these groups by comparing their prevalence amongst the living trees in the burnt and unburnt forest. Mann–Whitney U-tests were used to compare bark roughness scores, and the abund-

ance of latex and resin scores in both forest types. Analysis of covariance (ANCOVA) was used to control for the effects of tree size (dbh) in comparing the bark thickness in burnt and unburnt forest, and the fuel build-up between unbuttressed and buttressed trees. Paired t-tests were used to compare the bark thickness at 30 cm and 130 cm on buttressed and unbuttressed trees. Bark thickness was square-root transformed in all analyses. Spearman correlations were used to relate fuel-layer depth and char height with tree size.

Dbh, the presence of buttresses and burn height scores were used as independent variables to predict mortality in logistic regression models. Bark thickness was not included as the desiccated bark on dead trees was not considered to give an accurate measure of living bark thickness. Analyses were carried out separately for the burnt and the unburnt forest, and data from all sites were entered into the model. This was justified as Kruskal–Wallis tests showed that there was no significant difference between the prevalence of either the number of trees (either as a whole or grouped by dbh class) or of buttresses at the four burnt sites (J. Barlow, unpubl. data). Furthermore, site was not significant when entered in the model as a categorical variable, and did not influence the overall results. All analysis was undertaken in SPSS v. 10, and measures of variance around the mean are standard errors ( $\pm$ SE).

## RESULTS

A total of 2829 standing trees were recorded in all 24 forest plots, including 1075 within unburnt forest and 1754 within burnt forest. A total of 93 of these were palms, 33 were woody lianas, whereas 10 were trees that were fast-growing pioneer species considered to have grown to a girth of  $\geq 10$  cm dbh since the fires (*Cecropia* spp. and *Palicourea guianensis* Aubl.). Overall levels of detected mortality (measured as the death of all standing and recently fallen stems) in the burnt-forest plots (34%) were many times higher than the background levels in unburnt-forest plots (7%).

### Pre-burn forest similarity

The burnt forest had fewer trees per plot than the unburnt forest, this being due to the lower abundance of trees in the smallest size class (10–19.9 cm dbh; Table 1). Many more trees had fallen in the burnt forest (195) than in the unburnt forest (36), and there was no difference between burnt plots grouped by their location (Table 1). The proportion of trees with buttress roots per plot was very similar between unburnt-forest and burnt-forest plots both close to and far from the controls (Table 1), and buttressed trees were no more likely to have fallen than trees without buttresses ( $\chi^2 = 2.75$ ,  $df = 1$ ,  $P > 0.05$ ).

**Table 1.** Mean per cent of trees with buttresses, and the mean number of standing trees (excluding arborescent palms and woody lianas, and stems recruited after the fire) per quarter-hectare plot within each 10-cm dbh size class. Burnt forest RM indicates burnt plots from the Rio Maró which were close to the control plots. Burnt forest RA represent the eight plots from the Rio Arapiuns.

	Unburnt forest (n = 8)		Burnt forest RM (n = 8)		Burnt forest RA (n = 8)		F	P
	Mean	SE	Mean	SE	Mean	SE		
% buttressed	41.0	3.3	38.4	4.4	44.4	4.7	0.5	0.8
No. of fallen trees	4.5 <sup>1</sup>	0.9	12.3 <sup>2</sup>	1.7	12.1 <sup>2</sup>	2.4	6.4	0.007
All standing trees	134.4 <sup>1</sup>	5.5	113.3 <sup>1,2</sup>	3.4	104.8 <sup>2</sup>	7.6	4.9	0.02
Dbh class (cm)								
10–19.9	77.1 <sup>1</sup>	4.8	64.8 <sup>1,2</sup>	2.9	54.9 <sup>2</sup>	5.5	6.0	0.008
20–29.9	31.5	1.9	25.4	2.3	27.9	1.5	2.6	0.1
30–39.9	11.8	1.1	11.4	1.1	10.3	1.1	0.5	0.6
40–49.9	6.0	0.7	6	1.1	5.3	0.9	0.2	0.8
≥ 50	8.0	0.8	5.8	1.0	6.5	1.5	1.0	0.4

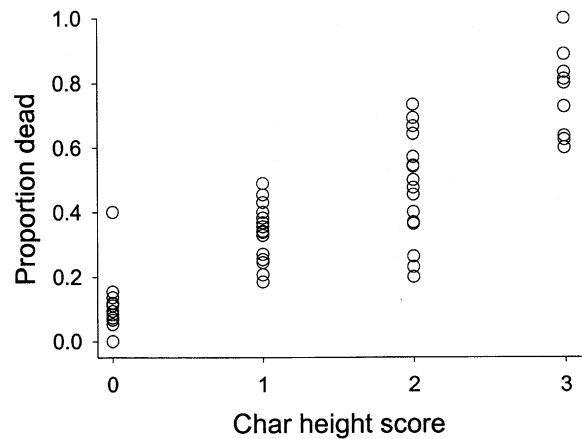
<sup>1,2</sup> Superscripts indicate significant subsets (Tukey’s HSD test).

