POTENTIAL ADAPTIVE SIGNIFICANCE OF VEGETATIVE REGENERATION IN THE MONODOMINANT TROPICAL TREE *DICYMBE CORYMBOSA* (CAESALPINIACEAE)

Lance P. Woolley

**ABSTRACT**

The tropical monodominant tree *Dicymbe corymbosa*, vegetatively regenerates via epicormic shoots and roots, resulting in multi-stemmed trees with stabilizing pseudotrunks and root mounds. In two 1-ha forest plots on the Guiana Shield, we quantified the regenerative structure and aboveground soil development of *D. corymbosa* individuals ≥ 10 cm dbh and investigated the potential adaptive significance of reiteration in terms of genet persistence and root exploitation of aboveground litter and soil accumulations. We also investigated the incidence of the heart rot fungus *Phellinus robustus* in *D. corymbosa* and examined its role in the reiteration process. Large trees contained more and larger shoots, greater trunk, root mound, and organic soil volumes, and a higher incidence of *Phellinus*. Roots and ectomycorrhizas were abundant in aboveground soils on the trees, occurred at higher densities than those from the surrounding forest floor, and may be important in recycling mineral nutrients. Shoot turnover and regeneration, while stimulated by *Phellinus* rot, appeared to be cumulative over time, resulting in stable, structurally complex trees of indeterminate lifespan which successfully recruit through mast fruiting. *Dicymbe corymbosa* provides a rare example of a tree species which exploits both persistence and recruitment niches.
ACKNOWLEDGEMENTS

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INTRODUCTION

In many woody plant species vegetative regeneration by stem and root sprouting can allow for the persistence of established individuals, influencing plant population structure over time (Paciorek et al. 2000, Bond & Midgley 2001, Del Tredici 2001, Bond & Midgley 2003). Nevertheless, vegetative regeneration has largely been neglected in models of plant demography and forest succession (Paciorek et al. 2000, Bond & Midgley 2001, Douhovnikoff et al. 2004). Despite the potential importance of vegetative regeneration, particularly in disturbance-prone environments, most studies involving woody plant population dynamics have focused on the "recruitment niche" (e.g., seed dispersal, germination, and seed and seedling banks), ignoring the impact of vegetative regeneration and resulting individual persistence (i.e., the "persistence niche" sensu Bond & Midgley 2001). In tropical systems, understanding of forest dynamics may be enhanced by documenting and interpreting the patterns of vegetative regeneration exhibited by individual trees (Putz & Brokaw 1989, Bellingham et al. 1994, Zagt 1997, Paciorek et al. 2000).

Here I examine vegetative regeneration and single-species dominance (i.e., monodominance) in the Neotropical tree *Dicymbe corymbosa* Spruce ex Benth. (Caesalpinioideae; Richards 1996a, Henkel 2003). The origin and maintenance of tropical monodominance such as that exhibited by *D. corymbosa* may result from life history traits of the dominant species that alter the understory environment, affect recruitment,
and promote clumped distributions (e.g., ectomycorrhizal habit, mast fruiting, limited dispersal, shade tolerance; Connell & Lowman 1989, Hart et al. 1989, Torti et al. 2001, Henkel et al. 2005). *Dicymbe corymbosa* is the only tropical monodominant species that appears to combine the aforementioned traits with intensive vegetative regeneration via epicormic stems and roots (Henkel 2003). Vegetative regeneration through seemingly spontaneous trunk sprouting, though better documented in temperate forests (Koop 1987, Sillett 1999), may be rare in tropical rain forest (Zagt 1997). In Guyana the majority of *D. corymbosa* trees are multi-stemmed, suggesting that vegetative regeneration facilitates monodominance by yielding large, reiterated individuals that control stand resources and contribute to sexual recruitment through successive rounds of mast fruiting (Henkel 2003, Henkel et al. 2002, 2005).

