

Functional explanations for variation in bark thickness in tropical rain forest trees

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Summary

1. The complex structure of tree bark reflects its many functions, which include structural support as well as defence against fire, pests and pathogens. Thick bark, however, might limit respiration by the living tissues of the trunk. Nevertheless, little research has addressed community-level variation in bark thickness, and to the best of our knowledge, no one has tested multiple hypotheses to explain variation in bark thickness.

2. We conducted an extensive survey of bark thickness within and among species of trees in the tropical rain forests of French Guiana. Trunk bark thickness increased by 1.2 mm per 10 cm increase in stem diameter, and varied widely at all taxonomic levels. Mean trunk bark thickness was 4.5 mm (range: 0.5–29 mm), which was less than that found in two Amazonian rain forests in previous studies. This survey of bark thickness should be of use for forest management since tree survival through fire is strongly predicted by bark thickness.

3. We combined the survey data with multiple datasets to test several functional hypotheses proposed to explain variation in bark thickness. We found bark to provide an average of 10% of the flexural rigidity of tree stems, which was substantially less than that found in the only other study of bark stiffness. Bark thickness was uncorrelated with species' association with fire-prone habitats, suggesting that the influence of fire on bark thickness does not extend into moist forests. There was also little evidence that bark thickness is affected by its function as a defence against herbivory. Nor was there evidence that thick bark limits trunk respiration.

4. A re-analysis of previously collected anatomical data indicated that variation in rhytidome (non-conducting outer bark) thickness explains much of the variation in overall bark thickness. As rhytidome is primarily involved in protecting the living tissues of the trunk, we suggest that bark thickness is driven mostly by its defensive function.

5. Functional explanations for the variation in bark thickness were not clear-cut. Nevertheless, this study provides a foundation for further investigation of the functional bases of bark in tropical trees.

Key-words: bark thickness, fire ecology, flexural rigidity, herbivore defence, periderm, rhytidome, trunk respiration

Introduction

Tree bark is one of the more salient aspects of tropical forests. Many foresters identify trees with nothing more than a

machete, using the diverse visual, textural, and olfactory clues of inner and outer bark to guide identification (Keller 2004). The term bark designates all tissues external to the vascular cambium, comprising secondary phloem, periderm and nonconductive tissues external to the periderm, i.e. rhytidome (Evert, Esau & Eichhorn 2006). This complex structure reflects the manifold functions of bark, which include structural support and protection against biotic and

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abiotic threats (Roth 1981). Thick bark might also have physiological consequences, potentially limiting trunk respiration. Nevertheless, few community-level surveys of bark thickness exist (Roth 1981; Uhl & Kauffman 1990; Hegde, Chandran & Gadgil 1998), and no study, to the best of our knowledge, has tested multiple hypotheses to explain variation in bark thickness. Though ecologists measure many characteristics of bark, including its density, moisture content and thermal conductivity (Uhl & Kauffman 1990; Cornelissen *et al.* 2003), we focus on the thickness of bark as a trait that integrates its multifarious functions.

The two objectives of this study are to describe taxonomic and intra-specific variation in bark thickness, and to test multiple functional hypotheses proposed to explain why there is such variation in bark thickness. We first surveyed the variation in bark thickness on the trunks and twigs of French Guianan rain forest trees. We then integrated multiple datasets to test several functional hypotheses posited to explain the variation in bark thickness, keeping in mind that they are not mutually exclusive since bark simultaneously performs a variety of functions. The functional hypotheses are summarized in Table 1. Most studies of bark thickness have been conducted in savannas and dry forests, where the effects of fire are likely to overwhelm any other factors that affect bark thickness (e.g. Pinard & Huffman 1997; Hoffmann, Orthen & Do Nascimento 2003a). By examining moist tropical forests of French Guiana, we expected that a more balanced understanding of bark's functions may be obtained. In the following paragraphs, we briefly introduce the various functions performed by tree bark.

Bark can help defend trees against abiotic and biotic threats. Regardless of the nature of the threat, if bark serves an important role in defence, its thickness should increase asymptotically as an individual grows, since beyond a certain limit additional thickness confers no further survival advantage (Wilson & Witkowski 2003).

Bark is an effective defence against fire (Harmon 1984). For trees exposed to fire, bark thickness is the single best predictor of cambium heating, and thus, the probability of survival (Vines 1968; Hoffmann & Solbrig 2003b; Van Nieuwstadt & Sheil 2005). This explains why the bark of trees of species associated with fire-prone Brazilian cerrado is, on average, three times thicker than the bark of forest-associated congeners (Hoffmann, Orthen & Do Nascimento 2003a). Yet fire-return intervals in many habitats are so long that many individual trees are unlikely to ever be exposed to fire. For example, in intact moist forests of the Neotropics,

fire-return intervals are estimated to be on the order of hundreds of years (Uhl 1998), though anthropogenically fragmented forests and forest-savanna ecotones are more fire-prone (Hammond & Ter Steege 1998; Malhi *et al.* 2008). Following droughts, especially, fire can kindle even in tropical moist forests, and such fires can decimate tree communities (Van Nieuwstadt & Sheil 2005). As frequent fires can impose a substantial selection pressure on bark thickness (Stephens & Libby 2006), species whose ranges include frequently burned habitats would be expected to have thicker bark than those whose range includes only habitats in which fires are infrequent.