**Burn height**

Nineteen per cent of all stems in burnt forest did not show obvious char marks, while 60% were classified as lightly charred (below 30 cm). Only 7% of stems (n = 120) were burnt above breast height (1.3 m). Of the three variables incorporated into the logistic regression model, burn height score was the best predictor of mortality status (Table 2). This strong effect of burn height upon tree mortality is also shown in Figure 1, where there was a positive relationship between the proportion of dead trees per plot (grouped by their char height score) and their char height score.

**Tree size**

Dbh was a significant predictor of mortality in the burnt forest (Table 2) and the only significant predictor of mortality in the unburnt forest, although the direction of its influence was reversed (Table 2). As expected from this size-dependent mortality, the mean dbh of live trees in the burnt forest plots was significantly higher than that in unburnt forest (Table 3). Dbh was also positively correlated with the maximum fuel depth in unburnt-forest plots and the burn height scores in burnt forest, these associations being significant for both buttressed and unbuttressed trees (Table 4).



**Figure 1.** Relationship between burn-height scores and tree mortality. Each point represents the proportion of trees that were dead within each burn class at each plot ( $r_s = 0.89$ ,  $n = 64$ ,  $P < 0.001$ ).

**Buttress roots**

The presence of buttresses augmented the probability of tree mortality in the burnt forest by 39% (Table 2). While there was no significant difference between the mean proportion of live trees with and without buttresses in unburnt forest, the mean proportion of live trees with buttresses in

**Table 2.** Logistic regression model considering the survival outcome of trees ≥ 10 cm dbh in both burnt and unburnt forest. B(constant) denotes the unstandardized regression coefficients, the Wald statistic is used to calculate significance, whilst ExpB is the odds ratio. The per cent change in the odds of mortality for each additional unit of an independent variable can be calculated by 1 – ExpB.

	B (constant)	SE	Wald	P	ExpB
Burnt forest <sup>1</sup>					
dbh	-0.02	0.005	17.0	< 0.00	0.98
Burn height	1.04	0.079	173	< 0.001	2.81
Presence of buttresses	0.33	0.114	8.17	0.004	1.39
Constant	-1.9	0.2	89.6	< 0.001	
Unburnt forest <sup>2</sup>					
dbh	0.02	0.006	8.8	0.003	1.02
Constant	-3.02	0.204	217	< 0.001	

<sup>1</sup>Burnt forest: 68.6% of all trees were classified correctly as either dead or alive, using an optimum cut-off value of 0.47.

<sup>2</sup>Unburnt forest: 92.8% of all trees were classified correctly as either dead or alive, using an optimum cut-off value of 0.4.

**Table 3.** Summary statistics and comparisons for all live trees (excluding palms and lianas) in the unburnt control plots and the eight burnt-forest plots close to the controls.

