



Soil and species effects on bark nutrient storage in a premontane tropical forest

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Abstract

Background and aims Bark contains a substantial fraction of the nutrients stored in woody biomass, however the degree of functional coordination of bark, wood, and foliar nutrient pools, and its relationship to soil nutrient availability remains poorly understood.

Methods Bark thickness and nitrogen, phosphorus, potassium, calcium, and magnesium concentrations were measured in 23 tree species present in two premontane wet tropical forests in western Panama differing in soil nutrient availability. Bark data were combined with existing wood and leaf data from the same species.

Results Bark nutrients were positively correlated with leaf and wood nutrients for all elements. The low fertility site had both lower bark nutrient concentrations and thicker bark, driven primarily by species compositional differences between sites, and secondarily by intraspecific variation. Across species, bark nutrient concentration varied 4 to 25 fold, with the highest variation for calcium. Overall, bark accounted for the largest percent of Ca in above-ground biomass nutrient pools (22–82%) and a large fraction of the other nutrients studied (N: 6–53%, P: 5–50%, K: 4–40%, and Mg: 2–35%).

Conclusions Bark represents a substantial, and highly variable, pool of biomass nutrients. The functional role of bark nutrients, the causes and consequences of this variation, and its relation to other bark traits, including bark thickness, deserve further study.

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Keywords Plant organ nutrient concentrations · Bark thickness · Wood · Leaves · Biomass nutrient budget · Nutrient allocation

Abbreviations

Ca	Calcium
C:N	Carbon to Nitrogen ratio
DBH	Diameter Breast Height
LMA	leaf mass per unit area
Mg	Magnesium
N	Nitrogen
P	Phosphorus
K	Potassium

Introduction

The productivity of tropical forests, which commonly grow on highly weathered soils, is widely considered to be limited by the availability of soil-derived nutrients (Vitousek and Sanford 1986). Consequently, the majority of nutrients cycled in tropical forests result from the decomposition of plant material, resulting in a positive feedback loop between plant nutrient allocation and soil nutrient availability (Wardle et al. 2004). While nutrient concentrations in plant biomass generally track the availability of nutrients in soil over broad fertility and climatic gradients in tropical forests (Fyllas et al. 2009; Ordoñez et al. 2009), there is considerable variability among co-occurring tree species in the allocation of nutrients to leaf (Townsend et al. 2007; Asner and Martin 2011) and woody biomass (Heineman et al. 2016). Furthermore, interspecific variation in nutrient acquisition and allocation may underlie variation in the importance and identity of limiting soil nutrients observed in nutrient addition experiments (Tanner et al. 1998; Mirmanto et al. 1999; Wright et al. 2010; Alvarez-Clare et al. 2013), and explain turnover in tree species composition across soil fertility gradients (John et al. 2007; Condit et al. 2013; Dalling et al. 2016).

Although nutrient allocation strategies are widely understood from the perspective of leaves, allocation of mineral nutrients to different non-photosynthetic organs is rarely measured, despite its importance to ecosystem function. Frequently, nutrient concentrations of all non-photosynthetic tissues are combined to provide estimates of nutrient stocks in woody biomass (Uhl and Jordan 1984; Tanner 1985; Bond 2010; Harrington et al. 2001). This approach, however, may obscure important tissue-specific variation in nutrient allocation with implications for nutrient cycling. In particular, bark can have 2–20 times the nutrient concentration of wood (Wang et al. 1991; Scatena et al. 1993), and represents a non-trivial, and highly variable, fraction of total above-ground biomass. Bark is estimated to make up 2–19% of forest biomass (Whittaker and Woodwell 1969; Whittaker et al. 1974; Alban et al. 1978; Van Lear et al. 1984; Scatena et al. 1993; Fearnside 1997; Hart et al. 2003; Gautam et al. 2011; Cai et al. 2013). Bark biomass and bark volume can be highly variable across species and DBH (Miles and Smith 2009; Arias et al. 2011). Consequently, variation among species and sites in nutrient allocation to bark, and in total biomass

investment in bark, may have a considerable impact on both tree and ecosystem nutrient cycling.

Bark not only influences nutrient dynamics within living trees but may also influence the rate of biomass decomposition post mortem. Because biomass concentrations of nitrogen (N), phosphorus (P), and the carbon:nitrogen ratio (C:N) are predictive of wood decomposition rates (Weedon et al. 2009; Zanne et al. 2015), the relatively nutrient-rich status of bark may facilitate wood decay (Dossa et al. 2016, 2018). Alternatively, bark and wood decay trajectories may be relatively independent (Freschet et al. 2012; Johnson et al. 2014; Shorohova et al. 2016). Understanding the magnitude of variation in bark nutrients, and the extent to which it correlates with wood and leaf nutrients could therefore improve trait-based models used to model rates of carbon turnover (Cornwell et al. 2009).

