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Influence of tree size, taxonomy, and edaphic conditions on heart rot in mixed-dipterocarp Bornean rainforests: implications for aboveground biomass estimates

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Abstract

Fungal decay of heartwood creates hollows and areas of reduced wood density within the stems of living trees known as heart rot. Although heart rot is acknowledged as a source of error in forest aboveground biomass estimates, there are few datasets available to evaluate the environmental controls over heart rot infection and severity in tropical forests. Using legacy and recent data from drilled, felled, and cored stems in mixed dipterocarp forests in Sarawak, Malaysian Borneo, we quantified the frequency and severity of heart rot, and used generalized linear mixed effect models to characterize the association of heart rot with tree size, wood density, taxonomy, and edaphic conditions. Heart rot was detected in 55 % of felled stems > 30 cm DBH, while the detection frequency was lower for stems of the same size evaluated by non-destructive drilling (45 %) and coring (23 %) methods. Heart rot severity, defined as the percent stem volume lost in infected stems, ranged widely from 0.1–82.8 %. Tree taxonomy explained the greatest proportion of variance in heart rot frequency and severity among the fixed and random effects evaluated in our models. Heart rot frequency, but not severity, increased sharply with tree diameter, ranging from 56 % infection across all datasets in stems > 50 cm DBH to 11 % in trees 10–30 cm DBH. The frequency and severity of heart rot increased significantly in soils with low pH and cation concentrations in topsoil, and heart rot was more common in tree species associated with dystrophic sandy soils than with nutrient-rich clays. When scaled to forest stands, the percent of stem biomass lost to heart rot varied significantly with soil properties, and we estimate that 7 % of the forest biomass is in some stage of heart rot decay. This study demonstrates not only that heart rot is a significant source of error in forest carbon estimates, but also that it strongly covaries with soil resources, underscoring the need to account for edaphic variation in estimating carbon storage in tropical forests.

1 Introduction

Fungal rot of secondary xylem causes hollows and regions of reduced wood density in tree stems. This type of fungal infection, commonly referred to as heart rot, stem rot, or butt rot, is important for the structure, dynamics, and functioning of forests, given that it may increase tree mortality (Franklin et al., 1987; Ruxton, 2015), facilitates the creation of cavity habitats for a diversity of wood-inhabiting and decaying species (Cockle et al., 2012; Stokland et al., 2012), and may act as a reservoir of nutrients sequestered in heart rot biomass (Swift, 1973; Janzen, 1976; Boddy and Watkinson, 1995). Moreover, the effect of heart rot on aboveground biomass is of particular importance for efforts to map carbon storage in tropical regions as part of global conservation and climate change mitigation strategies (Saatchi et al., 2011). However, because heart rot is difficult to detect by non-destructive means, we understand little about what controls its frequency and severity in tropical forests.

Most information available on heart rot in tropical forests comes from forestry studies exploring its influence on the volume and quality of timber. Among species commonly logged in old world dipterocarp forests, heart rot occurs up to 75 % of large *Shorea robusta* (Dipterocarpaceae), reducing stem volumes by 9–13 % (Bakshi, 1960; Bagchee, 1961). The majority of large mono-dominant *Shorea albida* (Dipterocarpaceae) individuals in Sarawak peat swamp forests have been extensively hollowed by fungi and termites (Anderson, 1964). In subalpine silver fir (*Abies densa*; Pinaceae) forests of the Eastern Himalayas, heart rot reduced timber yields < 33 % of those predicted from external stem volumes (Burgi et al., 1992; Gratzer et al., 1997). The influence of heart rot appears to be less in the Brazilian Amazon, where the average frequency of heart rot was 30 % in six commercial timber species in the eastern Amazon (Eleuterio, 2011), and estimation of stem volume hollowed by heart rot in the western Amazon was just 0.7 % (Noguiera et al., 2006). Together these studies provide evidence that the frequency and severity of heart rot influence AGB estimates, particularly those obtained using LiDAR and other remote sensing methods (Zhao et al., 2009). However, there

have been few systematic analyses of the interspecific variation in heart rot with intrinsic tree properties or extrinsic environmental factors that might mediate susceptibility and engender spatial variation in forest biomass lost to heart rot.

Understanding how patterns of heart rot infection vary with tree size is critical to assessing its influence over forest AGB and its estimation because big trees > 70 cm in diameter at breast height (DBH) explain 70 % of variation in pantropical AGB (Slik et al., 2013). Tree size may be among the best predictors of heart rot in tropical forests because old trees have lived long enough to incur butt, branch, and stem wounds that lead to fungal infection, and trees may become less resistant to infection as they senesce (Boddy, 2001). In temperate forests, where tree age can be estimated precisely through dendrochronology, heart rot frequency increases with age in longleaf pine (*Pinus palustris*; Hooper et al., 1988), and pedunculate oak (*Quercus robur*; Ranius et al., 2009). While tree size is an imperfect proxy of tree age (Ng, 2013), heart rot frequency increases with tree diameter in neotropical forests (Nogueria et al., 2006; Gibbons et al., 2008; Eleuterio, 2011). However, variation in the frequency of heart rot in a given size class among sites indicates that there may be interactions between tree size with the taxonomic and environmental factors.

Wood anatomical properties may also explain variation among trees in susceptibility to heart rot. Trees with dense wood may be less likely to experience branch and stem breakage due to wind disturbance (Putz et al., 1983) and are considered more durable to termite and fungal infection than trees with softer wood (Bultman and Southwell, 1976). Additionally, dense wood is associated with pathogen resistance in tropical tree species (Augspurger and Kelly, 1984) and slower fungal growth (Romero and Bolker, 2008), perhaps because the reduced permeability of dense wood impedes fungal hyphae (Merrill and Cowling, 1966). Within species, fast-grown trees with lower wood density are associated with faster decay rates by saproxylic fungi (Edman et al., 2006), although this pattern does not hold across all fungi (Yu et al., 2003). In an Amazonian forest, little or no covariation was found between species' wood density and frequency

of heart rot, although the probability of rot was significantly correlated with other wood traits, such as vessel lumen diameter and vessel density (Eleuterio, 2011).

The frequency and severity of heart rot may also vary with the availability with edaphic resources. For instance, low soil fertility and nutrient or water stress may predispose tissues to fungal infection (Shigo, 1984). There is also a potential indirect age effect, as trees tend to grow slower and live longer on infertile soils (Russo et al., 2005, 2008), and are therefore exposed to chance infection for longer. Conversely, forests on more fertile soils tend to grow faster, have less dense and softer wood and lower contents of defensive, mycostatic secondary metabolites, and such wood may be more prone to heart rot (Boddy, 2001). Variation in heart rot along edaphic gradients would enhance the importance of including soil parameters in models estimating forest storage and fluxes, especially in Southeast Asian forests where aboveground biomass varies with soil nutrient availability (Lee et al., 2002; Paoli et al., 2008).

We used legacy and modern data sets to quantify the covariation of taxonomy, tree size, wood density, and soil resource availability with the frequency and severity of heart rot in two Bornean mixed dipterocarp forests. We quantified the impact of heart rot on forest standing biomass, and evaluated the implications of soil-related variation in heart rot for stand-level variation in biomass. Efforts to quantify heart rot in tropical trees are hampered by the difficulty of evaluating rot without compromising the health of trees in long term monitoring plots. We therefore also compared methods for quantifying heart rot frequency, including the direct assessment of heart rot frequency based on destructive harvesting, with two non-destructive methods (coring and drilling).