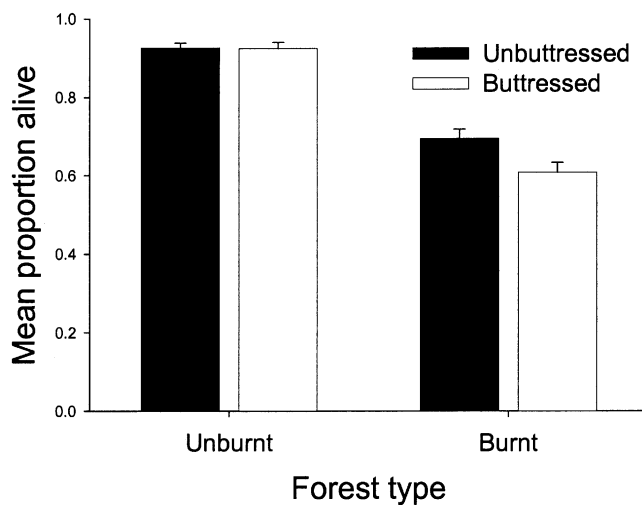
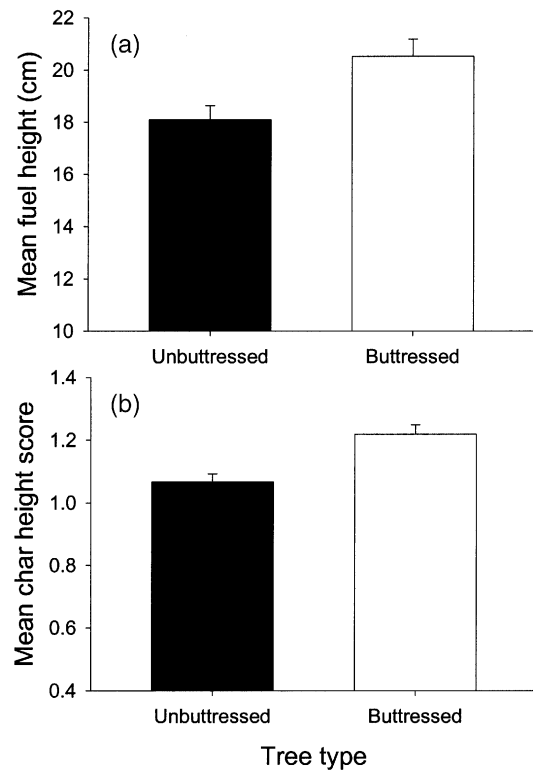
	Unburnt		Burnt		Z <sup>1</sup>	n	P
	Mean	SE	Mean	SE			
Dbh (cm)	22.63	0.47	23.6	0.58	-2.4	1488	0.02
Rank latex score	0.40	0.03	0.32	0.04	-1.6	1488	0.11
Rank resin score	0.35	0.02	0.25	0.03	-3.2	1488	0.001
Bark roughness – All (cm)	1.9	0.02	2.1	0.03	-5.1	1488	< 0.001
0.1–0.19 cm	1.69	0.06	1.7	0.13	-0.1	110	0.94
0.2–0.39 cm	1.69	0.03	1.84	0.04	-2.8	462	0.006
0.4–0.59 cm	1.89	0.03	2.04	0.05	-2.6	398	0.01
0.6–0.79 cm	2.08	0.04	2.14	0.06	-0.9	208	0.34
0.8–0.99 cm	2.14	0.07	2.19	0.07	-0.6	139	0.53
≥ 1 cm	2.36	0.06	2.44	0.08	-1.1	171	0.26

<sup>1</sup> Mann–Whitney U test.

**Table 4.** Spearman correlations between tree dbh and fuel depth in the unburnt forest and tree dbh and burn height in the burnt forest. Correlations in the unburnt forest include live trees only, excluding palms and lianas. Correlations in the burnt forest are for all standing trees excluding palms, lianas and those recruited after the fire. Correlations are shown for all trees, and for trees grouped according to their root type.

	r <sub>s</sub>	n	P
Fuel depth			
All trees	0.21	828	< 0.001
Buttressed only	0.23	323	< 0.001
Unbuttressed only	0.19	502	< 0.001
Rank burn height			
All trees	0.16	1645	< 0.001
Buttressed only	0.15	683	< 0.001
Unbuttressed only	0.15	940	< 0.001

the burnt forest was significantly lower than that for live trees without buttresses (Figure 2). Moreover, buttressed trees had a significantly higher burn-height score than unbuttressed trees (Figure 3b) and data from unburnt

**Figure 2.** The mean proportion of surviving trees with and without buttresses in burnt and unburnt forest. Unburnt forest: mean unbuttressed =  $0.926 \pm 0.01$ ; mean buttressed =  $0.924 \pm 0.02$ ;  $Z = -0.11$ ,  $n = 16$ ,  $P = 0.96$ . Burnt forest: mean unbuttressed =  $0.694 \pm 0.02$ ; mean buttressed =  $0.618 \pm 0.03$ ;  $Z = -2.32$ ,  $n = 32$ ,  $P = 0.019$ .**Figure 3.** (a) The mean litter depth at the bases of buttressed and unbuttressed trees. Means shown are adjusted by ANCOVA, using dbh class as the covariate. Original means were  $17.8 \pm 0.5$  cm for unbuttressed and  $20.9 \pm 0.7$  cm for buttressed trees. Corrected model;  $F_{2,822} = 30.8$ ,  $P < 0.001$ ; Root type;  $F_{1,822} = 8.03$ ,  $P = 0.004$ ; dbh class (covariate);  $F_{1,822} = 48.2$ ,  $P < 0.001$ . (b) The mean rank burn height on buttress and unbuttressed trees (data for live and dead trees, excluding palms, lianas and new recruits); mean unbuttressed =  $1.07 \pm 0.03$ ; mean buttressed =  $1.22 \pm 0.03$ ,  $Z = -4.0$ ,  $n = 1,623$ ,  $P < 0.001$ .