One challenge to incorporating bark into trait-based models is its striking diversity of morphologies, which includes variation in thickness, density, texture and persistence. The functional basis for this variation remains unclear (Paine et al. 2010). Although thick bark confers fire resistance (Pinard and Huffman 1997) and bark is thicker in fire prone environments (Pellegrini et al. 2017), thickness appears to be uncorrelated with an association for fire-prone habitats in widely distributed tropical trees (Paine et al. 2010). A test of additional hypotheses for bark function in the same study found only weak evidence for a role in defense against herbivores, and no support that it contributes to structural rigidity (Paine et al. 2010). However, in temperate rain forests in New Zealand that experience little fire, bark thickness is inversely correlated with soil fertility (Jager et al. 2015; Richardson et al. 2015). This raises the possibility that physical traits of bark might be related to protecting soil-derived nutrients that are costly to acquire. Furthermore, investment in bark storage proteins, which can serve as a mobile nutrient reserve, varies among temperate hardwood species (Wetzel and Greenwood 1991) and might therefore also co-vary with bark morphology. Alternatively, bark traits may simply co-vary with wood traits, reflecting the shared ontogenetic origin of both inner bark and wood from the vascular cambium (Rosell et al. 2014), and more broadly, existing axes of functional coordination between wood and leaves (Rosell et al. 2014; Heineman et al. 2016). For example, wood and bark densities (Rosell et al. 2014; Poorter et al. 2014) and wood and leaf nutrient concentrations (Heineman et al. 2016) are both

positively correlated. Bark nutrients might therefore be predicted to correlate with wood nutrients.

In this study, we measured the thickness and nutrient concentrations of bark in 23 tree species sampled in two premontane forest plots in Panama with contrasting soil nutrient availability. We combined data on bark physical and chemical traits, with wood and leaf nutrient data collected at the same sites (Heineman et al. 2016) to test two primary hypotheses: (1) Coordination of tree nutrient allocation results in covariation of bark, wood and leaf nutrient concentrations; (2) Soil nutrient limitation simultaneously constrains bark nutrient concentration and selects for increased bark thickness. We then combined site-specific bark nutrient data with soil, wood, and leaf nutrient content data to estimate the contribution of bark to above-ground biomass nutrient stocks.

Materials and methods

Site description

Bark, wood, and soil samples were collected from two sites, 9 km apart, in wet premontane forest at the Fortuna Forest Reserve in western Panama. The sites, Honda A and Hornito, are 1 ha forest dynamics plots that differ in rainfall and soil characteristics (primarily P and base cations; Prada et al. 2017; Table 1). The Honda A forest grows on soils derived from low fertility rhyolitic tuff, while those at Hornito are derived from dacite. Despite their proximity, the sites only share 45 out of 164 tree

species >10 cm diameter breast height (DBH), that occur at the two sites, and only one out of the ten most abundant species (*Dendropanax arboreus*; J. Dalling, unpublished data).

Sampling design

We sampled bark and wood from 23 tree species within 100 m of the edge of the 1 ha forest plots. The dataset included nine species sampled at both sites and seven species unique to each site (Supplemental Information Appendix S1). We chose the tree species based on their high abundance in the plots and/or their presence in both sites. In total, we sampled species that accounted for 44.4% of basal area at Honda A and 51.4% at Hornito. The sampled species unique to each site contributed the highest proportion of basal area at each site (Honda A: 31.5%; Hornito 10.1%), and therefore have the largest impact on biomass nutrient stocks. For these unique species, we sampled three individuals per species. For shared species present at both sites, we sampled five individuals per species per site to provide additional statistical power for analysis of intraspecific variation in bark nutrient concentration. When collecting bark, we used a chisel to remove a 9 cm × 9 cm sample of inner and outer bark from each tree at breast height. Bark thickness and area of the bark piece were measured to the nearest millimeter before samples were dried at 65 °C for 72 h. To calculate bark density, we multiplied the length, width, and thickness (cm) of each sample to calculate bark volume, and then divided the dry mass (g) by the volume.

Because bark thickness usually increases with diameter (Paine et al. 2010; Richardson et al. 2015), we compared the DBH of the trees sampled across sites. DBH differed significantly among species sampled (ANOVA $df=22$, $F=4.32$, $p<0.001$; range of species means = 9.2–63 cm) and sites (ANOVA $df=1$, $F=11.34$, $p=0.001$; average DBH at Honda A = 20.8 cm (± 15.4 SD) and Hornito = 30.0 cm (± 26.9 SD)), and site and species showed a significant interaction (ANOVA $df=8$, $F=2.91$, $p=0.007$). Tree diameter was therefore included in bark thickness analyses (see statistical methods below).

Wood and leaf nutrient concentration data were obtained for 14 species at Honda A and 11 species at Hornito (Heineman et al. 2016). For wood, three trees per species were cored using a 4.3-mm diameter Hagl of increment borer. Analysis of wood nutrients was

Table 1 Environmental characteristics of the two sampling sites

Site	Honda A	Hornito
Elevation (m)	1155	1330
Annual Rainfall (mm)	6255 ± 2350	5160 ± 570
pH	3.6 ± 0.2	5.0 ± 0.7
Total N (%)	1.1 ± 0.4	1.3 ± 0.6
Total P (mg/kg)	650 ± 209	1168 ± 300
Total inorganic N (mg/kg)	12.7 ± 6.7	12.6 ± 6.7
Resin P (mg/kg)	0.8 ± 0.6	9.4 ± 4.6
K (cmol/kg)	0.1 ± 0	0.7 ± 0.3
Ca (cmol/kg)	0.2 ± 0	20.3 ± 13.5
Mg (cmol/kg)	0.1 ± 0.1	3.8 ± 1.7

Soils data were collected from 13 locations at 0–10 cm depth in a one-hectare plot at each site. Values are means (± 1 SD). Modified from Prada et al. (2017) and B. L. Turner (unpublished data)

restricted to the outer 5 cm of wood, as the heartwood to sapwood transition is often hard to delineate in tropical trees (Jordan and Kline 1977). For leaf nutrients, three fully expanded shade leaves were collected with a pruning pole from three individuals per species.