2 Methods

2.1 Study sites

The data were collected in two locations in Borneo: Central Sarawak and Lambir Hills National Park, Sarawak (hereafter, Lambir) (Fig. 1). The Central Sarawak tree drilling

and felling data were collected during a timber inventory of lowland mixed dipterocarp rain forest (1°30′–2°50′ N, 112°20′–113°50′ E) (FIDP, 1974a). Annual rainfall averages 3000–3500 mm yr^{-1} in this region with no distinct dry season. The topography consists of long, steep-sided ridges on Tertiary sandstones and narrow valleys in softer shales. The soils are colluvial/residual Acrisols (Udults) and associated Cambisols (Udepts) (FAO, 2006). The coarse loams on sandstone ridges tend to be more stable and deeper than the shale-derived fine loams and clays of the lower slopes and valleys. All of the soils are acidic and leached, and exchangeable base saturations are usually < 10 %. Reserves of K and Mg are moderate, but those of P and especially of Ca are low. Mineral nutrient fertility increases with clay content, and the slope and valley clays are less dystrophic than the coarse loams on the ridges (Baillie et al., 1987). The mixed-dipterocarp forest at this site was among most diverse forests in the Paleotropics. The distributions of many tree species are associated with soil conditions, producing considerable changes in floristic composition on different soil types (Baillie et al., 1987; Ashton and Hall, 1992; Potts et al., 2002; Paoli et al., 2006). Average canopy height is 30–50 m, with emergent trees reaching 70 m, taller than many other tropical forests (Banin et al., 2014).

The Lambir tree coring data were collected in 2009 in Lambir Hills National Park (4°11′ N, 114°01′ E) in northern Sarawak. The physical environment is similar to that of the central Sarawak study area, with acid leached Acrisols and associated Cambisols (Baillie et al., 2006; Tan et al., 2009) on a sandstone cuesta (Yamakura et al., 1996), with shale below the scarp and on the lower dip-slope. Sampling was conducted on two contrasting soil types: clay/fine loam soil, which is more fertile for most nutrients and has greater cation exchange and water-holding capacity, and sandy loam soil, which has lower concentrations for most nutrients, lower cation exchange capacity, and is better drained (Baillie et al., 2006; Tan et al., 2009). The distribution of individual species, and the overall floristic composition, structure, and dynamics of the mixed-dipterocarp forest at Lambir are associated with differences in topography and soils (Lee et al., 2002; Davies et al., 2005; Russo et al., 2005, 2008; Heineman et al., 2011).

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2.2 Heart rot data

The Central Sarawak felling (1035 trees in 240 species in 32 families) and drilling (1780 trees in 242 species in 33 families) data were collected in 422 plots grouped in 80 clusters located (Fig. 1; Table 1). Nine plots were 3×3 square arrayed in each cluster at 80 m spacing (Fig. S1 in the Supplement). Plots were defined using a BAF 10 prism, so that all the stems with an angular diameter $> 1.74°$ when viewed from the center point were included in the plot. This standard forest inventory method (Avery and Burkhart, 2001) includes larger stems located relatively farther away from the center point, whereas small stems are only included if they are close. The plots were therefore irregularly shaped, and sizes ranged from ca. 200 to $> 2000 \, \text{m}^2$ (Fig. S1). On a random subset of 44 clusters, all trees that would produce at least one commercial log (i.e., 3.65 m long with minimum diameter at breast height (DBH) of 30 cm) were felled at breast height (1.3 m) (Fig. S2). Presence or absence of heart rot was recorded based on visual inspection of the log ends, and heart rot was scored as present when the wood contained voids or areas of darkened, soft, or brittle wood (Fig. S2). Logs that were sound at one end but rotten at the other were sawn in half to better quantify rot severity. For each cross-section, the total area and the area of rot were measured by grid counts on transparent overlays (Panzer, 1975). The volumes of the whole log and of the heart rot were computed based on tapering cylinders. The percent of heart rot for the tree was estimated as the sum of the rot volumes for each log as a percentage of the total stem volume. Early felling results revealed more frequent and severe heart rot than anticipated, so rot sampling was augmented with a drilling program. On 25 % clusters chosen randomly, all trees with at least one commercial log were drilled at 1.3 m perpendicular to the stem axis, with two drill holes at right angles to each other (Fig. S2). Presence or absence of heart rot was identified by visual inspection of the drilled debris using the above criteria. The accuracy of drilling was cross-validated on 419 stems, which were drilled prior to felling.

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Safety was a primary consideration, and felling crews had complete on-site autonomy to exclude trees with visible rot, asymmetric crowns or other features indicative of increased risk of the stem splitting during felling. The disproportionate exclusion of very large or obviously rotten stems, and species with very hard, heavy wood means that the felling data are probably conservative in their representation of rot in the forest as a whole. Safety was less of an issue for drilling, and the drilling data contain more very large trees, although species with very hard wood blunted drill bits, and were often excluded.

The heart rot data from Lambir were collected from 220 trees (22 species in 9 families; Table 1) with a 5 mm increment hand borer, bored to half of the DBH. Secondary xylem from extracted cores was examined for heart rot as above, and presence or absence of heart rot was recorded. Trees were sampled on two soil types, clay/fine loam and sandy loam, defined in previous research at the site based on elevation and soil properties (Davies et al., 2005; Russo et al., 2005).

2.3 Tree properties

DBH was recorded for all individuals in the drilling, felling, and coring datasets. Wood density (oven dry mass/fresh volume; $g\,cm^{-3}$) was estimated for each tree in the coring data. Wood cores were broken into segments no greater than 5 cm in length prior to analysis to account for radial variation in wood density. The fresh volume of each segment was estimated by water displacement (Archimedes' principle) for each tree in the coring data set. Mass was recorded for wood segments after drying at 60 °C for 72 h. The density for each core was calculated as the mean of segment densities weighted based on the proportion of the basal area occupied by that annulus.

2.4 Tree species properties

Each tree species in the three data sets was categorized according to its soil association. Generalists were species that are similarly abundant on all soil types. Species

with distinct soil associations were categorized as specialists of clay/fine loam, fine loam/loam, loam/sandy loam, in order of decreasing fertility and water retention. Assignments were based on analyses of species' distributions within the 52 ha forest dynamics plot at Lambir (Davies et al., 2005) and across a network of plots in Sarawak (Potts et al., 2002). For species not included in these studies, natural history data and personal observations (by P. S. Ashton) were used. The density of sound wood was assigned to stems in the felling and drilling datasets from timber group values (FIDP, 1974b) and from species average densities in the coring data.

2.5 Soil properties

Edaphic data (Table S1 in the Supplement) were collected for each plot in the Central Sarawak data. Soil morphology was described in shallow profile pits at plot centres (Baillie et al., 1987; Fig. S2). The profiles and augerings, located 2.5 m from the centre, were sampled at 0–10 and 45–55 cm, bulked by depth (topsoil and subsoil, respectively), and the soils analysed for pH electrometrically, organic carbon by Walkley Black acid dichromate oxidation, and total nitrogen by micro-Kjeldahl distillation. Exchangeable cations were extracted with $1 M NH_4OOCH_3$. Reserve nutrients and free Fe and Al sesquioxides were extracted with hot concentrated HCl. Extracted cations were assayed by atomic adsorption spectrometry, Fe and Al by titration, and P by molybdenum blue colourimetry. Particle size distribution was analysed by pipette sampling after oxidation with H_2O_2 and dispersion with sodium hexametaphosphate (Chin, 2002). For the coring data, the soil type of each tree was assigned to sandy loam or clay/fine loam (140 and 80 trees, respectively) based on the soil survey of the adjacent 52 ha forest dynamics plot (Baillie et al., 2006; Tan et al., 2009).