forest plots clearly show that they accumulated more leaf litter around their bases (Figure 3a).

### Bark thickness

Bark thickness (of live trees in unburnt forest) was very variable, ranging between 0.3 and 37.6 mm, with an over-

all mean of  $5.5 \pm 0.13$  mm for all trees  $\geq 10$  cm dbh and  $7.9 \pm 0.024$  mm for all trees  $> 20$  cm dbh. However, a vast proportion of all trees in this central Amazonian flora were typically thin-barked. A total of 59.4% of all trees, comprising 16% of the basal area, had a bark thickness of less than 5 mm whereas only 10.6% of trees (or 32% of the basal area) had a bark thickness of at least 10 mm. Bark thickness was significantly related to dbh (live trees only in unburnt forest;  $y = 1.76x + 0.016$ ,  $r^2 = 0.35$ ,  $F_{1,968} = 509$ ,  $P < 0.001$ ).

The mean bark thickness of live trees in burnt forest (eight plots in Rio Maro only) was significantly greater than that in unburnt forest, even when dbh was taken into account (mean unburnt forest =  $55 \text{ mm} \pm 1.3$ ; burnt forest =  $63 \text{ mm} \pm 1.6$ ; ANCOVA corrected model,  $F_{2,1485} = 422$ ,  $P < 0.001$ , forest type,  $F_{1,1485} = 26$ ,  $P < 0.001$ , dbh (covariate),  $F_{1,1485} = 26$ ,  $P < 0.001$ ). Although there was no significant difference in bark thickness between heights at 30 cm and 130 cm for unbuttressed trees (mean at 30 cm =  $0.49 \pm 0.03$  mm; mean at 130 cm =  $0.49 \pm 0.03$  mm; paired- $t = -0.08$ ,  $df = 97$ ,  $P = 0.93$ ), bark thickness at 30 cm height was significantly thinner than that at 130 cm for buttressed trees (mean at 30 cm =  $0.38 \pm 0.03$  mm; mean at 130 cm =  $0.49 \pm 0.03$  mm; paired- $t = 5.6$ ,  $df = 75$ ,  $P < 0.001$ ). Moreover, amongst all living trees in the unburnt forest, buttressed trees had significantly thinner barks at 130 cm than did unbuttressed trees (mean unbuttressed =  $0.6 \pm 0.02$  mm, mean buttressed =  $0.48 \pm 0.02$  mm;  $t = 4.6$ ,  $df = 969$ ,  $P < 0.001$ ).

### Other bark characteristics

There was no significant difference between the bark roughness, or the abundance of either latex or resin between all unburnt-forest and burnt-forest plots ( $P = 0.09$ ,  $0.23$  and  $0.39$  respectively). However, when this analysis was restricted to the eight burnt plots that were close to the control plots, resins were significantly less abundant and barks were significantly rougher in the burnt forest (Table 3). Because bark roughness was significantly correlated with bark thickness ( $r_s = 0.38$ ,  $n = 1013$ ,  $P < 0.001$ ), trees were grouped into six categories according to their bark thickness in order to test the effects of bark roughness independently of bark thickness. Bark was significantly rougher in trees in the burnt forest with a bark thickness of between 0.2–0.6 cm (Table 2).

## DISCUSSION

### Pre-burn forest similarity

Although there were significantly fewer stems  $\geq 10$  cm dbh in the burnt forest, this was largely a result of a numeric decline in the 10–20-cm dbh class in the Rio Arapiuns plots (Table 1). These smaller midstorey trees account for

only a small proportion of forest biomass, and were the most likely to have gone undetected in the survey of fallen wood in the burnt forest, especially as some may have either combusted or decayed. Furthermore, stems that had fallen before the fire were likely to have burnt and therefore been underestimated. Lower standing-stem densities following fires have also been found by Holdsworth & Uhl (1997) and, like them, we do not attribute the marginally lower stem density to any pre-burn differences. Furthermore, interviews with local communities at the four villages affected by this fire confirmed the assumption that these forests were structurally similar prior to the fires.