Nutrient analysis

Analysis of wood and leaf nutrients is reported in Heineman et al. (2016). An identical protocol was used for bark analysis. In brief, dried bark was ground to a fine powder using a mini Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). Sample percent N was determined using an elemental analyzer (Costech, Valencia, CA, USA). Concentrations of P, magnesium (Mg), calcium (Ca), and potassium (K) were determined by using inductively coupled plasma-optical emission spectrometry (ICP-OES) on an Optima 2000 DV (Perkin Elmer, Waltham, MA, USA). Samples were initially dry ashed at 550 °C for 3 h, and then dissolved in 1 M HNO₃ (Karla 1998). A standard control (apple leaves, NIST 1515) was included with all analyses.

Correlations of nutrient concentrations across plant organs

We compared wood, leaf, and bark nutrient concentrations to examine the coordination of nutrients across plant organs. Where possible, we calculated bark, wood, and leaf species mean nutrient concentrations using samples from both sites. For some species, wood and leaf nutrient data were only available from one site. When wood and leaf data were only available from one site, we used bark data from the site corresponding to the wood and leaf data to calculate bark nutrient means (Supplemental Information Appendix S1). To test for correlations of nutrient concentrations across tissue types, we used major axis regression implemented in the package *lmodel2* in R (Legendre 2018). We also calculated phylogenetically independent contrasts of each functional trait to evaluate if trait correlations persist after accounting for evolutionary history. We used a previously constructed tree for the species in this study built from the Angiosperm Phylogeny Group (APG III) using Phylomatic v3.0 (Webb and Donoghue 2005), fossil derived of tree taxa and Phylocom to construct the tree (see Heineman et al. 2016 for details). We then used the R package *ape* to calculate the phylogenetically

independent contrasts for the log of each species trait (Paradis et al. 2004).

Analysis of bark thickness and nutrient allocation between sites

We compared both bark thickness and relative bark thickness between sites, to assess whether bark thickness differed between sites and whether differences in bark thickness were explained by differences in DBH between sites. To explain variation in bark thickness, we used a linear model with DBH, species, and site as factors. We calculated relative bark thickness by dividing bark thickness by DBH (Jager et al. 2015) and used species and site as predictors in a linear model.

To examine variation in bark nutrient concentration, we natural log-transformed the nutrient concentrations to meet the linear model assumption of normality of errors. We explored intraspecific variation in bark nutrient concentrations using a linear model with DBH, site, and species as factors to analyze only the species that were sampled in both sites. We used AICc model selection to determine which terms to retain in the final model. We also calculated the variation explained by each factor using the *varpart* function in the *vegan* package in R (Oksanen et al. 2018).

We calculated the community weighted mean nutrient concentration for comparisons in nutrient concentration between the two sites and for the estimation of above-ground nutrient budget. To calculate the community weighted mean nutrient concentration, we used the basal areas calculated for each species in the 2013 census of the two plots (Prada et al. 2017). Species values were weighted by their respective basal area in each 1-ha plot. We then used the *Hmisc* package in R to calculate the basal area weighted mean and variance and performed a t-test (Harrell and Dupont 2018).

Estimation of above-ground nutrient budgets

Total above-ground biomass (AGB), including leaf biomass, was calculated for each tree using allometric equations for wet forests from Chave et al. (2005) where Eq. 1 is for trees with available height measurements and Eq. 2 is for trees without height measurements. We measured the height of the 30 largest diameter trees (as determined from the 2008 plot census) and a subset of 100 trees of varying sizes in each plot in Spring 2011 (K.

Heineman, unpublished data). We took the sum of AGB estimates for all trees in each plot to calculate plot AGB.

$$\text{AGB} = 0.0776 \times (\rho D^2 H)^{0.940} \quad (1)$$

$$\text{AGB} = \rho \times \exp\left(-1.239 + 1.980 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3\right) \quad (2)$$

Where AGB is above-ground biomass (kg), ρ is wood density (g/cm^3), D is diameter at breast height (cm), and H is the height of the tree (m).

The AGB nutrient pools found in each plant organ were calculated by estimating the proportion of AGB found in each plant organ and multiplying the estimated biomass by the organ-specific community weighted mean nutrient concentrations. To calculate leaf biomass, we multiplied leaf area index (LAI) and site-specific leaf mass per area (LMA). The leaf area index for both sites was estimated as $6 \text{ m}^2 \text{ m}^{-2}$ based on data compiled for tropical forests (Leigh 1999; Unger et al. 2013). Site specific LMA was estimated as 62 g m^{-2} for Honda A and 69 g m^{-2} for Hornito (K. Heineman, unpublished data).

