BUTTRESS CHARACTERISTICS IN RELATION TO TOPOGRAPHY AND CROWN ECCENTRICITY IN PLANTED AND NATURALLY-REGENERATED SHOREA LEPROSULA TREES

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INTRODUCTION

Buttress characteristics and contributions to tree stability have long attracted the attention of tropical ecologists (Richards 1952). Prominent buttresses are characteristics of some tree species (Chapman et al. 1998, He et al. 2012) and are particularly pronounced in freshwater swamp forests (Lewis 1988, Steege et al. 1997), but also occur on well drained soils (Nicoll & Ray 1996). Buttress size and distribution around boles of trees are reportedly related to gravitational forces (Ennos 1993). Given that flowering plants, i.e. angiosperms, form tension wood in response to gravity, buttresses are expected to be concentrated on the upwind and uphill sides of trees (reviewed by Henwood 1973 but see Lewis 1988). Similarly, for trees with eccentric crowns, maximum buttress formation should be on the opposite side of the trunk, as proposed and demonstrated for trees in Central America (Young & Perkocha 1994). We tested these and other buttress-related hypotheses with planted and naturally-regenerated Shorea leprosula trees in a dipterocarp forest in Indonesia.

If buttress development is a function of the forces to which tree stems are subjected, then it should increase with crown exposure which, in turn, generally increases with tree size. However, if buttress formation is slow, which may be expected given their high wood density (Woodcock et al. 2000), then if trees of the same size are compared, buttresses should be more pronounced on slower growing individuals. We tested this hypothesis by comparing buttress development on very fast-growing S. leprosula trees that were planted and tended along cleared lines through selectively logged forest with buttresses on slower growing and thus older trees of the same species and size in the strips of natural forest retained between planted lines.

From a timber stand management perspective,
support for this hypothesis would be good news insofar as timber recovery is lower on buttressed trees because the buttressed portion of the stem is often not harvested.

MATERIALS AND METHODS

Study site

The study was conducted at the Sari Bumi Kusuma concession in Central Kalimantan, Indonesia (0° 56' N, 111° 68' E) at elevations of 356–425 m with undulating topography. Precipitation for 2001–2012 averaged 3631 mm year^{-1} (3024–4762 mm year^{-1}) and there were no months with average rainfall of < 200 mm. Temperatures averaged 30–33 °C at midday and 22–28 °C at night (Suryatmojo et al. 2013). Soil is deep red-yellow clay loam (oxisols) with good internal drainage. Over the past 15 years (1999–2014), Sari Bumi Kusuma has already applied the selective cutting and strip enrichment planting silvicultural system (locally tebang pilih tanam jalur—TPTJ) to a third of its 147,000 ha concession. The minimum cutting cycle under TPTJ is 25 years. The oldest plantations we sampled will therefore be eligible for harvest of trees > 40 cm diameter at 1.3 m (dbh) after another 10 years. TPTJ guidelines continue to evolve, but in the 14- to 15-year-old plantations we sampled, nursery-grown seedlings of *S. leprosula* were planted at 5-m intervals along 3-m wide lines cleared at 20-m intervals through twice logged forest. Slashing of lianas, shrubs and non-commercial tree regeneration was continued for 3 years after planting. Sari Bumi Kusuma experimentally planted 23 commercial species but settled on *S. leprosula* and four other *Shorea* species of which *S. leprosula* was the most commonly planted. Another reason for our selection of this species was that it was by far the most common among the naturally-regenerated of the planted species.

Field data collection

Buttresses were measured on 100 randomly selected *S. leprosula* trees of 20–40 cm dbh, half of which were planted and tended along the planting lines and half naturally-regenerated in the interline strips of logged-over forest. We chose this dbh range because buttresses were poorly developed on smaller trees and because the largest of the 14- to 15-year-old planted trees were about 40 cm dbh. Buttresses were measured using the method of Chapman et al. (1998). Buttress height was measured from the ground to where the buttress became even with the trunk of the tree and buttress length was measured from its intersection with the bole of the tree to where the uppermost surface of the buttress first entered the ground. For each sampled tree, we recorded the steepest slope 5 m above and below the bole (%), the height and length of each buttress, the orientation of the tallest buttress relative to the slope (uphill, downhill or to the side), crown radii in the four directions relative to the slope and dbh. The same approach was used to determine orientation of the longest crown radii.