### Morphological correlates of tree mortality

Although the size-dependent mortality of trees is not a universal phenomenon following fires in tropical forests (Holdsworth & Uhl 1997) it has been frequently observed following low-intensity fires (Cochrane & Schulze 1999, Peres 1999, Pinard *et al.* 1999). The normal expectation is that small trees will be more at risk because of their thinner bark and the increased chance of complete flame coverage (Gutsell & Johnson 1996, Pinard & Huffman 1997, Uhl & Kauffman 1990). Although strong size-dependent mortality was detected in these forests both 1–2 mo after (Peres 1999) and 1 y after this fire (Barlow *et al.* 2002), the effects after 3 y appear to be weaker. Since small trees were apparently no more likely to fall than large trees (J. Barlow, unpubl. data), this may be attributed to a stronger physiological lag effect delaying the mortality of large, and initially more resistant, canopy trees.

Bark thickness of live trees at this site was similar to that observed in Paragominas, eastern Amazonia (Uhl & Kaufman 1990), and tree dbh explained very similar amounts of the variance (this study:  $r^2 = 0.35$ ; Uhl & Kauffman 1990:  $r^2 = 0.38$ ). Because live trees had significantly thicker barks in the burnt forest, we can surmise that thin-barked trees were most susceptible to the fires. Our results therefore support the conclusions of studies on fire disturbance in both eastern Amazonia (Uhl & Kauffman 1990) and eastern Bolivia (Pinard & Huffman 1997) that bark thickness is an important morphological correlate of tree survival. Both bark roughness and the presence of resins appeared to be important determinants of tree mortality. Rougher bark may increase the boundary layer (Dickinson & Johnson 2001) resulting in lower surface bark temperatures (Uhl & Kauffman 1990). Although our findings of fewer resin-secreting trees in the burnt forest are contrary to the findings of Hegde *et al.* (1998), they are not surprising as many of the resins produced by *Protium* spp. and *Hymenaea* spp. are flammable. However, these results should be viewed with caution because of our lack of 'before' control plots providing background data on pre-burn resin and latex abundance. Experimental

burns within smaller areas would allow these effects to be examined in more detail.

Surprisingly, and contrary to our initial expectation, buttressed trees were significantly *more* likely to succumb to fire-induced mortality. This runs against previous conjectures that buttresses might be able to protect vital cambium tissues from fire damage, thus aiding the probability of tree survival (Pinard & Huffman 1997, Uhl & Kauffman 1990). This could have two explanations. First, buttressed trees tended to collect more leaf litter at their bases, which in turn apparently contributed to their higher burn heights. Second, the higher probability of mortality for buttressed trees may relate to bark thickness differences. Not only do buttressed trees have significantly thinner barks for their size, they also have thinner bark at their bases, coinciding with the area of maximum flame temperature during surface wildfires (see Gill 1995).

#### Burn intensity and fuel depth

Although results from this study are generally consistent with the notion that some of the morphological traits of trees can influence their fire tolerance (Pinard & Huffman 1997, Uhl & Kauffman 1990), local fire intensity appeared to be the most important determinant of tree mortality. The strong relationship between burn severity and mortality rate is very similar to that uncovered by Holdsworth & Uhl (1997), whilst Pinard *et al.* (1999) also found dead trees to exhibit significantly higher char heights. Because of the importance of burn intensity in determining mortality, an understanding of its environmental determinants will aid our ability to predict and perhaps avert the potential consequences of fires.

At one hypothetical extreme, burn intensity could be purely stochastic and determined by the local combination of humidity, wind and temperature, and the coarse and fine fuel-load conditions on the forest floor. Just as logging increases the intensity of fires by opening up the canopy (thereby reducing humidity and augmenting fuel dry-down rates: Holdsworth & Uhl 1997) and increasing the fuel load on the forest floor (Uhl & Kauffman 1990), so may natural treefall gaps. It is perhaps noteworthy that the figure of 7% of severely burnt trees closely resembles the proportion of typical unburnt primary forest occupied by treefall gaps (J. Barlow, unpubl. data). Further variation in burn intensity may stem from the fact that parts of this forest burned twice in the same year, with smouldering logs re-igniting the fresh leaf fall from severely heat-stressed trees in the immediate aftermath of the fires (C. Peres, pers. obs.).