The threat posed to trees by pathogens and sap-feeding herbivores may also affect bark thickness. In addition to the wide variety of insects that consume cambium and phloem, among which Cerambycid beetles feature prominently (Tavakilian *et al.* 1997), vertebrates specialized to feed on tree exudates occur on most continents. In the Neotropics, Marmosets (*Callithrix* spp.) feed on exudates from holes they gouge in trees (Coimbra-Filho & Mittermeier 1976). In North America, sapsuckers (*Sphyrapicus* spp.) extract sap from the extensive series of holes they drill through bark, preferentially selecting species that produce more sap (Eberhardt 2000). Once damaged, furthermore, trees vary widely in the rate at which bark grows to close the wound (Romero & Bolker 2008). If pathogens and sap-feeding herbivores impose significant selection pressures, we would predict a suite of defensive traits to be expressed. These may include physical traits, such as thicker bark, and chemical traits, such as latex and secondary metabolites. Two contrasting patterns may be expected. If allocation to overall defence is fixed, then there may be negative correlations between the degree of physical and chemical defences. If, alternatively, there are deeper physiological trade-offs between allocation to growth and defence, then positive relationships may be expected between physical and chemical components of defensive strategy (Agrawal & Fishbein 2006).

Given its position on the exterior of stems, bark could make a substantial contribution to mechanical rigidity so long as it is sufficiently stiff and thick, relative to the stem radius. Using a simple formula, Niklas (1999) calculated that wood and bark contribute equally to flexural rigidity when bark stiffness is half that of wood, and bark constitutes approximately one-third of stem radius. The structural role of bark may be particularly important for branches and twigs, as bark thickness, as a fraction of stem diameter, is greater on small-diameter stems (Fig. 1d,e).

Table 1. Summary of hypotheses to explain variation in bark thickness

Hypothesis	Role	Predictions
Defence	General	Asymptotic thickness/diameter relationships in trunk and twig
	Fire	Positive relationship between bark thickness and association with fire-prone habitats
	Herbivory	Negative relationship between physical defences (bark thickness) and chemical defences (terpenes and latex)
Biomechanical	Support	Bark thickness and stiffness combine such that bark contributes substantially to the flexural rigidity of stems
Physiology	Respiration	Lower rate of CO ₂ efflux from trunks in thicker-barked individuals