Bark biomass is difficult to predict from the data we collected, because bark thickness differs between branches and boles (Paine et al. 2010). We calculated the range of bark biomass percentages (2–20%) as a percent of forest biomass that has been reported in previous studies (Whittaker and Woodwell 1969; Whittaker et al. 1974; Alban et al. 1978; Van Lear et al. 1984; Scatena et al. 1993; Fearnside 1997; Hart et al. 2003; Cai et al. 2013). We reported the calculations of bark as 10% of AGB in Table 3.

Results

Coordination of wood, leaf, and bark nutrient concentrations

Bark, leaf, and wood nutrient concentrations were positively correlated, although the range of nutrient concentrations differed greatly between plant organs. Bark and leaf species mean nutrient concentrations were positively correlated for all nutrients examined (Ca, K, Mg, N, and P, Fig. 1, Supplementary information Table S1). When data from the two sites were analyzed separately, bark and leaf nutrient concentrations were positively

correlated for all nutrients examined except for Ca (Supplementary information Table S2 and S3). Species mean nutrient concentrations were higher in leaves compared to bark for all nutrients except for Ca, which was higher in bark than leaves (Fig. 2). Similarly, bark and wood species mean nutrient concentrations were positively correlated for all nutrients examined (Fig. 1). When sites were analyzed separately, bark and wood nutrients were positively correlated except for Ca and Mg (Supplementary information Table S2 and S3). Species mean bark nutrient concentrations were 2–10 times higher than that of wood nutrient concentrations (Fig. 2). Slopes of the relationships between log-transformed wood and bark species mean nutrient concentrations did not differ from 1 for any nutrient except for P (slope < 1), indicating that the magnitude of tissue nutrient concentrations did not impact its relative allocation to bark versus wood (Fig. 1, Supplementary information Table S1). In contrast, slopes for leaf and bark species mean nutrient relationships were more than 1 except for P and K (Fig. 1, Supplementary information Table S1). When evolutionary relationships were taken into consideration, bark was still positively correlated with leaves and wood for all nutrients except Mg, which was not correlated between bark and wood (Supplementary information Table S1, Fig. S1).

Site effects on bark thickness, nutrient concentration, and community weighted mean nutrient concentrations

For species sampled at both sites, Honda A had thicker bark and higher relative bark thickness than Hornito (Table 2). The community weighted mean bark thickness was thicker at Honda A, the lower fertility site ($0.57 \text{ cm} \pm 0.17 \text{ SD}$), than at Hornito ($0.32 \text{ cm} \pm 0.11 \text{ SD}$, $t = 4.8$, $df = 26$, $P < 0.001$), despite the significantly higher mean DBH of trees at Hornito. In contrast to bark thickness, when analyzing species found in both sites bark nutrient concentrations were significantly higher at Hornito for all