For the central Sarawak data, we used principal component analysis (PCA) to create a reduced number of orthogonal axes of soil variation, using the function *prcomp* in the statistical software, R (R Core Team, 2014). Prior to PCA, we used multiple imputation to replace sparse missing values in the soil data matrix using the function *aregImpute* in R because PCA cannot be performed on a matrix with missing values, and we sought

to maximize sample size for statistical power. We included the first four PC axes in analyses, which together explained 58 % of the variance in soil properties (Table S2).

2.6 Data Analysis

Linear mixed effect models with type III tests of fixed effects were used to evaluate: (1) if the detection of heart rot presence/absence differed among datasets (2) if genera differed in the frequency and severity heart rot and (3) if heart rot frequency and severity varied significantly with species, tree, and edaphic covariates. Mixed-effect models were necessary because variable numbers of individuals and species were included in each dataset. All datasets were filtered to include only species with > 5 individuals after observations with missing values in the ecological covariates were deleted (Table 1).

In models testing variation in the frequency of heart rot, we employed generalized linear mixed models (GLMM) with a binomial probability distribution and logit link function using the Laplace method and Cholesky root algorithm for parameter estimation (Bolker et al., 2009). Linear mixed models (LMM) with restricted maximum likelihood parameter estimation and degrees of freedom estimated using the Kenward-Roger method were used to evaluate variation in heart rot severity (percent stem volume lost to heart rot), which was log transformed to meet the assumption of normality of residuals. GLMM and LMM models were fit using PROC GLIMMIX and PROC MIXED in SAS version 9.3 (SAS Institute, Cary NC).

We included DBH as a fixed effect in the GLMM testing for differences among datasets in heart rot detection on the aggregated data to account for differences among datasets in size range of trees measured. Because the effect of dataset on heart rot frequency was significant, we fit models for all subsequent tests separately for each dataset. Differences among genera in the frequency of heart rot (drilling, felling, and coring data separately) and heart rot severity (felling data) were tested with GLMMs and LMMs, respectively, with genus and DBH as a fixed effects and species as a random effect.

We fit two models testing the effects of ecological covariates on heart rot frequency and severity, depending on the availability of fixed-effect covariates and their collinearity: (1) main effects: DBH, wood density, soil PC1, soil PC2, soil PC3, soil PC4; 2-way interactions: wood density × DBH; (2) main effects: DBH, wood density, soil association; 2-way interactions: DBH × wood density, soil association × DBH, soil association × wood density; 3-way interaction: DBH × wood density × soil association. For the coring data, soil type (clay or sandy loam) replaced the soil PCs. To decide which fixed-effect interactions should be retained, we used manual stepwise removal of interaction terms with comparison of model Akaike's Information Criterion between models with and without interaction effects (AIC, Burnham and Anderson, 2002). We retained an interaction term if its removal increased model AIC by > 2. We used post hoc analysis of GLMM and LMM fits to determine the statistical significance of differences among levels of categorical predictors.

We examined the variance in heart rot probability and severity explained by variables in the GLMM and LMMs using two approaches. We determined the proportion of variance explained by random and fixed effects using pseudo-R squared (pR^2) metrics (Nakagawa and Schielzeth, 2013). The marginal pR^2 is the proportion explained by the fixed effects alone, and the conditional pR^2 is the total proportion explained by the model when fixed effects are conditioned on the random effects. We used hierarchical variance partitioning in the *hier.part* package in R (Olea et al., 2010; Walsh and MacNally, 2013) to rank the importance each factor in explaining variance in heart rot frequency and severity. Hierarchical partitioning reduces collinearity by determining the independent contribution of each explanatory variable to the response variable and separating it from the joint contributions, allowing an evaluation of the relative importance of species soil association and soil properties, which were modeled separately in mixed-effect models. Variance partitioning analyses included all species, individual, and soil factors evaluated for each heart rot frequency and severity dataset. Log likelihood was used as the goodness of fit metric.

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2.7 Biomass lost to rot

To evaluate how the patterns of heart rot frequency and severity among individual stems influenced stand level carbon stocks, we estimated maximum percent of stem biomass lost to heart rot ($Loss_{max}$) and correlated it with soil habitat variables for each cluster of plots sampled in the felling dataset. $Loss_{max}$ for each cluster was calculated as:

$$Loss_{max} = \frac{\sum_{i=1}^{n} TSV \cdot Wood\ Density \cdot Percent\ Rot}{\sum_{i=1}^{n} TSV \cdot Wood\ Density} \tag{1}$$

for each of n trees sampled in each cluster of the drilling and felling data, where TSV is the total stem volume from the base of the tree to the first branch. We included only clusters with > 10 felled trees > 30 cm DBH. Cluster-level soil parameters were averages of the plot-level soil measurements in each cluster. Because plots were variable in size and shape, it was impossible to calculate stem biomass lost per unit ground area. $Loss_{max}$, will not generate the same value as the average percent stem volume lost across individual tree stems because $Loss_{max}$ accounts for differences among species in wood density and weights the contribution of individual trees to stand biomass loss by tree size. $Loss_{max}$ is the maximum amount of biomass lost to heart rot because our calculations assume rotted areas were hollow, as no data was collected on how much wood density was reduced in these areas. Pearson correlation tests were used to determine if $Loss_{max}$ correlated with the first four soil PC axes and the six soil chemical variables in the topsoil (pH, total N, reserve P, and exchangeable Ca, K, and Mg) that were used in the PCA. Soil cations (Ca, K, and Mg) were log transformed to meet the assumption of normality.

3 Results

3.1 Frequency of heart rot

There was substantial variation between datasets in the frequency of heart rot (Fig. 2a), which occurred in 11 % of cored, 46 % of drilled, and 55 % of felled stems. The classification error of the drilling method was 18 % for the 419 trees scored for rot by first drilling and then felling, where felling observations were taken to be correct. Of the stems misclassified by the drilling method, 58 of the 77 errors were false negatives, in which drilled stems were scored as having no rot, but rot was later observed when the stem was felled. The average percent rot was substantially less severe in rotted stems misclassified by the drilling method (5 %) than in rotted stems trees correctly categorized by drilling (19 %), indicating that the drilling method was effective for scoring stems with extensive rot.

The discrepancy in prevalence of rot between the central Sarawak and Lambir datasets may be caused in part by differences in the tree sizes sampled: at Lambir 80 % of the cored trees were < 30 cm DBH, whereas 98 % of trees drilled or felled in Central Sarawak were > 30 cm DBH (Fig. 2b). We investigated these possibilities by sub-setting the data to include the same DBH range across all datasets and testing for differences between datasets in the probability of a tree having heart rot, while accounting for DBH. After sub-setting, heart rot probability increased with DBH in all datasets, and there was no difference in the slope of this relationship across data sets (DBH, $F_{1,1270} = 21.33$, $p < 0.001$; DBH × dataset interaction, $F_{2,1270} = 1.2$, $p = 0.305$). However, datasets differed in the mean probability of heart rot at a given diameter ($F_{2,1270} = 13.40$, $p < 0.001$). For a tree 50 cm at breast height, the probability of finding rot in the coring dataset was 25 % in the coring dataset, compared to 45 % in the drilling and 55 % in the felling datasets.