Data analysis

Buttress characteristics are represented by both maximum buttress height and total buttress area per quadrant (uphill, downhill and on the two sides). Buttress area was calculated from height and length along the ground with the assumption of triangularity. Crown area and eccentricity were calculated based on the method described in Hardiansyah et al. (2015). Generalised linear model (GLM) analysis was used to assess the main effect on buttresses (maximum height and total area) of planted or naturally-regenerated, with dbh, slope and crown area as covariates. A GLM approach was used because it permitted fitting of linear models to distribution functions in the exponential family (e.g. Gaussian, Poisson, binomial, gamma) and to directly fit the expected mean of the dependent variable, thereby avoiding the biases of transformed linear models (McCullagh & Nelder 1989, Saha et al. 2014). The parameter estimates of model and their confidence intervals are presented on the graphs. The centre dots indicate predicted values, the thick horizontal bands show the 68% confidence intervals and the thinner wider bands indicate the 95% confidence intervals. A predictor is significant if its confidence interval does not contain 0. All predictors were scaled to a standard deviation of 1, and centred around 0 to improve interpretability of the relative strength of influence of the predictor on the predicted variable compared with the other predictors.
A stepwise approach using Akaike Information Criterion was applied in model selection.  The assumption that naturally-regenerated trees of 20–40 cm dbh were much older than the 14- to 15-year-old line-planted and tended trees was supported by data from permanent plots in the same stands we sampled (Pamoengkas et al. 2014, T Inada & S Purnomo, personal communications). Diameter growth of S. leprosula trees in logged-over forest averaged 0.5–0.7 cm year\(^{-1}\) which meant that naturally-regenerated trees of 20–40 cm dbh were expected to be 28–80 years old. Differences in bark texture were also evident, with smooth and fissured bark on the planted and naturally-regenerated trees respectively (FE Putz, personal observation). Chi-square tests were used to evaluate the contingency of the location of the tallest buttress relative to the direction of slope and longest crown radius. All statistical analyses were conducted in R (2013). Raw data from this study will be available in September 2015 from the Dryad Data Repository (http://datadryad.org/).

RESULTS AND DISCUSSION

Buttress height and surface area

Maximum buttress heights (Figure 1) and total buttress area (Figure 2) both increased with tree dbh. However, only buttress height was greater on naturally-regenerated than on planted trees (p < 0.001 and p = 0.394 respectively, Figures 3 and 4). The tallest buttresses on naturally-regenerated trees [(0.49 ± 0.03 m (± standard error)] averaged 0.14 m (41%) taller than on planted trees (0.35 ± 0.02 m, df = 96, p < 0.001, independent sample t-test). This finding suggested that development of tall buttresses was a function of tree age as well as tree size. Given that the seeds and wildlings that were subsequently planted were collected from the same area, there was no reason to expect genetic differences between the planted and naturally-regenerated trees. We therefore assumed that the observed differences in buttress characteristics were due to environmental factors. From a timber recovery standpoint, this result represent good news since the buttressed portions of harvested trees are often discarded by felling crews or the trees are cut above the buttresses. However, with maximum buttress heights of < 1 m, financial consequences of this effect are modest. Contrary to buttress heights, total buttress surface area of naturally-regenerated trees was slightly smaller than that of planted trees (0.41 ± 0.43 and 0.48 ± 0.41 m\(^{2}\); Kruskal-Wallis \(X^{2}=1.82, p=0.18, N=50\)). As the planted trees were probably exposed to more wind, this finding may support the idea that buttresses are mechanical adaptations to counter incidental stresses (Chapman et al. 1998). That planted trees have larger crowns than naturally-regenerated trees of the same size (Hardiansyah et al. 2015) may also help explain this finding. Furthermore, it remains to be seen whether buttress development accelerates on the planted trees during the 10 years that remain before their planned harvest.

Maximum buttress heights increased somewhat with slope (p < 0.05, Figure 3), but total buttress surface area did not (p = 0.377, Figure 4). When regressions were run separately for the naturally-regenerated and planted trees, slope was significant for both. The regression coefficient for naturally-regenerated trees was seven times larger than that of planted trees. Contrary to our predictions, neither buttress height nor surface area increased with crown size (p = 0.267 and 0.387 respectively, Figures 3 and 4).

Buttress orientation relative to slope and tree crown

Slopes in the sample area ranged from 3.5 to 48%, with mean of 17%. There was no difference in slope distribution between planted and naturally-regenerated trees (Kruskal–Wallis \(X^{2}=1.6383, p=0.20\)). Contrary to our expectations, the tallest buttresses were not found more often than expected on the uphill slope \((X^{2}=0.213, p=0.64; \text{Figure 5})\) nor on the side of the trunk opposite the longest crown radius \((X^{2}=1.92, p=0.166)\). As expected, the longest crown radius was downslope \((X^{2}=17.28, p<0.001; \text{Figure 6})\), which was presumably associated with increased access to light. These results did not change when analyses were carried out separately for planted and naturally-regenerated trees. These findings suggested that buttresses on S. leprosula trees were not responding to gravitational forces (Richter 1984, Lewis 1988). In the study from Central America that reported buttresses to be best developed on the side of the trunk opposite
the centre of mass of eccentric crowns (Young & Perkocha 1994), we suspected that some of the trees sampled were much larger than those we measured in Kalimantan (< 40 cm dbh), although the minimum size was the same (20 cm dbh).

CONCLUSIONS

Our data indicated that at least in *S. leprosula*, buttress development was a function of tree age as well as dbh. Determination of the universality of this conclusion awaits data on other species.
Figure 3  Coefficients for the model of tallest buttress height as function of naturally-regenerated or planted trees (NPP), diameter at 1.3 m (dbh), slope and crown area; dbh is a significant predictor and slope is marginally-significant, positive estimate indicates that higher values of that predictor correspond to higher buttresses, thus, maximum buttress height increases with dbh but is much lower on planted trees.

Figure 4  Coefficients for model of total buttress surface area as function of naturally-regenerated or planted trees (NPP), diameter at 1.3 m (dbh), slope and crown area; only dbh is a significant predictor.
grown under different environmental conditions. This finding suggested that butt log timber recovery will be greater from planted than naturally-regenerated trees. This good news from a timber stand management perspective needs to be tempered by the possibility that relatively low buttresses on planted trees will render them susceptible to being toppled.

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