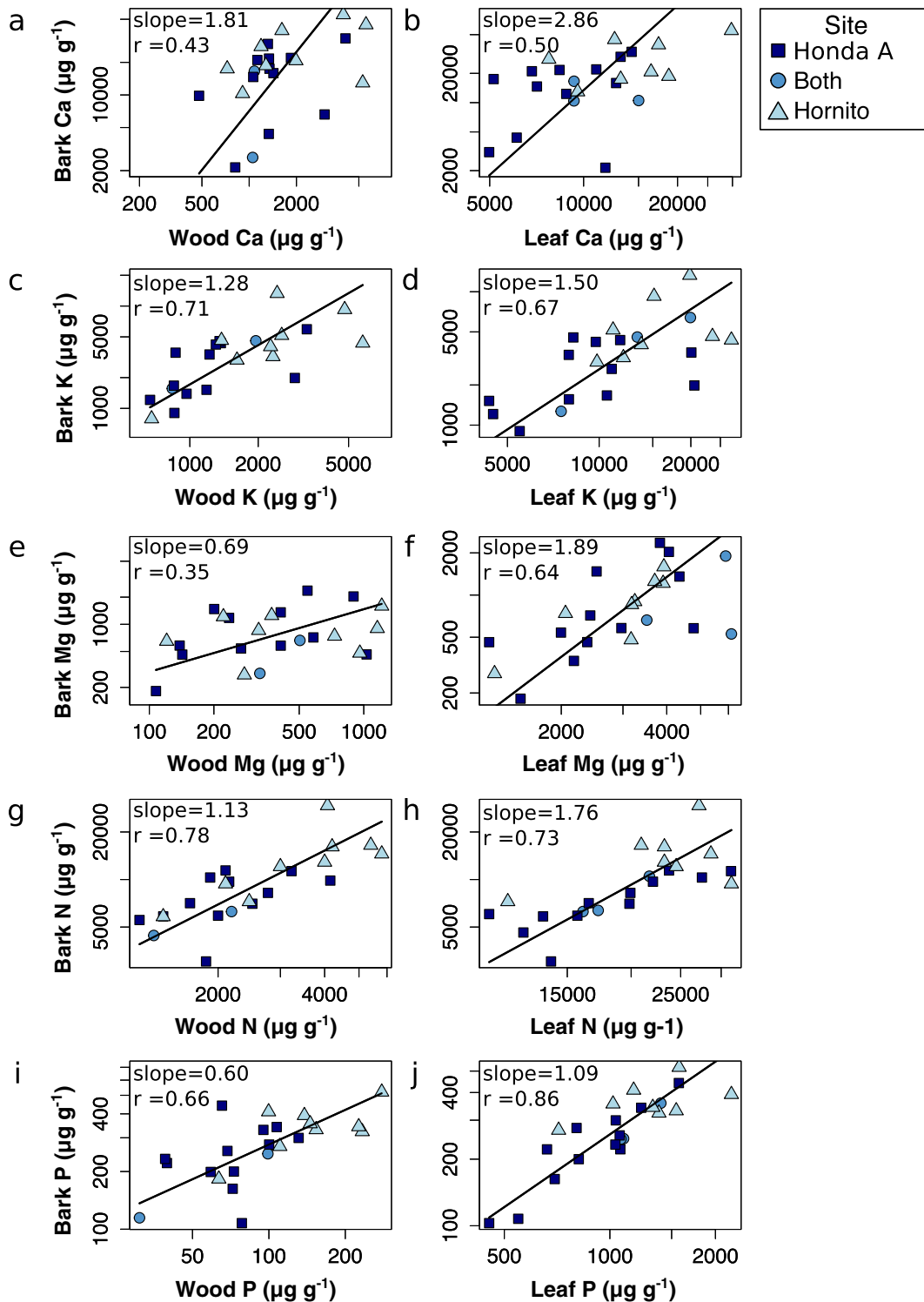


Fig. 1 Major axis regression lines between bark and wood species mean nutrient concentrations ($N = 23$) and bark and leaf species mean nutrient concentrations ($N = 23$). Lines represent significant correlations ($P < 0.05$)

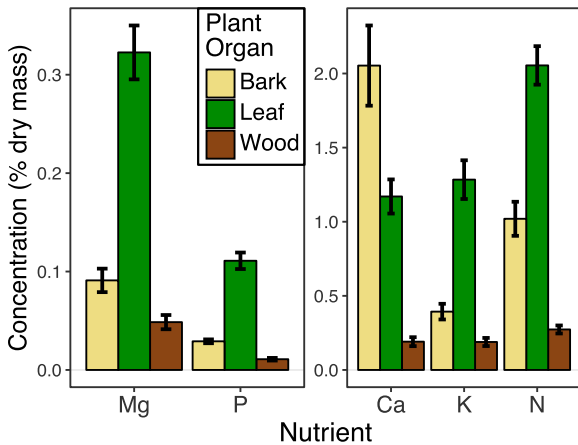


Fig. 2 Mean and standard error bars of species mean nutrient concentration (dry mass %) ($N=23$) by plant organ. Wood and leaf data from Heineman et al. (2016)

nutrients except K (Table 2, “All species” bars in Fig. 3). The basal area weighted means of all nutrients were also significantly higher at Hornito than Honda A (Fig. 4, Supplementary information Table S4). Average percent differences in bark nutrient concentrations for species in common between the two sites were smaller (15%–42%) compared to the difference in community weighted means (32%–80%).

Contribution of bark to above-ground biomass nutrient stores

We used basal area weighted means of bark nutrient concentration to estimate the contribution of bark to biomass nutrient storage at each site. Because the allocation of biomass to bark is difficult to estimate, we calculated the nutrient contents in bark for a range of potential bark biomass percentages (2–20%). For both sites, bark contains 6–53% of the N, 5–50% of P, 4–40% of K, and 2–35% of Mg (Supplemental Information Appendix S2). Bark contains a much higher percentage of Ca (22–82%) than other nutrients (Supplemental Information Appendix S2).

While the proportion of the biomass nutrient stock stored in wood was similar across the two sites, the total nutrient content (kg ha^{-1}) differed greatly (Table 3, Appendix S2), reflecting differences in species composition. When bark is estimated as 10% of AGB, the total nutrient storage in bark in the high fertility site of Hornito was three times that of Honda A for K, approximately 1.5 times higher for Ca and Mg, and two times higher for N and P (Table 3).

Table 2 Linear regressions explaining bark thickness and bark nutrient concentrations with diameter breast height (DBH, natural log transformed), species (Sp), and site

	Bark thick.	Relative bark thick.	Ca	K	Mg	N	P
DF	66	59	57	58	65	41	65
AICc full model	152.2	−455.1	165.7	233.4	184.7	88.0	124.1
AICc reduced model	63.1	−491.0	88.2	172.7	100.2	88.0	36.3
Variables							
DBH	26.9***	—	2.4	20.7***	11.2**	8.4**	10.7**
Species (Sp)	3.5**	8.9***	40.2***	11.4***	12.0***	17.5***	13.6***
Site	6.5*	18.1***	13.1***	—	14.9***	8.2**	26.0***
DBH × Sp	—	—	—	2.0	—	0.6	—
DBH × Site	—	—	—	—	—	0.7	—
Sp × Site	—	2.8*	2.2*	—	—	0.4	—
DBH × Sp × Site	—	—	—	—	—	2.5*	—

Only species sampled at both sites were used in this analysis. F values are presented from the model with stars indicating level of significance. The “—” for model variables indicate that the term was removed during AICc-based model selection