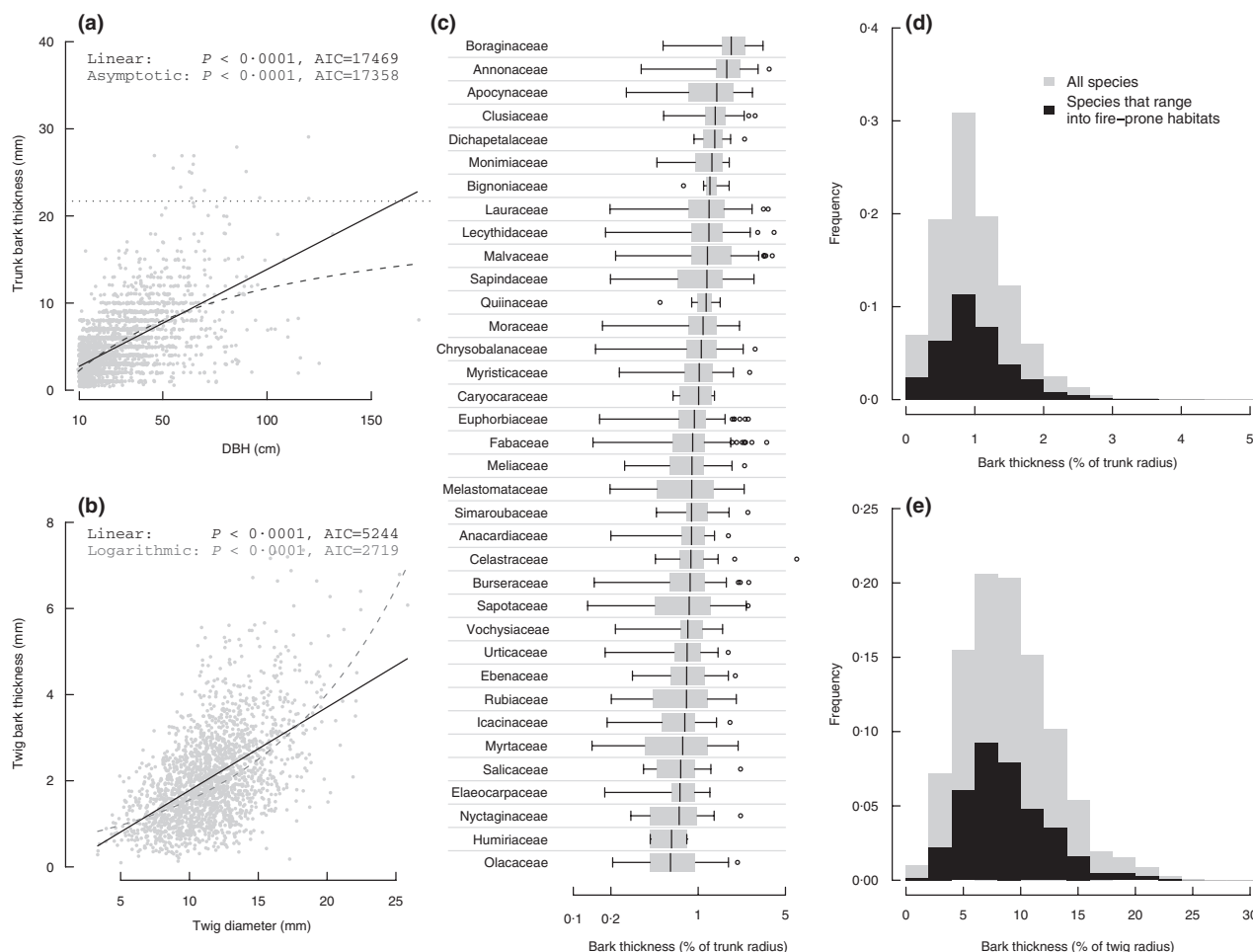


Fig. 1. A survey of the variation in bark thickness in rain forest trees of French Guiana. There are strong positive relationships (a) between diameter at breast height (DBH) and trunk bark thickness as well as (b) between twig diameter and twig bark thickness. In (a) and (b), dashed lines indicate the asymptotic and logarithmic fits, respectively, whereas solid lines indicate the linear fits. The dotted horizontal line in (a) indicates the predicted asymptotic bark thickness. (c) Trunk bark thickness, as a percentage of DBH, varies widely among families. To ease comparisons among families, only data from individuals < 20 cm DBH is shown. For both (d) trunks and (e) twigs, bark thickness varies widely as a percentage of stem radius. Species not associated with fire-prone habitats display as wide a range of bark thickness as do all species combined, suggesting fire-association to be of relatively little importance in explaining variation in bark thickness. Note log scale of x-axis in (c).

Increased bark thickness could, however, have physiological consequences. Bark limits the diffusion of water, oxygen and CO_2 between the vascular cambium and the atmosphere (Teskey *et al.* 2007). The strength of this limitation can increase with the thickness of bark, and the degree to which bark is impregnated with suberin, lipids and waxes (Lendzian 2006). In a broad survey of a Costa Rican rain forest, Cavaleri, Oberbauer & Ryan (2006) concluded that thick bark limited respiration by the living tissues of the trunk, since they observed significantly greater respiration rates (on a mass basis, $\text{nmol kg}^{-1} \text{ s}^{-1}$), in smaller-diameter stems, which bore thinner bark. This pattern was also found in a second study, though bark thickness was not measured (Meir & Grace 2002).

Materials and methods

This study was conducted in nine one-ha permanent plots in coastal French Guiana. All plots were located in moist tropical never-flooded

terra firme forest, where precipitation ranged between 2 and 4 m annually. The plots were censused in the context of the BRIDGE project, in which each tree was identified to species and sampled for functional traits including bark thickness; details on field sampling can be found in Baraloto *et al.* (2010) and at <http://bridge.ecofog.gf/>.

In four plots, every tree was sampled for trunk bark thickness, whereas in the remaining five, at least three individuals of each species were sampled. We measured bark thickness at a height of 1.4 m with increment hammers (Haglöf Sweden AB, Långsele, Sweden), which give accurate readings for bark less than approximately 15 mm thick. For trees with thicker bark, we used bark thickness gauges (Suunto Oy, Vantaa, Finland). Trunks were lightly brushed to dislodge loose flakes before measuring. Twig bark thickness was assessed on every tree in two plots, three individuals per species in five plots, and was not available in the final two plots. Twig samples of approximately 1-cm diameter were obtained by professional tree climbers. Twig diameter and bark thickness were measured from high-resolution scans of twig cross-sections.

In this study, we seek functional explanations of the variation in bark thickness in addition to describing patterns of variation in

tropical tree bark thickness. There is a strong, pervasive relationship between stem diameter and bark thickness for both trunks and twigs (Fig. 1, see *Results* for details). This relationship may obscure other effects shaping bark thickness. Thus, in the subsequent functional analyses, we use the residuals of the diameter–thickness relationship, rather than absolute bark thickness, as a response variable.

DEFENCE AGAINST HERBIVORY

Trade-offs between bark thickness and defensive chemistry would suggest that an important function of bark is to deter herbivory. Though many secondary metabolites deter herbivores, bacteria and fungi, we focus on volatile terpenes as they are among the most important, diverse, and easily measured (Phillips & Croteau 1999; Singh *et al.* 2007). During field sampling, we obtained samples of bark for volatile terpene analysis with a 1-cm diameter leather punch from one individual each of 202 species. Previous analyses indicated that there is little within-species variation in terpene composition (Courtois *et al.* 2009). Monoterpenes and sesquiterpenes were extracted from bark samples by Solid Phase Micro Extraction, a fast solvent-free technique, followed by GCMS (gas chromatography/mass spectrometry) analysis in order to obtain the terpene composition. As this method cannot reliably estimate the abundance of molecules, we report presence/absence data (Courtois *et al.* 2009). Herbivory defence analyses were performed at the species level, thus we summarized per-species terpene diversity as the total number of monoterpenes and sesquiterpenes that we detected, and related these values to species-mean bark thickness. Latex quantity can vary among individuals within species, depending largely on water availability. Despite the intra-species variability, we (CETP and CB) categorized species on the basis of latex quantity (None, Scant, Moderate and Abundant), based on field observations and published literature (Roth 1981; Keller 2004). In an ANCOVA, we predicted the residuals of the bark–diameter relationship on the basis of latex quantity and terpene richness. As the interaction of latex quantity and terpene richness was non-significant it was dropped from the model.