The reiterative stem and root structure exhibited by *D. corymbosa* may enhance persistence of individual trees and subsequently influence forest dynamics. Multiple rounds of regeneration in *D. corymbosa* appear to yield large, structurally complex individuals, consisting of woody stems of various diameters and heights, an intricate common trunk composed of anastamosed stem bases and descending woody roots (hereafter “pseudotrunk” *sensu* Jeník 1994), hollow stem trunks, and decaying stumps from turnover of previous iterations (*e.g.*, Figures 1a-e, 2a-d; Henkel 2003). Additionally, large conical root mounds form through anastamosis of adventitious roots arising from the developing pseudotrunk (Henkel 2003). There are a number of potential advantages to the multi-stemmed physiognomy of *D. corymbosa*. Multiple stems could spread the risk of parent tree mortality among many stems (Eriksson & Jerling 1990,
Lacey & Johnston 1990) and buffer individual stems from damage (Peterson & Jones 1997). Additionally the pseudotrunk and root mound may increase physical stability and reduce tip-up incidence, possibly enhancing tree longevity and reducing population turnover (Peterson & Jones 1997, Bond & Midgley 2001, Henkel 2003). Such consequences of multi-stemmed physiognomy may restrict or limit recruitment opportunities for competing species, resulting in increased monodominance (Henkel 2003). From an evolutionary standpoint, each additional stem ramet may enhance the fitness of the genet, through increased survivorship, prolonged seed production, and production of ensuing ramet generations (Fischer & van Kleunen 2002, Pan & Price 2002, Douhovnikoff et al. 2004).

Large *D. corymbosa* individuals may also command a major share of above- and belowground stand resources. Cumulative stem production of *D. corymbosa* appears to result in crown enlargement and replacement, yielding a sun-exposed overstory and stratified understory and presumably effective photosynthesis (Richards 1996a, Henkel 2003). Following windthrow of upper canopy stems, pre-existing understory stems may rapidly exploit the resulting gaps, providing for effective light harvesting in space and time (Ohkubo et al. 1996, Zagt 1997, Paciorek et al. 2000, Henkel 2003). *Dicymbe corymbosa* may also be effective at recycling mineral nutrients through the accumulation of decomposing plant matter on the root mound and pseudotrunk. Organic soils can be up to 50 cm deep on the root mound and occur up to 4 m height on reiterated trees (Henkel 2003, Mayor & Henkel 2006). Soil accumulations within trunk cavities appear to coincide with the presence of the wood decay fungus *Phellinus robustus* (P. Karst.)
Bourd. & Galzin (Hymenochaetales, Basidiomycota), a known heart rotter (T. Henkel pers. obs., Bakshi & Singh 1970, Sunhede & Vasilaukas 2002). Aboveground soil accumulations and decaying wood of *D. corymbosa* may create favorable substrata for adventitious root development and mineral nutrient recycling, as demonstrated for other tree species in tropical and temperate forests (Jeník 1978, 1994, Longman & Jeník 1987, Sanford 1987, Nadkarni 1994). Overall, the vegetative regeneration exhibited by *D. corymbosa* may result in high levels of productivity, competitive advantage for seedling recruitment and self-replacement, and a greater ability to survive disturbances, ultimately promoting stable, persistent monodominant stands.

The purpose of this study was to explore the role of *D. corymbosa* vegetative regeneration in tree development and its potential impact on stand structure. We asked: 1) To what extent is vegetative regeneration in *D. corymbosa* cumulative over time, indicating potential for risk spreading, gap exploitation, and resource acquisition?, 2) Do soils accumulate as a result of reiterative tree physiognomy, and, if so, what is their potential for providing mineral nutrients to trees?, and 3) What the incidence of *P. robustus* in *D. corymbosa* trees, and what role may the wood decay fungus play in vegetative regeneration?
MATERIALS AND METHODS

Field site

Research was conducted during 2004-2005 in the central Pakaraima Mountains of western Guyana. The region is densely forested with the seasonal evergreen *Eschweilera – Licania* association (Fanshawe 1952) with elevations ranging from 700-2200 m. In the intermountain valleys of the Upper Potaro River Basin, a major watershed originating in the Pakaraimas, a mosaic of primary monodominant *D. corymbosa* stands of one- to many hectares in extent occurs in a matrix of mixed-species forests lacking *D. corymbosa* (Fanshawe 1952, Henkel 2003, Henkel *et al.* 2005). For further details of the climate, geology, and soils of the area see Henkel 2003, Henkel *et al.* 2005, and Mayor & Henkel 2006.