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

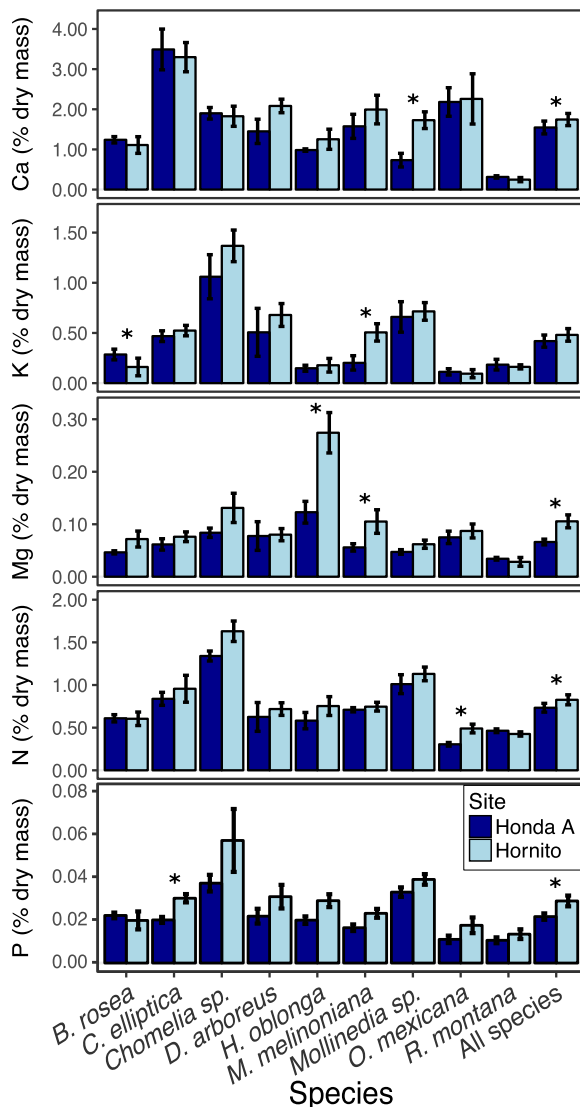


Fig. 3 Mean bark nutrient concentration (% dry mass) and standard error bars for species sampled in both sites across site. Stars are for significantly different linear contrast statements

Discussion

We observed considerable variation among species in bark traits, which contributed to large differences in total above-ground nutrient stocks between our two forest sites. These findings support both hypotheses posited in this study. First, bark nutrient concentrations were significantly positively correlated with both wood and leaf nutrients, suggesting functional coordination of nutrient allocation across these disparate tissue types. Second, as hypothesized, we found lower bark nutrient concentrations (with the exception of K) and thicker

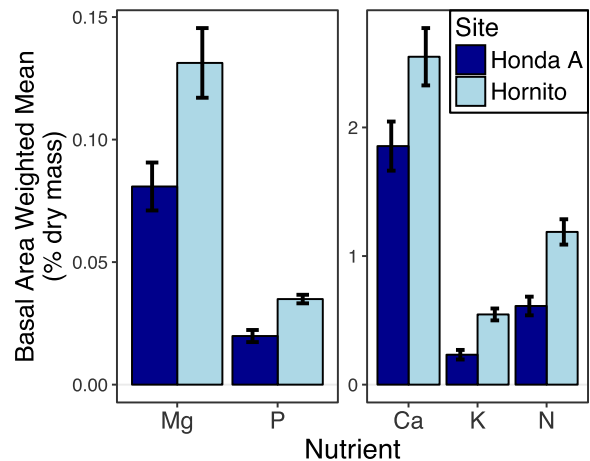


Fig. 4 Mean basal area weighted bark nutrient concentration (% dry weight) with standard error bars between sites

bark in our low nutrient site (Honda A), suggesting that soil nutrient availability constrains uptake or storage of a variety of nutrients within species. In addition, we also found large differences in community weighted bark nutrient concentrations between sites, which is evidence that species composition contributes to differences in nutrient storage across sites differing in soil nutrient availability. Finally, in the species we studied, we found substantial differences in nutrient storage in bark between the two sites. Using bark biomass as 10% of AGB, we found that bark accounts for, on average, 20–50% of the above-ground biomass nutrient pool, therefore representing a significant investment of plant nutrients.

Coordination of biomass nutrient pools

Bark, wood, and leaf nutrient concentrations were significantly correlated for all nutrients studied, with the strongest relationships for N, P, and K. Previous analysis from trees sampled across 10 sites (including the two sites sampled here) revealed that wood nutrients are remarkably variable, with >30 fold variation in Ca, K, Mg and P across 76 tree species (Heineman et al. 2016). In this study we found that wood nutrients varied 4–10 fold among 23 species sampled at two sites, while leaf nutrients varied 2–5 fold. Interspecific variation in bark nutrient concentrations was even higher, with 4–25 fold variation for the same elements. Species mean bark nutrient concentrations were intermediate between those of leaves and wood with one exception. Bark Ca concentration was nearly twice that of leaves and ten-fold

Table 3 Estimated bark nutrient content (kg/ha) and percent of total above-ground biomass nutrient pool found in bark