ASSOCIATION WITH FIRE-PRONE HABITATS

We evaluated the degree to which association with fire-prone habitats shapes bark thickness. We extracted from the Global Biodiversity Information Facility database (<http://gbif.org>) all records of geo-referenced herbarium voucher specimens from Central and South America of taxa pertaining to the 57 families occurring in our field inventories. Brazilian samples were poorly represented in the GBIF dataset, so we supplemented Brazilian records with those available in the SpeciesLink database (<http://splink.cria.org.br/>). Each record was assigned to a habitat by joining the specimens dataset to an ArcGIS 9.3 (ESRI, Redlands, CA, USA) shapefile of terrestrial ecoregions developed for the World Wildlife Fund by Olson *et al.* (2001, <http://www.worldwildlife.org/science/data/item1875.html>). We collapsed the fourteen terrestrial ecoregions of Olson *et al.* (2001) into three habitats: wet, moist and mangrove forest; dry and Mediterranean-type forest; and savanna, shrubland and cerrado. Henceforth, we refer to these habitats as moist forest, dry forest and savanna, respectively. A fire-association index was calculated for each species using the following formula: $n_{ij}f/(n_{ji})$, where n is the number of specimens, f is fire return interval, and i and j indicate indices over species and habitats respectively. In other words, the occurrence of each species in each habitat is weighted by the fire recurrence interval in that habitat, and scaled by the product of the total number of occur-

rences in that habitat and the relative abundance of that species. The index was multiplied by n (698 044) to avoid working with numbers of extremely small magnitude. Fires in intact closed-canopy moist forest are exceedingly rare, since high humidity renders the understory largely incapable of sustaining fire (Uhl & Kauffman 1990). The fires that do occur in these forests tend to be associated with droughts associated with El Niño–Southern Oscillation events (Hammond & Ter Steege 1998). Based on the investigations of Hammond & Ter Steege (1998), we estimate the fire return interval in moist tropical forest to be 100 years, acknowledging that return intervals may be far longer. Return intervals for dry forest and savanna were taken as 4 and 2 years respectively (Coutinho 1990; Cochrane *et al.* 1999). For taxa present in the field inventories but not the herbarium specimen dataset, fire-association indices were calculated at the next higher taxonomic level. The relationship between the fire-association index and the thickness-diameter residuals was evaluated with a linear regression on species-mean data.

BIOMECHANICAL MEASUREMENTS

We evaluated the contribution of bark to flexural rigidity at one site included in the BRIDGE project, and three others in Western coastal French Guiana. Doing so required precise measurements of the stiffness and diameter of fresh stems with and without bark. In each site, species were chosen to represent a wide taxonomic range. Even so, the taxa subjected to biomechanical measurements largely overlapped with those of the BRIDGE dataset. We selected straight stems 0.5–1.6 cm in diameter and 0.2–0.5 m in length from the branches of adult trees and the primary axis of saplings. Stiffness (Young's modulus of elasticity) was measured using a custom three-points bending test apparatus on the same stems before and after bark was stripped from them. For some stems, stiffness with bark was measured on a longer stem before it was cut into 0.14 m length segments, after which the bark was removed and stiffness of wood alone was measured. Diameters were measured in three points along the stems using digital calipers (Mitutoyo Corporation, Tokyo, Japan). Where multiple measurements were made on an individual, data were summarized to provide one mean per part (trunk or branch) of each individual. The ratio of the contributions of bark and wood to the flexural rigidity of stems was calculated as $E_b/E_w((R_b/R_w + 1)^4 - 1)$, where E indicates stiffness, R indicates radius and the subscripts b and w refer to bark and wood, respectively (rearranged from Niklas 1999 Fig. 7a).

PHYSIOLOGICAL MEASUREMENTS

We measured the rate of CO₂ respiration by trunks in two plots also sampled in the BRIDGE campaign as well as two other nearby plots. We sampled only trees with fully or mostly exposed crowns. Measurements, one observation per tree, were made between 9:00 and 16:00 h on sunny days. CO₂ diffusion from trunks was measured using an infrared gas analyzer (EGM1 or EGM4; PPSystems, Hitchin, UK) attached to a sampling chamber strapped to a gently cleaned area of the trunk at about 1.3 m above ground. Trunk efflux (Et) was calculated and expressed on the basis of trunk area as:

$$Et = \Delta[CO_2]/t * D_{ch} * v * 273/T_{air} \quad \text{eqn1}$$

Where $\Delta[CO_2]$ is the increase in CO₂ concentration over the sampling duration t (ppm s), D_{ch} is the depth of the chamber (m), v is the

volume of a mole of CO₂ (0.045 mol L⁻¹) and T_{air} is the air temperature (°K). E_t was standardized at 25 °C as:

$$Et_{25} = \frac{Et}{Q_{10}^{(T_{\text{air}}-25)/10}} \quad \text{eqn2}$$

where Et_{25} is the CO₂ efflux at 25 °C and Q_{10} is the relative increase in E_t for a temperature increase of 10 °C, which was fixed at 2 (Cavaleri, Oberbauer & Ryan 2006).