Study plots

To quantify vegetative regeneration in *D. corymbosa* and explore its influence on forest dynamics, two locally-disjunct 1-ha study plots (50 m × 200 m) were randomly chosen within larger areas of primary *D. corymbosa*-dominated forests, within 5 km of a permanent base camp located along the Upper Potaro River at 5° 18' 04.8" N; 59° 54' 40.4" W (Henkel 2003, Henkel *et al.* 2005). Plot 1 (P1) was established 1.5 km southeast of the base camp on a gentle E-SE facing slope at 720 m elevation on ironstone clay soil. Plot 2 (P2) was established 5 km southwest of base camp on the crest of a E-SE ridgeline at 740 m elevation on lateritic clay soil with outcroppings of ironstone boulders. Signs of anthropogenic disturbance were undetected in both plots. To compare tree species
richness and *D. corymbosa* dominance levels with those of previous studies, trees ≥ 10 cm diameter at breast height (dbh; diameter at 1.37 m above the ground) for all species were numbered and measured for dbh (Henkel 2003, Henkel *et al.* 2002, 2005). Each tree was identified to genus and species when possible, or otherwise assigned to morphospecies (Richards 1996b).

**Regenerative structure of *Dicymbe corymbosa***

For each *D. corymbosa* tree ≥ 10 cm dbh in P1 and P2, basal diameter (*i.e.*, diameter, at ground level, of the trunk or pseudotrunk, if original trunk was obscured by regenerative growth), pseudotrunk diameter (*i.e.*, diameter immediately below the first pseudotrunk split) and pseudotrunk height (*i.e.*, vertical distance from ground level to the first pseudotrunk split) were recorded. Each live stem ≥ 5 cm in diameter was measured for implantation height (*i.e.*, vertical distance from ground level to point of origin on the trunk or pseudotrunk) and basal diameter, as well as distance and compass angle relative to the central longitudinal axis of the trunk/pseudotrunk. In addition, dead stems occurring on a tree as standing dead or fallen stem traces emanating from the pseudotrunk were measured for basal diameter. In P1 dead stems ≥ 10 cm in diameter were put into the following decay classes: (1) solid wood with some leaves and/or fine twigs still attached, (2) moderately decayed wood, with rotten, sloughing bark and wood that could be broken when kicked, (3) extremely decomposed wood infiltrated with roots and being incorporated into the soil (*i.e.*, log trace), and (4) decayed stumps attached to pseudotrunks with no attendant log trace detectable on the ground. Decay classes were modified from the classification schemes of Triska & Cromack 1980 and Harmon *et al.*
1995. Decay classes 1-4 were presumed to represent increasing periods of time since stem death. Live and dead stems < 5 cm in diameter were summed for each tree. To characterize crown dimensions of multi-stemmed trees, a subsample of six trees was selected in P1 over a range of basal diameters, and each stem was measured for top height, top distance, crown diameter, and crown depth, using an Impulse 200LR Laser Rangefinder (Laser Technology, Inc., Centennial, Colorado).

Root mound radial length was measured in four cardinal directions from the base of the pseudotrunk to the point where the mound leveled out. Using a probe, root mound depth from the suspended litter horizon to the mineral soil was measured along each of the cardinal directions at three positions: immediately adjacent to the base of the pseudotrunk (this measurement was also used as the height of the root mound in volumetric calculations), the middle of the mound, and at the extreme margin. From the above measurements, root mound volumes were calculated using the equation for the volume of a conic frustum (i.e., volume = height × \( \pi/3 \times [\text{lower radius}^2 + (\text{lower radius} \times \text{upper radius}) + \text{upper radius}^2] \)); also used to calculate pseudotrunk volume). From two destructively-sampled trees outside the study plots, root mound volume between the upper suspended litter/root layer and the underlying mineral soil layer was determined to be ~ 50 % air space. Consequently, calculated root mound volumes were halved to more accurately represent the volume of humus and roots within the mounds.