After accounting for DBH, genera varied in the probability of heart rot in the felling ($F_{7,641} = 3.71$, $p = 0.006$) and drilling ($F_{6,578} = 4.77$, $p < 0.001$) datasets, but not in the coring dataset ($F_{3,140} = 9.55$, $p = 0.164$, Table S3). Among the three most well sampled

genera (all Dipterocarpaceae) in the felling dataset, heart rot occurred significantly more frequently in *Dryobalanops* (66 % of stems) and the red meranti section of *Shorea* (61 % of stems) than in *Dipterocarpus* (26 % of stems; Fig. 3a).

Heart rot increased in probability with tree diameter in all three datasets (Fig. 2). Indeed, DBH was the only significant predictor in any of the coring data models (Table S4). Across all datasets, the frequency of rot shifted drastically among size classes: stem rot was present in 11 % of stems 10–30 cm DBH, 37 % of stems 30–50 cm DBH, and 56 % of stems > 50 cm DBH.

The probability of finding heart rot covaried significantly with species wood density in the drilling (Table 2; Fig. S4), but not in the felling or coring datasets (Tables 2, S4). In the drilling data, the probability of heart rot increased with wood density, but the strength of this effect diminished with increasing DBH. In other words, for species with low wood density, smaller trees had a lower probability of being infected than larger trees, but at high wood density, the differences in heart rot incidence with tree size diminished (Fig. S4).

Heart rot incidence varied significantly with edaphic variables. In the drilling data, heart rot decreased in probability with increasing values of soil PC2, which were associated with high pH and high exchangeable Mg in both topsoil and subsoil (Table 2; Fig. S5a). In felling data, the probability of rot increased significantly with soil PC3 (Table 3; Fig. S5b), which had a strong negative association with reserve and exchangeable Ca in the topsoil and varied in the same direction with respect to Mg and pH in topsoil as soil PC2. Overall, these results suggest that the incidence of heart rot in Central Sarawak was more frequent on lower fertility soils with reduced cation availability. In the Lambir coring dataset, the probability of heart rot did not differ between sandstone and shale soil types (Table S4).

Species soil associations showed significant covariation with the presence of heart rot in both the drilling and felling (Table 2), but not the coring (Table S4) data. The rank order of mean heart rot probability among habitat association groups was similar in the drilling and felling data, but the significance of these differences varied. Heart rot prob-

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ability was lowest in stems of species associated with more fertile, finer textured soil, intermediate for generalists, and highest in specialists of dystrophic coarser textured soils (Fig. 4). In the felling dataset, the effect of DBH on the incidence of stem rot varied significantly among soil associations (DBH × soil association $F_{3,615} = 3.69$, $p = 0.012$):

5 in species associated with high fertility clay and fine loam soil, the probability of rot did not increase with DBH, whereas the probability of rot significantly increased with DBH in all other soil association groups (Fig. S6).

Overall, the amount of variation in the probability of a tree having heart rot that was explained by the fixed effects in our models differed among the data sets, ranging from

10 the lowest marginal pR^2 values of 8 % in the felling data to the highest of 33 % in the coring data (Table S5). The variance explained increased with the inclusion of the species random effect by 12–45 % (conditional pR^2; Table S5), indicating that species differed in heart rot probability even after accounting for variation due to the fixed effect predictors.

15 In variance partitioning analyses, species identity had the highest independent contribution to model variance in all three datasets (Table 4), ranging from 58 % in the coring to 73 % in the felling datasets. DBH was the second most important variable in all datasets, and had a much larger contribution in the coring relative to the drilling and felling datasets (Table 4). Among soil variables significantly associated with heart rot

20 frequency in the drilling and felling datasets, the independent effect of species soil association (12 %) was much greater than soil PC2 (6 %) in the drilling dataset, whereas the soil association (4 %) and soil PC3 (3 %) had smaller and more similar independent contributions in the felling dataset.

3.2 Severity of heart rot

25 For the 57 % of felled trees showing heart rot, the percent of stem volume lost to heart rot (severity) averaged 17 %, but ranged widely, from 0.1–82 %. Genera varied significantly in heart rot severity (Fig. 3b; Genus: $F_{1,7} = 4.43$, $p = 0.002$). Unlike the probability of rot, heart rot severity did not significantly covary with DBH directly ($F_{1.358} = 0.04$,

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$p = 0.847$), but DBH did influence the severity of rot in a three-way interaction with species wood density and soil association ($F_{3.355} = 3.92$, $p = 0.009$; Table 3). This effect was driven primarily by soil generalist species, for which the severity of rot decreased with DBH and increased with species wood density relative to the other soil habitat groups (Fig. S7).

Heart rot severity increased with larger values of soil PC3 (Table 3), indicating that, as with frequency, heart rot was more severe on soils with low exchangeable and reserve Ca. Alone, the fixed effects explained a very small proportion of variance in heart rot severity (range of marginal $pR^2 = 0.02$–0.11). A larger proportion of variance was explained when fixed effects were conditioned on the random effect of species identity (range of conditional $pR^2 = 0.18$–0.24; Table S5), suggesting that heart rot severity differed among species due largely to characteristics not measured in this study, and the majority of overall variation in heart rot severity remained unexplained by the tree and environmental properties measured.

Similar to variance partitioning results for heart rot frequency, species identity was by far the largest independent contributor to model variance in heart rot severity (85 %; Table 4). However, soil PC3 (6 %) explained slightly more variance than soil association (4 %), and no other covariate independently contributed more than 1 % of model variance.

3.3   Biomass lost to heart rot

Our estimate of the maximum percent of forest stem biomass lost to heart rot, $Loss_{max}$, ranged substantially among spatial clusters of trees (0.03–20.9 %), and a significant proportion of this variation was explained by soil variables. $Loss_{max}$ was significantly correlated with two soil principal component axes, soil PC2 ($r = -0.40$, $P = 0.016$) and soil PC3 ($r = 0.38$, $p = 0.022$), although the correlation with soil PC3 was strongly influenced by one cluster and was no longer significant without it ($r = 0.21$, $p = 0.113$). $Loss_{max}$ was also marginally associated with soil PC4 ($r = -0.31$, $p = 0.060$) (Fig. 5). With respect to specific aspects of soil chemistry, the estimated amount of stem

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biomass lost to rot declined with topsoil exchangeable Ca ($r = -0.59$, $p < 0.001$) and Mg ($r = -0.50$, $p = 0.002$), but there was no relationship between Loss$_{max}$ with topsoil measures of soil pH, reserve P, or exchangeable K (Fig. 6).

4 Discussion

Our understanding of the ecology of heart rot in tropical forests is limited primarily by the scarcity of both heart rot observations and associated explanatory ecological data. The extensive legacy and recently collected data analysed here allow examination of the influence of tree characteristics and locally-measured edaphic properties on heart rot frequency and severity in taxonomically resolved tropical trees. Our study is the first to highlight the importance of edaphic properties, along with tree size and taxonomy, in explaining the frequency and severity of heart rot among trees. Together, these factors generated spatial variation among forest stands in the estimated proportion of biomass lost to heart rot, and this variation was correlated with soil resource availability. Moreover, our finding that 9 % of stem volume is in some stage of wood decay in this mixed-dipterocarp forest justifies greater consideration of heart rot in tropical forest biomass estimates, and underscores the need for standardized methods of heart rot detection to be applied across forest types.