We regressed bark thickness against trunk diameter for the trees in the physiological dataset. We then constructed a linear mixed model to assess the relationship between CO₂ efflux and the residuals of this relationship. Initially, we included DBH as a continuous covariate and species identity, site, and sampling date as categorical covariates. We then dropped out covariates, using Akaike's information criterion to choose the most appropriate model. The best model retained only species identity as a covariate.

All analyses were conducted in the R statistical computing environment, version 2.10.1, using the nlme package (Pinheiro *et al.* 2009; R Development Core Team, 2009).

Results

VARIATION IN BARK THICKNESS

We measured bark thickness on the trunks of 3657 trees, 1971 of which were also measured for twig bark thickness, representing 57 families of angiosperms. The thickness of bark varied greatly within and among species. Mean bark thickness on trunks was 4.53 mm (range: 0.5–29.0 mm). Within species, the greatest source of variation in bark thickness was individual size. Diameter at breast height (DBH) was strongly positively correlated with bark thickness (Fig. 1a), as were twig bark thickness and twig diameter (Fig. 1b). Even accounting for the relationship between DBH and bark thickness, and only considering trees < 20 cm DBH, variance in bark thickness occurred at all taxonomic levels (Table 2 and Fig. 1c). Family median bark thickness varied from 0.60% (Olacaceae) to 1.8% (Boraginaceae) of trunk radius. Even within genera there was great variation in bark thickness. For example, the genera *Pouteria* (Sapotaceae) and *Inga* (Fabaceae: Mimosoidae) showed ranges of trunk bark thickness from 0.5–7.0 mm and 0.5–7.1 mm, respectively (again, considering only trees < 20 cm DBH). For the community as a whole, bark consti-

tuted a mean of 1.01% of trunk diameter and 8.97% of twig diameter (Fig. 1d,e).

GENERAL DEFENCE

Should bark play an important role in defence against either herbivores or fire, a positive asymptotic relationship between DBH and bark thickness would be expected. Combining all species together, both linear and asymptotic relationships between DBH and trunk bark thickness were significant ($P < 0.0001$), and each explained a similar amount of variance (linear: $R^2 = 0.38$, asymptotic: $R^2 = 0.39$; Fig. 1a). Using Akaike's information criterion (AIC), there was more support for an asymptotic relationship than for a linear relationship ($\text{AIC}_{\text{linear}} = 17\,469$, $\text{AIC}_{\text{asymptotic}} = 17\,358$), with a predicted asymptotic bark thickness of 22 mm. Support for an asymptotic relationship was undermined, however, as the half-asymptotic DBH was 85 cm, a diameter attained by only the largest 1.2% of the individuals in the dataset. Credence in the asymptotic relationship declined further when species were analysed separately. Of the 30 most-common species (those with more than 25 individuals), only one (*Carapa procera* [Meliaceae]) was fit better by an asymptotic model than a linear model (Fig. S1). Moreover, the asymptotic bark thicknesses predicted for individual species were frequently biologically implausible, as they were greater than the maximum bark thickness observed for that species in this study. In twigs, an asymptotic fit could not be parameterized because there was an accelerating relationship between twig diameter and twig bark thickness, which provided a superior fit to that of the linear relationship (Fig. 1b).

DEFENCE AGAINST FIRE AND HERBIVORES

The association of species with fire-prone habitats varied extensively. For example, *Parinari campestris* (Chrysobalanaceae) was collected four times in cerrado, once in dry forest and 40 times in moist forest, whereas its congener, *P. montana*, was only ever collected in moist forests. Considering all species together, there was no relationship between the fire-association index of a species and the residuals of the bark thickness–diameter relationship ($P = 0.64$, Fig. 2a). Similarly, among those species that range into fire-prone habitats, there was no significant relationship with the fire-association index ($P = 0.052$). These relationships were weak because the distributions of bark thickness (as a fraction of stem diameter) did not differ between species that range into fire-prone habitats and all species together (Kolmogorov–Smirnov test, Trunk: $P = 0.97$, Twig: $P = 1.00$, Fig. 1d,e).

If herbivore defence is an important factor affecting variation in bark thickness, we would also expect species with thicker bark to have either less latex or less diversity of defensive compounds (or both). This hypothesis was assessed for 202 species from 47 families. There was a significant trend for latex-rich species to bear thicker bark after accounting for the relationship between bark thickness and diameter ($P = 0.044$, Fig. 2b). This trend was weak, as the mean bark

Table 2. Partitioning of variance in trunk and twig bark thickness among taxonomic levels. For trunks, to limit variation attributable to differences in individual stature among taxa, only individuals < 20 cm DBH are included. In both trunk and twig bark, there is far more variation within species than among taxa (See Fig. 1a,b)

Taxonomic level	Percent variance explained	
	Trunk	Twig
Family	11.3	17.8
Genus	7.8	4.8
Species	17.3	22.9
Intra-species	63.6	54.6