Incidence of *Phellinus robustus*

Each *D. corymbosa* individual, including dead and fallen stems ≥10 cm in diameter, was inspected for the presence of *P. robustus*. Incidence was assessed in two
ways: (1) presence of basidiomata (hereafter “signs”) and/or (2) presence of decayed wood (hereafter “indications”) typical of many *Phellinus* spp., a white pocket rot with brown setal hyphae (Sunhede & Vasiliauskas 2002). Presence and extent of *P. robustus* decay was determined by cutting into dead stems and roots with a machete. No living stems were destructively sampled for decay presence. For each standing dead and fallen stem the maximum diameter and length of the *P. robustus* decay column were recorded. Voucher specimens for *P. robustus* basidiomata and decayed wood are housed at Humboldt State University.

**Organic Soil accumulations**

Location, number and dimensions of organic soil accumulations occurring up to 4 m elevation on each *D. corymbosa* tree were recorded. Soil accumulations were divided into two types based on parent material and location: (1) aerial soil occurring in junctions between shoots composed of freshly fallen litter and humus, derived from abscised leaves and other organic materials (*e.g.*, bark, twigs, invertebrate frass), or (2) cavity soil occurring in shoot cavities and the interior of pseudotrunks, composed mainly of decayed wood and invertebrate frass. Length, width, and depth of each soil accumulation were measured using a probe. Five to ten depth measurements were taken to obtain an average depth for the entire accumulation. Soil accumulation volume was calculated as the product of the surface area of an ellipse (*i.e.*, \( \pi \times \frac{\text{accumulation length}}{2} \times \frac{\text{accumulation width}}{2} \)) and mean depth (Sillett & Bailey 2003).

**Forest floor root density**

To estimate *D. corymbosa* root density on the forest floor (*i.e.*, away from root
mounds) 12 randomly positioned 3.8 l cores were excavated in each plot from the H horizon (defined here as the organic rich surface layer, 10-15 cm deep in our case; Van Breeman & Buurman 2002). *Dicymbe corymbosa* roots were separated from non-*Dicymbe* roots based on gross morphology, washed with water, cleaned of debris, field dried over a constant low heat for 72 hours, packaged in air tight containers, and stored at 5° C upon returning from the field. In the laboratory roots were separated into ≤ 2 mm diameter (fine roots; Vance & Nadkarni 1992) and > 2 mm diameter size classes, dried further at 60° C until a constant weight was obtained, and weighed.

**Organic soil accumulation root density**

Root density was estimated in 3.8 l cores extracted from aerial, cavity, and root mound soil accumulations of 12 randomly selected *D. corymbosa* trees ≥ 105 cm basal diameter. Of the 12 trees selected, six contained at least one aerial soil accumulation and the other six contained at least one cavity soil accumulation equal to or greater in volume than the 3.8 l core. For root mound sampling, one core was randomly positioned on the central mound in one of the four cardinal directions and extracted from each of the 12 trees. For aerial and cavity sampling, the 3.8 l core was positioned in the central portion of the soil accumulation and extracted. In total, 12 root mounds, six aerial, and six trunk cavity soil accumulations were sampled. The samples were processed for root density as described previously.

**Mycorrhization of fine root tips**

From each forest floor and soil accumulation fine root sample, three one gram subsamples were randomly selected, cut into one-cm lengths, suspended in a Petri dish
containing water, and randomized (Brundrett et al. 1994). The percentage of EM rootlets was quantified by scoring each rootlet that intersected the lines of a one cm grid subtending the Petri dish and scoring it as EM (mantle evident) or not EM (mantle not evident). If mantle was evident, the EM morphotype was recorded. Based on mantle and rootlet morphology three consistently occurring EM morphotypes were distinguished. The presence of a Hartig net, verified in the field with hand sections and light microscopy, confirmed the EM status of each morphotype (Agerer 1991).