4.1 Methodological variation in heart rot detection

While our results affirm previous findings that heart rot infection is frequent and often severe in dipterocarp forests (Bakshi, 1960; Bagchee, 1961), regional comparisons are complicated by discrepancies in methods among studies. Heart rot occurred in 50 % of drilled, 57 % of felled stems > 30 cm DBH, and encompassed 9 % of stem volume on average in central Sarawak, which greatly exceeds observed volume losses to heart rot (0.7–4 %) reported in neotropical forests (Brown et al., 1995; Clark and Clark, 2000; Noguiera et al., 2006). However, these studies measured only the hollow frac-

tion of stems, whereas our study quantified the volume of wood in any stage of decay visible in the field. Therefore, our methods would inherently generate larger estimates of volume loss. Additionally, approaches that quantify heart rot in decomposing stems, such as stumps cut along access roads (Brown et al., 1995) or in naturally fallen logs in coarse woody debris censuses (Clark and Clark, 2000), may quantify rotting that occurs *post mortem* or, conversely, may be biased toward logs that are resistant to decomposition. Noguiera et al. (2006), measured the hollow area in cross-sectional discs of freshly felled stems, but included only five individuals > 80 cm DBH compared to the 100 included in our study. While there is no equivalent measure of heart rot severity in the literature, our measure of heart rot frequency via drilling was similar to Eleuterio (2011), which evaluated wood decay in the debris created by plunging a chainsaw into the stem of trees to be logged in the eastern Brazilian Amazon. This study found wood decay in only 30 % of stems > 45 cm DBH for the six most common timber species, providing evidence that heart rot may be more prevalent in Sarawak that other tropical forests. Because of the great number of large stems examined destructively for both heart rot presence and severity, our study presents robust and well-constrained estimates of heart rot frequency and severity compared with others in tropical forest literature to date.

While logging concessions may be opportunistically exploited for detailed evaluation of heart rot, accurate non-destructive measures are needed to estimate heart rot where destructive harvest is impossible. Drilling proved to be an accurate means of scoring trees for heart rot, correctly characterizing heart rot in 80 % of trees. The majority of misclassifications likely occurred because drilling tested for areas of wood softness only at breast height, missing rot occurring higher up in the stem. However, classification error diminished to 8 % for stems that had lost more than 10 % of their volume to rot, indicating that drilling at breast height is a reliable means of identifying trees containing large sections of rot. Combined with the under-sampling of very large trees in the felling data, results of felling and drilling analyses require subtly different interpretations, with the felling dataset exploring the controls over heart rot infection overall,

and the drilling dataset exploring the controls over severe heart rot infection. There was no way to validate the accuracy of the coring method; however, the probability of detecting rot was lower at a given stem diameter in the coring dataset relative to the drilling dataset. Assuming that the true dependence of heart rot frequency on DBH was the same in Lambir and the Central Sarawak sites, then we suspect the drilling method may have been more effective at detecting rot because it was conducted in two perpendicular directions at breast height, whereas trees in the coring dataset were bored only once. Despite inconsistencies among methodologies, inclusion of all three datasets not only allowed assessment of non-destructive methodologies for estimation of heart rot, but also improved inference of the controls over heart rot by increasing the size range to include the small and large trees included in the coring drilling datasets, respectively. Sonic tomography has been applied to non-destructively evaluate both the frequency and severity of hollows in tree stems (Nicolotti et al., 2003; Wunder et al., 2013). In the absence of access to this costly equipment, drilling may be a viable, less expensive alternative for assessing the presence of heart rot in remote tropical forests.

4.2 Controls over heart rot in individual stems

Understanding the environmental and intrinsic tree correlates of heart rot provides a window into the mechanisms that govern heart rot and its implications for forest ecosystem processes. Tree size was the only factor significantly associated with rot in all three datasets, and was the only significant predictor in the coring dataset. These findings support previous observations of stark increases in heart rot frequency with diameter in tropical forests (Noguiera et al., 2006; Eleuterio, 2011). It is unclear what role heart rot plays in tree senescence, although rot has been implicated as an important impetus for tree mortality (Franklin et al., 1987). However, given that tree size was not a significant predictor of the percent stem volume lost to rot in infected trees, the advancement of stem rot infection may depend less on tree age than on the identity of the pathogen and the physical and chemical properties of the heart wood (Rayner and Boddy, 1983).

Species wood density was not a significant predictor of stem rot frequency or severity in the felling or coring datasets, consistent with findings from an Amazonian forest (Eleuterio, 2011). However, there was a significant interaction between wood density and DBH in the drilling dataset, in which the probability of heart rot increased with wood density in smaller trees with the effect levelling off with increasing tree size. This result is somewhat surprising, as high wood density has been associated with pathogen protection in tropical tree species (Augspurger and Kelly, 1984). However, wood density is inversely correlated with mortality and growth rates (King et al., 2006), and so trees with higher wood density may be older than trees of the same size with low wood density, and so an increase in heart rot frequency is detected among smaller stems. At large diameters, however, variation in wood density may have little effect on the probability of heart rot, as most trees have likely had enough time to develop rot. The detection of this interaction may have been limited to the drilling dataset because it included more trees > 80 cm DBH than the others. Wood anatomical features related to wood density may also be influential, such as lumen diameter and vessel density, which are significantly correlated heart rot frequency in Amazonian tree species (Eleuterio, 2011).

Heart rot was significantly more frequent and severe in trees on low fertility soils in central Sarawak, but heart rot frequency did not differ between edaphic habitats in the smaller trees cored at Lambir. Our results do not identify which soil nutrients directly correlate with heart rot, but they appear to include Ca and Mg, which have been found to correlate strongly with Bornean species distributions (Baillie et al., 1987) and explained significant variation in fine root growth at Lambir (Kochsiek et al., 2013). This result is initially counter-intuitive, as the forest processes on high fertility sites are generally more dynamic (Coomes and Grubb, 2000), and generate more frequent canopy disturbance, causing wounds and opportunities for infection (Boddy and Rayner, 1983). Furthermore, stem tissues under nutrient stress may be more prone to infection, as resources to produce secondary compounds may be limited. Lower nitrogen concentrations in wood and soil may also cause wood-decay fungi on low fertility soils to excavate greater volume of wood to satisfy nutrient requirements (Boddy, 2001). However, vari-

ation among soil habitats in heart rot may also be driven by the change in species composition of the tree community combined with differences among taxa in susceptibility to heart rot. Although our observational datasets cannot definitively distinguish direct and indirect effects of soil fertility, variance partitioning analysis indicated that soil properties and tree species soil associations explain similar independent proportions of variance in stem rot frequency and severity in the felling dataset, whereas soil association contributed twice as much to variance compared to soil properties in the drilling dataset. The significant three-way interaction between soil association, DBH, and wood density explaining the severity of heart rot remained difficult to parse, aside from the indication that the influence of habitat on heart rot is variable across size classes and woods of different properties. The frequency of heart rot differed significantly among soil associations in both the felling and drilling datasets. Because drilling was less effective at detecting heart rot in partially rotted stems, these results may suggest that overall heart rot infection may be more frequent in species associated with low/intermediate fertility soils and that extensive stem rot is much less likely to be observed in species associated high fertility soils. As with wood density, the fertility effect may be acting as a proxy for tree age, as growth and mortality rates are low on the more dystrophic and drought-prone sandstone soils (Russo et al., 2005), and, therefore, may have more frequent heart rot by virtue of longer exposure time to stochastic infection risk. Regardless of whether soil-related variation in heart rot is driven by species differences or nutrient availability, it has important implications for spatial variation in biomass in tropical forests.