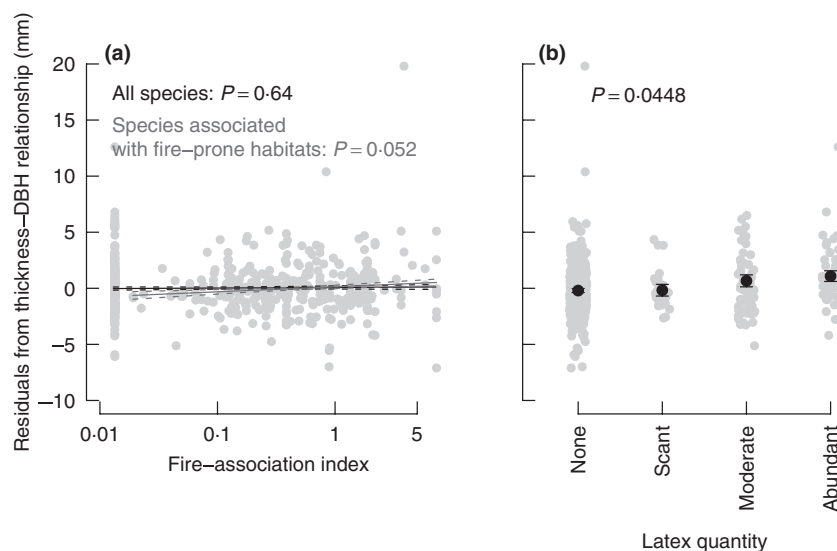


Fig. 2. There is little evidence that defence against fire or against herbivory explains variation in bark thickness in the forests of French Guiana. Species-mean residuals from the bark thickness–diameter relationship are unrelated to (a) association with fire-prone habitats but are (b) weakly and positively correlated with latex quantity.

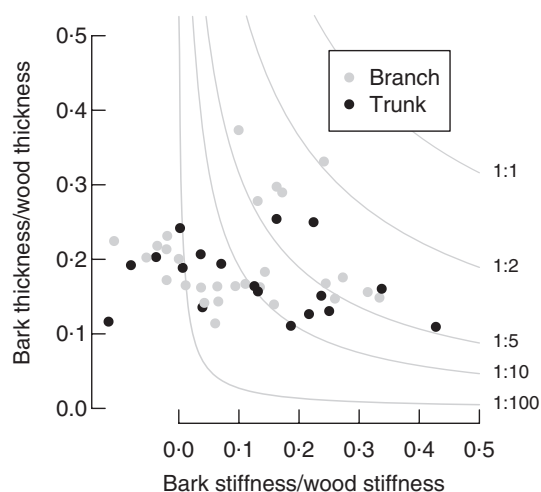


Fig. 3. The contribution of bark to flexural rigidity of a stem is proportional to the product of the ratio of bark thickness to wood thickness and the ratio of bark stiffness to wood stiffness. Isoclines connect points that have equivalent flexural rigidities, and are labelled with the ratio of the relative contributions of bark and wood. The isocline labelled 1 : 10 passes through the cloud of points, in accord with our estimation that bark contributes approximately 10% of the flexural rigidity of an average stem, with little difference between branches and trunks. Measurement error caused some samples, in which the ratio of bark stiffness to wood stiffness was small, to appear to have negative stiffness. Bark thickness, as a fraction of stem thickness, was relatively great in this dataset owing to the relatively small diameter of the stems measured.

thickness of species with abundant latex was only 1.3 mm greater than that of non-lactiferous species. The diversity of defensive compounds, whether considering monoterpenes or sesquiterpenes separately, or considering all volatile terpenes together, was unrelated to bark thickness ($P > 0.17$, Fig. S2).

BIOMECHANICAL SUPPORT

The flexural rigidity provided by bark is proportional to the product of its stiffness and its thickness. To assess the magnitude of the contribution of bark to flexural rigidity, we sampled 40 trees representing 18 families, with six trees yielding both trunk and branch samples. A mean of 10.8% of the flexural rigidity of stems was attributable to bark, with little difference between trunks and branches (10.0% and 11.3% respectively; Fig. 3). This relatively minor contribution occurred despite the proportionately greater thickness of bark (mean bark thickness: 18.5% of stem radius) on the small-diameter stems of this dataset (mean overbark diameter: 7.1 mm). Rather, the contribution of bark to flexural rigidity was limited by its lack of stiffness, which was on average just 12.1% that of wood.

PHYSIOLOGICAL CONSEQUENCES

Bark that is thicker may be expected to be less permeable to gasses than thinner bark. We assessed CO_2 efflux from the trunks of 314 trees representing 24 families. There was no evidence that thicker bark reduces CO_2 efflux ($P = 0.34$, Fig. S3).

Discussion

Bark thickness varies strongly with stem diameter both for trunks and twigs (Fig. 1a,b), in accordance with the results of previous studies (Uhl & Kauffman 1990; Pinard & Huffman 1997; Nefabas & Gambiza 2007). Among species, bark thickness varies widely at all taxonomic levels (Table 2). There have been two previous surveys of bark thickness with wide taxonomic sampling in the Neotropics: Uhl & Kauffman (1990) measured 699 trees with DBH ≥ 20 cm in Paragominas, Para state, Brazil, and Roth (1981) measured 263 trees in

Venezuela with DBH ≥ 10 cm. Like the current study, these studies were conducted in lowland closed-canopy moist forest. Considering only trees ≥ 20 cm DBH to make the three datasets comparable, Uhl and Kauffman found a mean bark thickness of 7.1 mm (SEM: 0.14 mm), Roth found a mean of 10.4 mm (SEM: 0.38 mm), and we found a mean of 6.4 mm ($n = 1648$, SEM: 0.10 mm, Fig. 1a). The mean bark thickness in the forests of French Guiana is thus significantly less than the other two sites (one-sample *t*-tests, $P < 0.0001$). These differences, though slight, may be enough to affect the probability of an individual tree's survival through fire, since this probability is strongly predicted by the thickness of its bark. Experimental studies have shown thicker bark to significantly reduce cambium heating, thus promoting survival through fire (Uhl & Kauffman 1990; Pinard & Huffman 1997). Moreover, bark thickness is a better predictor of cambium heating than are bark density and moisture content (Pinard & Huffman 1997). These results suggest that the forests of the Guiana Shield may be somewhat more susceptible to fire than are those of Venezuela and Para. Thus, our survey of bark thickness should be of use in refining mechanistic models of land-cover change in the face of global climate change.