However, our measurements of fuel depth in the unburnt forest show that the distribution and accumulation of fine fuel is not random, with the stem bases of large trees and buttressed trees contacting heavier fuel loads. In

the case of tree size, heavier fuel loads may explain the weak effect that tree girth had upon the likelihood of mortality; while the thicker bark surfaces afforded by these trees may have conferred greater insulation from lethal heat stress, the greater fuel depth may have contributed to the increased char heights on large stems (although it is difficult to separate this from the effect that leeward vortices may have had in determining char height: Dickinson & Johnson 2001). Indeed, dbh was not a significant determinant of mortality in the logistic regression models unless the char height was added as a covariate. In the case of buttressed trees, heavier fuel loads may have contributed directly to their mortality rates, though it is difficult to dissociate this from the influence of their thinner bark.

#### Fire tolerance of Amazonian forests

Overall, the majority of trees in the forests of the Arapiuns region appeared to be extremely intolerant to the levels of thermal stress generated by surface fires. Although true levels of tree mortality were probably higher than those reported here (some stems may have burnt, or fallen and gone undetected in the dense regeneration), the detected mortality of around 34% of all trees  $\geq 10$  cm dbh is still high compared with mortality rates of between 8–23% documented for forest sites at the fringes of the Amazon basin (Barbosa & Fearnside 1999, Pinard & Huffman 1997, Santos *et al.* 1998) where a repeated history of fires may have exerted stronger selective pressure on the evolution of fire tolerance, or traits conferring some mechanism of fire resistance. As in other regions that could be described as core Amazonian forest (Uhl & Kauffman 1990), trees in our study area are typically characterized by thin bark, perhaps reflecting the extremely rare history of fires in these regions. Although data on carbon-dated charcoal from the Arapiuns forests remain unavailable at present, we predict that the periodicity of major fires in this area is far less frequent than those at the edges of the Gran Savannah of southern Venezuela (Sanford *et al.* 1985). In addition, our measurements of bark thickness along the trunk of a large set of trees in central Amazonia are in stark contrast to those in fire-adapted temperate forests where thick bark near the basal tree trunk can aid survival in low-intensity ground fires (Harmon 1984).

#### Fire-prone Amazonian forests in the future

Although our results indicate that some morphological traits such as thick bark and cylindrical trunks can confer survival advantages, the regional extinction of many fire-intolerant species following a light burn is unlikely because of the considerable spatial heterogeneity of burn intensity. Furthermore, the future composition of these forests will depend on much more than the tolerance of

mature individuals of each species to low-intensity burns. Species persistence will be determined by the survival of their seeds within the seedbank, their abilities to germinate in the post-fire microclimatic environment and compete with light-demanding pioneer vegetation such as lianas and herbaceous vines (Pinard *et al.* 1999, Uhl *et al.* 1988) as well as by the responses of their pollinators and seed dispersers. Although the ability to resprout from the base following fires has also been considered an important aid to survival following forest clearance (Uhl *et al.* 1982) and low-intensity burns in *terra firme* forests (Pinard *et al.* 1999, Uhl *et al.* 1988), this was rarely observed during this study. This is in agreement with the findings of Woods (1989), and indicates that the heat stress at the base of trees that had died was also sufficiently lethal to destroy the dormant meristematic tissue (Uhl *et al.* 1988).

But by far the greatest threat to species persistence is that posed by high-intensity recurrent burns (Cochrane & Schulze 1999, Goldammer 1999, Nepstad *et al.* 1999). The increased severity of a recurrent burn can be expected to kill a much greater proportion of the seedbank, whilst the dispersal of many large-seeded species will be hindered by the absence of many large-bodied vertebrate dispersers from forest that has burnt more than once (J. Barlow, unpubl. data). Furthermore, given the frequency of the current El Niño-mediated fire regime in tropical forests (Goldammer 1999, Nepstad *et al.* 1999, Siegert *et al.* 2001), post-burn saplings and juveniles are unlikely to have enough time to grow into a size class that will enable them to survive a recurrent burn. Moreover, the close proximity of any resprouting stems to the woody fuel from neighbouring dead stems may make them especially vulnerable to future fires. It may be that the frequency of repeated fires mediated by the present day El Niño periodicity will create conditions unsuitable for tree regeneration, converting forested areas threatened by fire into rather simplified scrub savannas.

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