Study	Units	Biomass	N	P	K	Ca	Mg
Honda (this study)	kg/ha	3.61x10 ^e	223	7	81	666	30
	%		26	19	20	60	19
Hornito (this study)	kg/ha	4.02x10 ^e	535	15	255	1021	43
	%		33	22	23	66	12
41 yr. old loblolly pine ^a	kg/ha		123	0.9	3.9	12.8	17.3
	%		12	9	7	12	36
Appalachian Hardwood ^b	kg/ha		–	–	37.5	422.7	17.3
	%		–	–	16	77	36
Sub-tropical eucalypt forest ^c	kg/ha		30.6	0.8	110.6	103.9	135.9
	%		7	4	57	30	18
Sub-tropical wet forest ^d	kg/ha		24.8	1	19.4	31.8	3.9
	%		4	3	23	7	3
Northern Hardwood ^e	kg/ha		5.25	3.0	19.5	128.5	4.5
	%		10	3	4	26	9
40 yr. old aspen stand ^f	kg/ha		115	16.4	86	435	20.5
	%		25	25	23	41	27
40 yr. old spruce stand ^f	kg/ha		43	8.2	31	161	7.3
	%		10	13	12	20	16
40 yr. old red pine stand ^f	kg/ha		42	6.4	16	70	8.3
	%		10	13	8	21	12
40 yr. old jack pine stand ^f	kg/ha		33	4.7	12	56	5.7
	%		11.1	16	10	23	13
Warm temperate forest ^g	kg/ha		128.5	30.1	117.3	792	17.9
	%		29	22	21	70	23

For this study, bark nutrient content and percentages reported in this table were calculated using bark estimated as 10% of AGB (Appendix S2)

^a Van Lear et al. (1984). Pine plantation, South Carolina, USA. Excludes tree crowns and below-ground nutrient pools

^b Day and Monk (1977). Coweeta, North Carolina, USA. Above ground biomass only. Bark data not available for N and P

^c Westman and Rogers (1977). Queensland, Australia

^d Scatena et al. (1993) Bisley watershed, Puerto Rico. Excludes below-ground nutrient pools

^e Whittaker et al. (1979) Hubbard Brook, USA. Stem bark only as a fraction of above- and below-ground nutrient pools

^f Alban et al. (1978). Forest stands on similar soils in Minnesota, USA

^g Hart et al. (2003). *Nothofagus* (beech) dominated forest, New Zealand. Above-ground nutrient pools only

higher than wood. This is consistent with previous studies that have highlighted exceptionally high Ca concentrations in bark (e.g., Stone and Boonkird 1963; Woodwell et al. 1975; Day and Monk 1977), potentially associated with cambial activity and xylem development (Fromm 2010). Alternatively, Ca allocation has been interpreted as a defense against chewing insects (Franceschi et al. 2005), even though it may induce bark stripping by mammals (Nichols et al. 2016). More generally, bark has been proposed as a potential storage

organ for nutrients, including N in temperate trees (Wetzel et al. 1989) and P in eucalypts (Dell et al. 1987). Although bark may be important for the storage of N and mineral nutrients in tropical trees, we did not find evidence consistent with differential investment of nutrients in bark versus wood; slopes of major axis regressions of wood versus bark nutrient concentrations did not differ from one, except for P, which had a slope of less than 1. In contrast, the slopes for the major axis regressions of bark and leaf nutrients differed from one,

indicating different controls on leaf and bark nutrient concentration.

Allocational response to nutrient limitation

Correlations of bark, wood, and leaf nutrient concentrations also reflect coordinated responses to soil nutrient availability. When the wood nutrient data included in this study were combined with those from other sites at Fortuna and the Panama Canal watershed, significant correlations with soil nutrients were found for Ca, K, and P (Heineman et al. 2016), consistent with reported strong responses of foliar Ca, K, and P to soil nutrients in Amazonian forests (Fyllas et al. 2009). Considering only the two sites included in this study, and excluding K, both species-level and community weighted mean bark nutrient concentrations were lower at the low-fertility Honda A site, than Hornito. Although we included fewer sites than Heineman et al. (2016), in this study we sampled from the same species at both sites, allowing comparisons of both interspecific and intraspecific variation in bark nutrients. As with previous studies (Day and Monk 1977; Scatena et al. 1993), we found wide variation among species in bark nutrient concentrations; when species and site were included together in models, species accounted for more variation in bark nutrient concentration than site and DBH for all nutrients examined (Supplementary information Table S5). Thus, more constant species-level allocation to bark (or leaf and wood) nutrient pools may constitute a component of environmental filtering responsible for species distributions along soil fertility gradients (Baltzer and Thomas 2010; Dalling et al. 2016; Heineman et al. 2016). Nonetheless, we did find significant intraspecific variation in bark nutrients as well. Comparing the nine species present at both sites, there were lower nutrient concentrations at Honda A for all elements except K (Table 2).

In addition to reduced nutrient concentrations, we also found that bark was significantly thicker at the lower nutrient site. This is consistent with the observation that investment in bark was inversely correlated with soil fertility across a network of plots in warm temperate forest in New Zealand (Richardson et al. 2015) and thicker on ridges than slopes (Jager et al. 2015). Greater investment in bark on poor soils has been interpreted as reflecting selection for resource storage, or in the context of plant defense theory, where investment in protecting cambial tissue should be maximized

under conditions where the cost of tissue replacement is highest (Richardson et al. 2015). Inclusion of bark nutrient data in this study failed to provide evidence to support the hypothesis that thicker bark protects greater nutrient reserves. Instead we found thicker bark was associated with lower bark and wood nutrient concentrations. Conversely, bark defenses may be more related to the composition of the bark than the bark thickness (Pausas 2015).