FUNCTIONAL EXPLANATIONS

Despite the broad variation in bark thickness we observed, we found little support for most functional hypotheses explaining this variation (Table 1). Bark appears, in general, to be too thin and too flexible to generate substantial structural rigidity. Nor was there conclusive evidence that bark plays a substantial role in defence, neither against fire nor against herbivory. Finally, there was no evidence that thicker bark limits trunk respiration. Our results, therefore, do not allow sweeping conclusions to be drawn regarding the functions of bark in tropical moist forests. In the following section, we interpret our results in light of the current literature.

Given the potential for injury from fire and herbivores, we expected that much of the variation in bark thickness would be associated with bark's defensive function. We found little evidence, however, that defence against either herbivory or fire explains the variation in bark thickness in French Guianan rainforests. We were surprised to not find significant relationships with fire association, since defence against fire is suggested to be one of the primary factors shaping bark thickness (Uhl & Kauffman 1990; Hoffmann & Solbrig 2003b; Van Nieuwstadt & Sheil 2005). It appears that bark thickness is evolutionarily labile, such that closely related species may have greatly differing bark thicknesses (Fig. 1c). Thus, individual trees in the humid forests of French Guiana can bear bark of any thickness, regardless of their associations with fire-prone habitats (Fig. 1d,e).

A positive decelerating relationship between tree size and trunk bark thickness has been previously interpreted to mean that bark thickness is strongly influenced by its defensive role. According to this hypothesis, which assumes that bark production is costly, defensive properties (both insulational and herbivory-reducing) of bark should be satisfied by a certain

thickness, beyond which additional thickness renders no additional survival advantage (Wilson & Witkowski 2003). In this study, AIC suggested that an asymptotic fit of trunk bark thickness against DBH with an asymptote of 22 mm should be preferred over a linear fit (Fig. 1a). Nevertheless, we do not put much credence in this result, since the predicted asymptotic bark thickness was so great that very few individuals ever attain it. Furthermore, only one of the 30 most-common species showed an asymptotic diameter–thickness relationship (Fig. S1). Roth (1981) noted that an asymptotic diameter–thickness relationship is expected only for species with bark that desquamates (i.e. flakes off). Species with fibrous or smooth bark, of which there are many in French Guianan forests, should be more likely to show linear diameter–thickness relationships.

Bark thickness weakly increased with latex quantity, but showed no relationship with the diversity of defensive compounds (Fig. 2b; Fig. S2). We were surprised by these results, given the diversity of sap-feeding vertebrates and invertebrates, and the damage they can cause (Goldingay 2000). As latex and terpenes are but two among the various classes of chemicals implicated in deterring herbivory, ours is a rather limited evaluation of the herbivore-deterrence functions of bark. Furthermore, investment in certain chemical defences, such as latex, can lead to specialization by certain herbivorous taxa (Tavakilian *et al.* 1997). A stronger test, beyond the scope of our study, would be to compare the characteristics of trunks observed to be attacked by herbivores with those that are not attacked, controlling as well as possible for species and individual stature (Eberhardt 2000). Moreover, inverse relationships between chemical defences and the physical defence that thick bark represents are only to be expected if trees have a limited defence budget. If there are also deeper allocation trade-offs, between allocation to growth and allocation to defence, we may expect positive correlations between physical and chemical defences. Such trade-offs may include wood density, as very dense wood is generally pest-resistant, and may obviate the need for exterior defences such as thick bark or toxic chemicals. An allied study of correlations among functional traits in the BRIDGE dataset, however, showed bark thickness to be uncorrelated with wood density in both trunks and twigs (Trunk: $r = -0.08$, Twig: $r = 0.03$; C. Baraloto, unpublished data). Nevertheless, a strong test of the defensive role of bark would include assessments of the physiological trade-offs that shape allocation to growth, respiration and defence.

A simple formula proposed by Niklas (1999) estimates the contribution of bark to the flexural rigidity of a stem based upon its thickness and stiffness. Our biomechanical measurements indicate that in an average stem, bark provides about 10% of the flexural rigidity, with the remainder provided by wood (Fig. 3). It appears that the contribution of bark is limited by the relative lack of stiffness of bark, which we found to be, on average, 12% of wood stiffness. Little data is available on bark stiffness in general, but Niklas (1999) reported bark stiffness to be approximately 50% that of wood for three temperate species. This difference in stiffness probably explains

the disparate results between our study and that of Niklas (1999). Several considerations shape our inferences from the biomechanical results. In the biomechanical dataset, bark made up an average of 18% of stem diameter, which is much more than in the general bark-thickness dataset, in which bark constituted 1% of trunk diameter and 9% of twig diameter (Fig. 1d,e). Furthermore, stems in the biomechanical dataset were thinner than those of the larger dataset. These observations, together with our estimate of bark stiffness, suggest that the mechanical contribution of bark to the stability of larger branches and trunks will be at most 10%, and is likely to be far less. More extensive surveys of bark stiffness would allow the mechanical function of bark to be more conclusively determined.