4.3 Taxonomic variation in heart rot

While tree size, wood density, and edaphic factors were all significantly associated with the heart rot infection, these factors together explained a relatively small fraction of the variance in the frequency of heart rot, and even less for heart rot severity. Variance partitioning indicated that species identity was by far the most important predictor of stem rot frequency and severity, meaning that the occurrence of heart rot had

a strong taxonomic component due to species properties other than wood density and soil association. Some of the taxonomy-related variation in the susceptibility to heart rot may be due to differences in induced and constitutive defences against fungal or insect pathogens (Taylor et al., 2002). When wounding allows exposure to pathogens, anatomical modification of xylem in the living sapwood, including compartmentalization, limits the spread of infection (Shigo, 1984), and the extent and effectiveness of this response likely differs among species. Interspecific variation in defense may also occur in the heart wood, which is suffused with secondary metabolites considered inimical to fungal growth. Some dipterocarps are known for copious resin exudation from wounds (Mantel et al., 1942), and differ widely in the composition and probably also effectiveness of these compounds (Bisset et al., 1971; Norhayati et al., 2013). The high heart rot frequency and severity among these Bornean species is surprising in this light, and yet their great longevity (Whitmore, 1975) suggests the capacity to tolerate heart rot. Even after accounting for species identity, most variation in heart rot frequency and severity remained unexplained. Heart rot infection may be highly stochastic because it appears to require both wounding and subsequent colonization by fungal spores or insects, which have varying dispersal capacities (Peay and Bruns, 2014) and host requirements (Gilbert et al., 2002). Density-dependent population dynamics caused by the differential susceptibility of tree species to pathogens has been hypothesized to explain the relative abundance of tree species in forest communities (Comita et al., 2010; Mangan et al., 2010). This, and the possibility that interactions between host trees and heart rot fungi are neutral or even mutualistic, are topics that merit more investigation in tropical forests.

4.4 Implications of tree level variation for forest biomass

When the tree-level influence of heart rot was scaled to the stand-level, we found large spatial variation in the potential ecosystem biomass lost to heart rot in central Sarawak that was partially explained by stem diameter, edaphic variables, and tree species properties. Stems of trees > 30 cm DBH account for ~ 70 % of the standing AGB in mature

mixed-dipterocarp forests (Yamakura et al., 1986), and the trees > 70 cm DBH make up 40 % of the AGB in southeast Asian forests (Slik et al., 2013). From these regional estimates of AGB in large stems, we conservatively predict that approximately 7 % of woody biomass in the central Sarawak site is in some stage of stem decay. More-over, Bornean dipterocarp forests are taller, with more large-diameter trees, thus having larger AGB than many other tropical forests (Yamakura et al., 1986; Slik et al., 2013; Banin et al., 2014). These differences may be reduced by heart rot in mixed-dipterocarp forests, as considerably lower estimates of biomass lost to heart rot have been reported in neotropical forests. The effect of heart rot on standing biomass showed strong spatial variation, and was significantly greater for stands growing on less fertile soil. An anal-ysis in a lowland Bornean rainforest found that AGB positively correlated with surface soil nutrient concentrations, including P, K, and Mg, due to the increased stem density of trees > 120 cm DBH on high fertility soils (Paoli et al., 2008). Our results suggest that the discrepancy in AGB between soils low and high fertility may in fact be even larger because large stems on low fertility sites are more likely to contain hollow sections of extensive rot.

It is difficult to determine if current methods of biomass estimation adequately ac-count for heart rot in tropical trees. Heart rot is implicitly incorporated into allometric equations used to estimate AGB from forest inventories (e.g., Chave et al., 2005), which are empirically derived from datasets likely to include trees with heart rot. However, the largest trees are often under-represented in these datasets. The potential for heart rot-induced underestimation of AGB may be worse for LIDAR-based estimates, depending on how estimates are calibrated with site-specific biomass data. Moreover, the strong variability in biomass loss among edaphic habitats in this study and the possible dis-parity in rot losses between the Paleotropics vs. Neotropics indicate that site-specific corrections for heart rot may be needed. Thus, greater consideration of local-scale soil conditions and broader-scale quantification of heart rot using standardized methods are critical to improving the estimation of carbon sequestration in tropical forests.

Influence of tree size, taxonomy, and edaphic conditions on heart rot

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5   Conclusions

Heart rot is a poorly quantified source of error in aboveground biomass estimation throughout the tropics. Our study of heart rot frequency and severity in mixed-dipterocarp forests in Sarawak Borneo, indicates that considerable spatial variation in biomass losses to heart rot exists at local scales due to soil-related factors, as well as tree and species-level properties. Moreover, comparison with similar studies in other tropical regions suggests that aboveground biomass estimation of Bornean forests, which have been considered to have large carbon sequestration capacity, may be particularly affected by heart rot. Using standardized, nondestructive methods to quantify heart rot across environmental gradients and compare its frequency and severity across tropical regions would help better constrain the contribution of heart rot to error in estimation of carbon stored in tropical forests.

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Table 1. Ranges and sample sizes for predictor variables for felling, drilling, and coring data sets by species and trees.

	Felling		Drilling		Coring	
	Species	Trees	Species	Trees	Species	Trees
Soil association						
Loam/sandy loam	7	66	7	54	9	90
Fine loam/loam	15	260	11	284	3	31
Clay/fine loam	13	206	12	196	6	61
Generalist	7	129	7	82	4	38
DBH (cm)	–	27.5–105.8	–	26.2–157.3	–	1.3–89.0
Wood density ($g\,cm^{-3}$)	0.450–1.120	–	0.530–0.940	–	–	0.204–1.020
Soil type						
Sandy loam	–	–	–	–	17	140
Clay/fine loam	–	–	–	–	12	80
Total	42	661	37	616	22	220

Table 2. Type III tests of generalized linear mixed model fixed effects for associations of the probability of heart rot in trees of mixed dipterocarp rain forest, Central Sarawak, Borneo, in the drilling and felling datasets. If they are not listed in the table, then two- or three-way interactions were not statistically significant.

Predictor variable	Dataset	Num. df	Den. df	F value	P value
Model 1	Drilling				
DBH		1	572	8.34	0.004
Species wood density		1	572	2.17	0.142
Soil PC1		1	572	1.22	0.269
Soil PC2		1	572	10.49	0.001
Soil PC3		1	572	2.57	0.11
Soil PC4		1	572	0.99	0.321
DBH × Species wood density		1	572	4.05	0.045
Model 2	Drilling				
DBH		1	576	7.94	0.005
Species wood density		1	576	4.08	0.081
Soil association		3	576	3.05	0.007
DBH × Species wood density		1	576	3.82	0.051
Model 1	Felling				
DBH		1	614	31.09	< 0.001
Species wood density		1	614	0.06	0.81
Soil PC1		1	614	0.1	0.751
Soil PC2		1	614	1.05	0.307
Soil PC3		1	614	6.32	0.012
Soil PC4		1	614	0.16	0.687
Model 2	Felling				
DBH		1	615	28.12	< 0.001
Species wood density		1	615	0.4	0.526
Soil association		3	615	1.81	0.144
DBH × Soil association		3	615	3.69	0.012

Table 3. Type III tests of LMM fixed effects for associations of heart rot severity in the Central Sarawak felling dataset. If they are not listed in the table, then two- or three-way interactions were not statistically significant.