Finally, our results add to the growing evidence that bark traits only partially align with the existing plant or wood economics spectrum (Paine et al. 2010; Richardson et al. 2015, but see Rosell et al. 2014). A key conservative plant trait associated with slow growth, high survival and low fertility environments is high wood density (Muller-Landau 2004; Slik et al. 2010). Consistent with a conservative life history, wood P (and therefore bark P) declines with increasing wood density (Heineman et al. 2016), however an earlier study observed the opposite relationship for wood N (Martin et al. 2014). In another example using leaves and bark, Richardson et al. (2015) found that there was no relationship between bark thickness and, another key functional trait, leaf mass per unit area (LMA).

Contribution of bark to biomass nutrient budgets

The nutrients stored in bark at Hornito was approximately twice that at Honda A for all macronutrients measured for the species we studied. This difference largely reflects the abundance of species with higher nutrient concentrations at Hornito. Despite their proximity, the two sites differ greatly in tree species composition, with only one shared species among the ten most abundant species. This is characteristic of tree species composition in the neotropics more broadly, where species composition is sensitive to soil fertility at a variety of spatial scales (John et al. 2007; Condit et al. 2013; Prada et al. 2017).

The diversity of species found in the tropics can also present challenges when making generalizations about nutrient budgets. We prioritized sampling from the species with the most basal area in both our plots, but despite sampling 23 tree species, we only captured species that represented 44.4% of basal area at Honda A and 51.4% at Hornito. If tree species that we sampled are biased in their nutrient concentrations, then community weighted means may not reflect true nutrient concentration means (Sandel et al. 2015). Unfortunately, in

our data, these biases are difficult to identify and account for as the number of species in each plot is so high.

Bark contains a substantial fraction of the above-ground biomass nutrient pool. Of the elements that we studied, bark accounted for more than half of the above-ground biomass pool of Ca, and ~ 20% of the N, P, K and Mg pools, when estimating bark as 10% of AGB. The large fraction of biomass Ca stored in bark is consistent with most previous nutrient budgets that separate the bark fraction. However, bark Ca content is clearly highly variable (range 7–70% of published biomass nutrient budgets, Table 3). Some of this variation probably reflects different methodologies to characterize nutrient pools, but also suggests large interspecific variation in bark Ca accumulation. In this study, bark Ca concentration varied 22-fold within a single site from 0.25% of dry mass in *Roupala montana* (Proteaceae) to 5.6% in *Peltostigma guatemalense* (Rutaceae). In comparisons with published data, bark Ca content was notably lower in the five conifer and eucalypt dominated stands (Table 3). Ca allocation to bark, and therefore whole-plant Ca-use efficiency, may therefore play a role in environmental filtering of tree communities. The potential for Ca to structure tropical tree communities was indicated by an analysis of a plot network in the Panama Canal watershed, where Ca was the third most important environmental variable (after rainfall and P) influencing tree species distributions (Condit et al. 2013). Allocation of P to bark may also impact species distributions. P availability is correlated with tree species distributions at Fortuna (Prada et al. 2017), and at Barro Colorado Island, Panama, where foliar P concentrations are significantly positively associated with species affinities for high P soils (Dalling et al. 2016).

In addition to overall investment of nutrients in plant tissues, nutrient-use efficiency is also influenced by the ability to reallocate tissue nutrient reserves. Several studies have shown strong seasonal fluctuations in bark nutrients (Helmisaari and Siltala 1989; Wetzel et al. 1989; Fromm 2010). Potential causes for these fluctuations include using bark as a nutrient storage organ during leaf senescence for both N (Rennenberg et al. 2010) and P (Netzer et al. 2017) and during seasonal variation in soil nutrient availability (Rennenberg et al. 2010). At Fortuna, seasonal growth flushes of understory saplings are associated with mobilization of a substantial fraction of wood P (K. Heineman, unpublished data); the degree to which bark P can also be

remobilized is currently unknown. More generally, the importance of nutrient allocation to bark as a constraint on plant growth will also be influenced by the bark turnover rate, or the shedding of bark, which is currently poorly understood (Richardson et al. 2015). Additionally, bark characteristics may influence the decomposition of bark (Dossa et al. 2018). Furthermore, given the relatively large fraction of nutrient pools held in bark, bark turnover rate and decomposition rate will influence the cycling of nutrients in ecosystems.

While the total nutrients found in bark differed widely between the high fertility and low fertility sites, the percentage of total biomass nutrients stored in bark did not differ as much. This suggests that at small spatial scales the percentage of nutrients stored in bark is relatively stable across soil fertilities, although there is much greater variation in percentage of nutrient stored in bark when considering studies outside the tropics (Table 3). Nevertheless, the high percentage of total nutrients in plant biomass stored in bark, and the different ecosystem residency times of bark and wood (Richardson et al. 2015), suggest that bark should be treated separately from wood in carbon cycling models. Lastly, the high variation in bark (and wood) nutrient concentrations should motivate further studies to explore the mechanisms, and functional significance underlying differences in nutrient allocation to these biomass pools.

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