A consequence of thicker bark may be to limit the diffusion of gasses between respiring trunk tissues and the atmosphere. We found no relationship between bark thickness and CO₂ efflux from trunks, but bark thickness is not the only factor that affects diffusion resistance. Resistance to CO₂ efflux depends not only on bark thickness, but also the degree to which bark tissues are impregnated with suberins, lignins and waxes (Lendzian 2006; Teskey *et al.* 2007). Trunk aeration thus mainly occurs through lenticels, and through the loose parenchyma of rays (Roth 1981). Thus, increasing bark thickness does not necessarily affect rates of CO₂ efflux. Rather, diffusion rates can be more closely related to lenticel density and size, which vary substantially among species. Bark density and lenticel quantification, unfortunately, were beyond the scope of this study.

INFERENCES FROM ANATOMY

As a final approach to gain insight into the factors shaping bark thickness in tropical trees, we analysed the detailed anatomical data provided by Roth (1981) in her authoritative book on the structure of tropical tree bark. Together with many other observations, Roth reported the thickness of bark components, including phelloderm, rhytidome and overall bark thickness, on one individual of each of 265 species of lowland tropical moist forest in Venezuela. As well, she

counted the number of superimposed periderms. Though it is frequently assumed that bark is universally formed as a single periderm (plane of division), she found a median of two superimposed periderms, and a maximum of 21. Using the data provided by Roth (1981, Tables 1–48), we correlated total bark thickness with the thickness of its two primary components: phelloderm (internal to the innermost periderm) and rhytidome (external to the innermost periderm). Total bark thickness was strongly and positively correlated with rhytidome thickness but not phelloderm thickness (Fig. 4a,b). Moreover, the number of superimposed periderms in the bark accurately predicted bark rhytidome thickness (Fig. 4c). Thus, variation in rhytidome thickness generates the majority of the observed variation in overall bark thickness. This suggests, in turn, that the functional roles that lead to variation in bark thickness in tropical trees are those that are performed by the rhytidome. As rhytidome is non-conductive, and frequently impregnated with lignins and waxy compounds, it is an important defensive barrier. We suggest, therefore, that a generalized defensive function against biotic and abiotic threats is one of the most important factors shaping bark thickness.

Conclusions

The question remains: Why is tree bark of such varied thickness in tropical moist forests? Functional explanations are not clear-cut. Perhaps because bark must simultaneously perform so many functions, no single function emerges as a dominant influence on thickness. It should also be noted that there are other potentially important functions of bark, the investigation of which lay beyond the scope of this study, such as photosynthesis, maintenance of water relations and the storage of non-structural carbohydrates (Roth 1981). Furthermore, some hypothesized functions, such as defence, could be more rigorously examined by sampling bark thickness across gradients of fire frequency or pest pressure (Hoffmann, Orthen & Do Nascimento 2003a; Fine, Mesones & Coley 2004). Nevertheless, we hope that our investigation of multiple functional hypotheses for the variation observed in

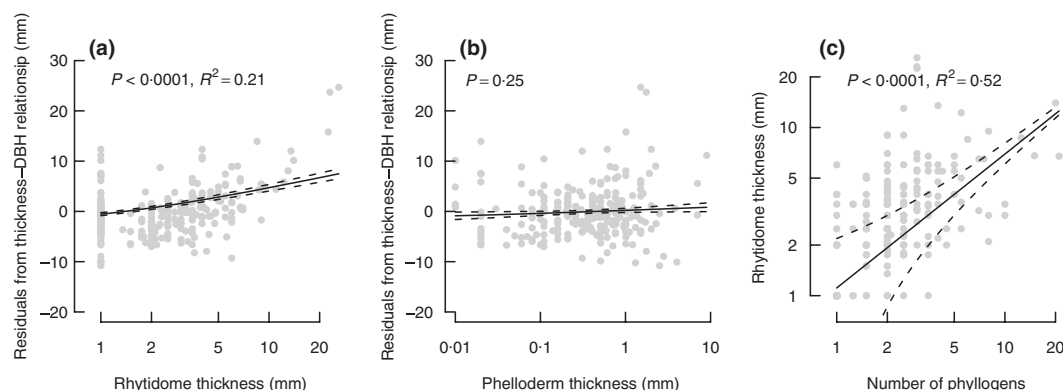


Fig. 4. Bark thickness variation results principally from variation in rhytidome (outer bark) thickness, rather than phelloderm (inner bark) thickness. (a) Rhytidome thickness, but not (b) phelloderm thickness, predicts overall bark thickness. (c) The number of overlapping periderms is a strong predictor of rhytidome thickness. Note logarithmic scale on all x-axes, and y-axis of (c). Data from Roth (1981).

bark thickness will provide a foundation for stronger tests in the future. Understanding the patterns in bark thickness variation and the functional bases of this variation will continue to increase in importance, since bark can limit trunk heating during forest fires, which are expected to increase in frequency and intensity in Neotropical forests (Malhi *et al.* 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Trunk bark thickness–stem diameter relationships for the 30 most-common species.

Figure S2. Terpene richness is not related to trunk bark thickness.

Figure S3. Bark thickness is not related to the rate of CO₂ efflux from trunks.

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