Predictor variable	Num. df	Den. df	F value	Prob.
Model 1				
DBH	1	364	0.54	0.461
Species wood density	1	29.2	0.02	0.901
Soil PC1	1	363	0.01	0.941
Soil PC2	1	363	0.78	0.378
Soil PC3	1	363	7.45	0.06
Soil PC4	1	363	0.44	0.509
Model 2				
DBH	1	358	0.4	0.847
Species wood density	1	274	0.04	0.843
Soil association	3	250	2.70	0.046
DBH × Wood density	1	360	0.18	0.672
DBH × Soil association	3	357	3.93	0.009
Wood density × Soil association	3	246	2.55	0.056
DBH × Wood density × Soil association	3	355	3.92	0.009

Table 4. The percent independent contribution of taxonomic, tree, species, and soil covariates to variance explained in heart rot frequency and severity. Variance partitioning of the covariates of heart rot frequency was conducted separately for the drilling, felling, and coring datasets.

| | Heart Rot Frequency | | | |
	Drill	Fell	Core	Heart Rot Severity
Species	63.1	72.5	58.0	85.8
DBH	14.7	18.6	39.4	0.9
Wood Density	0.9[a]	0.0[a]	1.1[b]	1.1[a]
Soil Association	12.0	4.3	0.9	4.4
Soil PC1	1.0	0.1	–	1.0
Soil PC2	5.7	0.8	–	0.2
Soil PC3	2.0	3.1	–	6.2
Soil PC4	0.5	0.5	–	0.3
Soil Type	–	–	0.7	–

[a] Species wood density.
[b] Individual tree wood density.
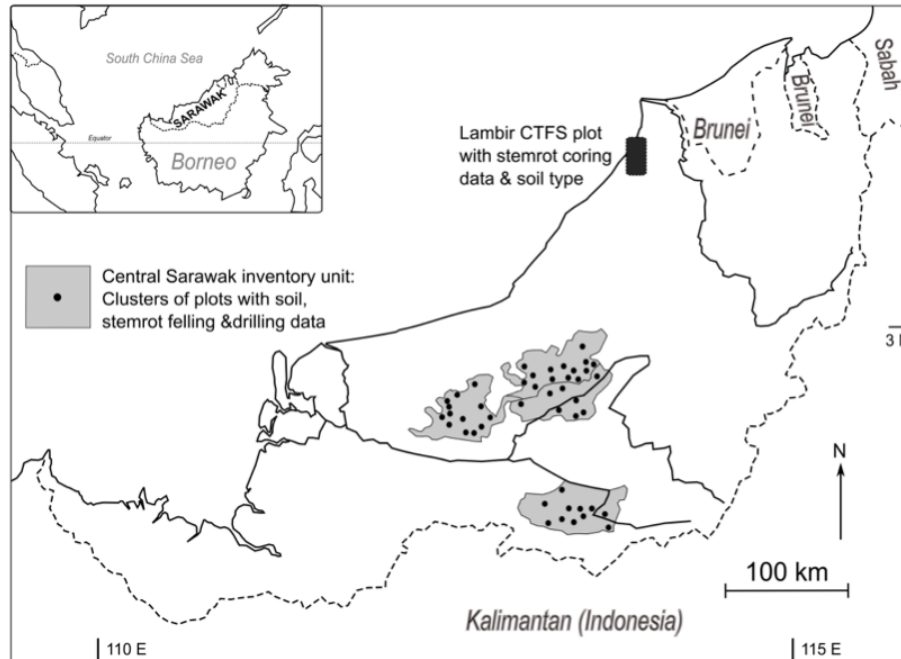
Figure 1. Location of study sites in Sarawak, Malaysian Borneo. Shaded areas are the Central Sarawak inventory units for heart rot felling and drilling data, with clusters of plots indicated by black dots. The black rectangle indicates the location of the Lambir Hills National park study site for the heart rot coring data.
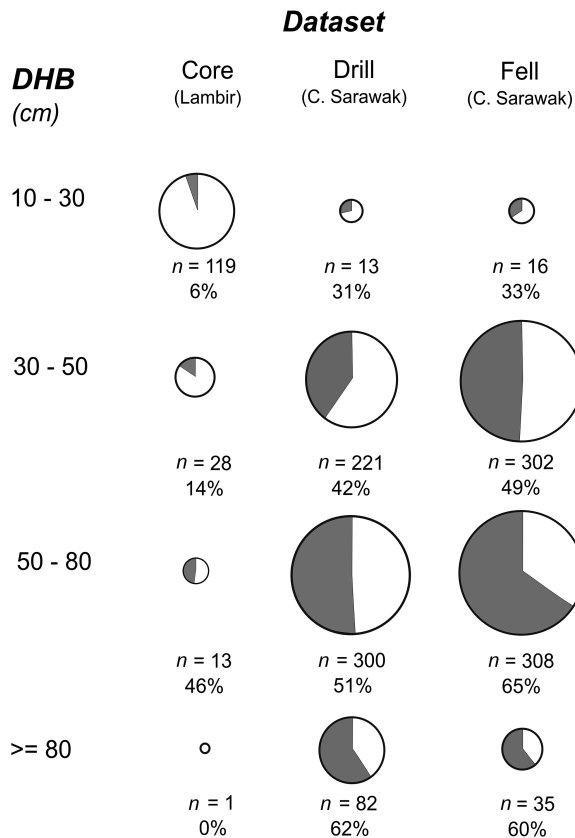
Figure 2. Variation in the frequency of heart rot found in trees in mixed dipterocarp rain forest of Central Sarawak, Borneo. Pie charts show the percentage of individuals with heart rot (shaded), with pies sized according to the total number of sampled stems (*n*), in each DBH size class and dataset.

(a) Frequency (% felled stems infected)

Dipterocarpus (Keuring) *n* = 94

Dryobalanops (Kapur) *n* = 146

Shorea (Red meranti) *n* = 249

27%

66%

57%

54 cm 22.2 m

57 cm 19.3 m

52 cm 19.9 m
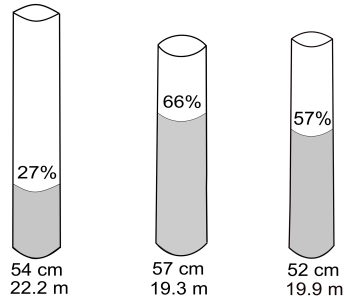
(b) Severity (Mean % volume loss in infected stems)

Dipterocarpus (Keuring) *n* = 25

Dryobalanops (Kapur) *n* = 96

Shorea (Red meranti) *n* = 143

10%

13%

14%

60 cm 24.3 m

60 cm 21.2 m

55 cm 20.3 m
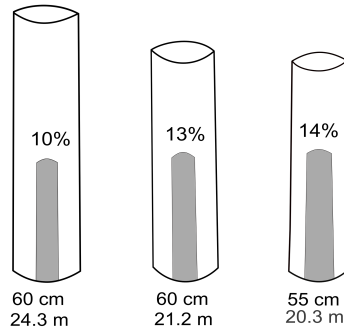
Figure 3. Variation in the frequency and severity of heart rot among important dipterocarp genera in rain forest of Central Sarawak, Borneo, based on the felling data. Local names for genera are in parentheses. Mean diameter at breast height (DBH; cm) is below, and mean stem length (m) is to the left, with cylinders sized accordingly. The shaded portions represent frequency, the percent of felled trees with heart rot, listed to the right in **(a)**, and severity, the mean percent volume lost to heart rot, listed to the right in **(b)**.
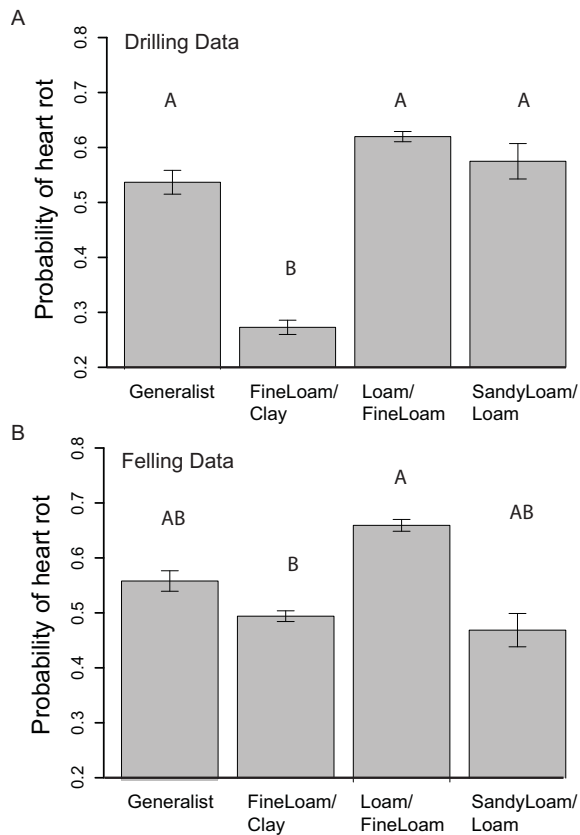
Figure 4. Variation in the probability of heart rot among tree species with different soil associations in mixed dipterocarp rain forest of Central Sarawak, Borneo, in the drilling **(a)** and felling **(b)** data. Bars are means, and error bars are ±1 standard error. Letters above bars indicate statistically significant differences among soil association groups.

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Influence of tree size, taxonomy, and edaphic conditions on heart rot

K. D. Heineman et al.

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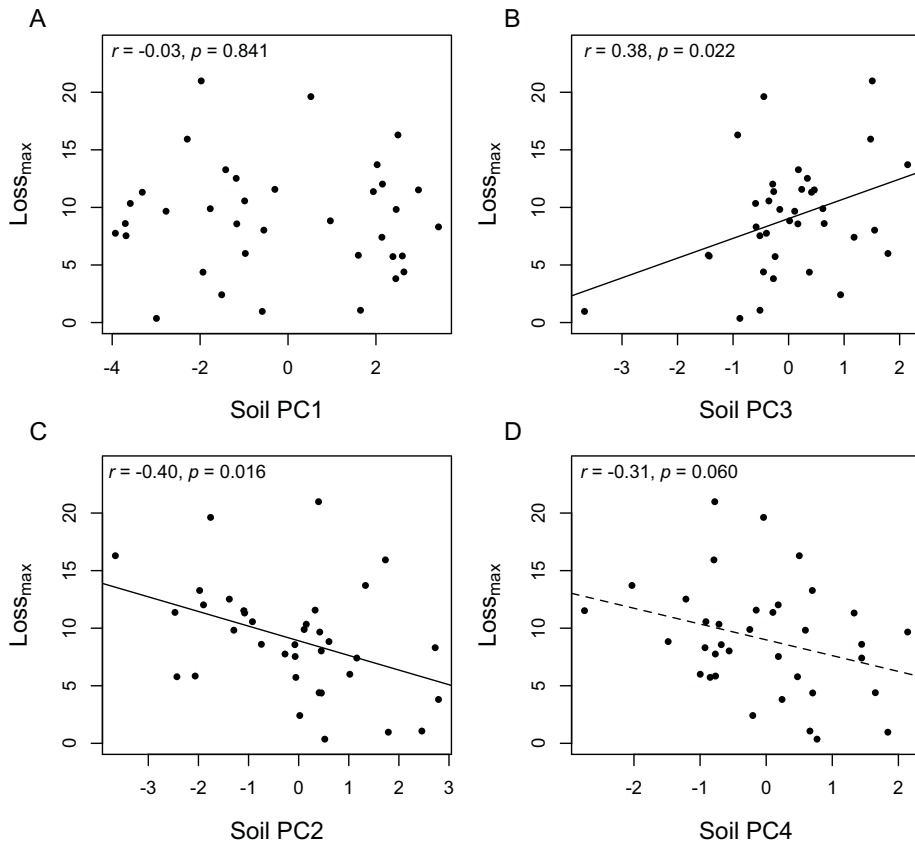Printer-friendly Version

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Figure 5. The relationship between the percent stand biomass lost to heart rot ($Loss_{max}$) among trees sampled in a cluster and mean values of the first four soil principle component (PC) axes for 36 tree clusters containing at least 10 trees > 30 cm DBH. The Pearson correlation coefficient (r) and associated probability of each relationship is in its respective panel. Soil concentrations are expressed in units of milliequivalents per 100 g of soil (me%), parts per million (ppm), or percent dry weight (%).
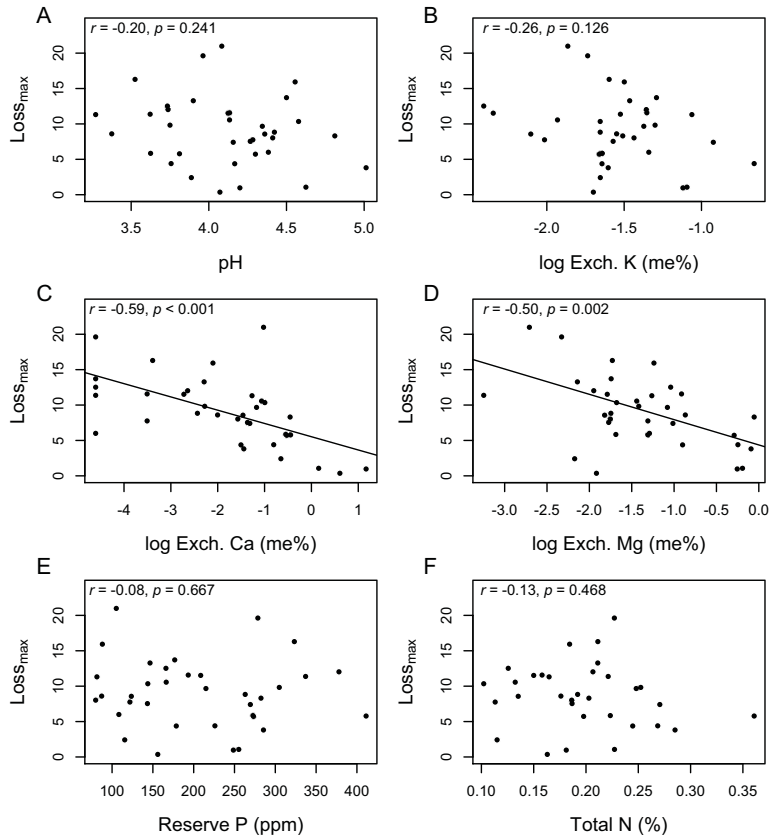
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Figure 6. The relationship between the percent stem biomass lost to heart rot ($Loss_{max}$) among trees sampled in a cluster ($Loss_{max}$) and mean soil chemical properties for 36 tree clusters containing at least 10 trees > 30 cm DBH. The Pearson correlation coefficient (r) and associated probability of each relationship is in its respective panel. Soil concentrations are expressed in units of milliequivalents per 100 g of soil (me%), parts per million (ppm), or percent dry weight (%).

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