**Data Analyses**

Linear regression was employed on the total sample of 307 *D. corymbosa* trees to examine relationships among tree structural variables, including basal diameter, total stem basal area (live + dead), live stem basal area, number of live stems, total number of stems (live + dead), pseudotrunk volume, and root mound volume (NCSS 2004). To further examine potential differences between small, medium, and large trees, the 307 trees were arbitrarily divided into three equal groups according to basal diameter: ≥ 10 cm ≤ 47 cm (diameter class 1, \( N = 102 \)), > 47 cm < 105 cm (diameter class 2, \( N = 102 \)), ≥ 105 cm (diameter class 3, \( N = 103 \)). In each of these basal diameter classes the number of multi-stemmed individuals was summed, as well as stems in the following diameter classes: < 10 cm, ≥ 10 cm < 20 cm, ≥ 20 cm < 50 cm, and ≥ 50 cm.

Relationships between total soil volume (aerial soil + cavity soil) and tree structure variables were analyzed with a stepwise multiple regression (SAS 2001). Total soil volume (aerial + cavity) was designated as the dependent variable. Due to large inter-tree variability in root mound soil volume this variable was excluded from the
multiple regression. To eliminate multicollinearity among the tree structure variables, principal components analysis (PCA) was used to derive orthogonal components of tree structure (McCune & Medford 1999). Analysis was restricted to trees with two or more stems $\geq 5$ cm diameter and one or more soil accumulations ($N = 118$). The relationship between cavity soil volume and incidence of *P. robustus* was assessed with Pearson's correlation.

Root samples obtained from randomly selected trees were grouped according to source (forest floor H horizon, root mound, aerial soil, and cavity soil), and differences in total and fine root density, and percent mycorrhization of fine roots among these groups were analyzed with a one-way ANOVA (NCSS 2004).
RESULTS

Forest structure

*Dicymbe* stands reported here covered the range in structure and composition seen in other *D. corymbosa*-dominated forests in the area (Henkel 2003, Henkel et al. 2002, 2005). In P1, *D. corymbosa* composed 113/316 trees/ha (36%) and 36.5/50.6 m²/ha (72%) of basal area. In P2, *D. corymbosa* composed 194/279 trees/ha (70%) and 29.3/33.2 m²/ha (88%) of basal area. Plot 2 was more purely monodominant, although the presence of several extremely large *D. corymbosa* (> 250 cm basal diameter) in P1 yielded higher basal areas, despite having lower *D. corymbosa* density than P2. Tree species richness ranged from 32-37 spp./ha (P1/P2). The most common co-occurring canopy species was *Eschweilera sagotiana* (Lecythidaceae), with 22 percent of trees in P1, and 5 percent in P2. See Henkel (2003) for a list of additional commonly-occurring canopy trees.

Regenerative structure of *Dicymbe corymbosa*

*Dicymbe corymbosa* trees exhibited abundant vegetative regeneration through epicormic stem and root production (Figures 1a-e, 2a-d). Overall, 243/307 (79%) of *Dicymbe* trees ≥ 10 cm dbh had at least two stems. On the 243 multi-stemmed trees, 2996 stems < 10 cm in diameter, and 628 stems ≥ 10 cm in diameter were recorded. The mean number of living stems per tree was 14.7 (range 1-96). The mean height of stem implantation on the pseudotrunk was 1.1 m (range 0-5.9 m), while mean stem base distance to the center of the pseudotrunk was 0.5 m (range 0-2.8 m). When portioning
the total tree sample into three basal diameter classes, small trees were more likely to have a single stem, while larger trees were more likely to be multi-stemmed and highly reiterated (Table 1).

Figure 1. *Dicymbe corymbosa* physiognomy in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. (a) single boled *D. corymbosa*; (b) young *D. corymbosa* with developing epicormic stems; (c) adventitious root development prior to root mound formation; (d) mature *D. corymbosa* with well developed root mound; (e) mature *D. corymbosa* with multiple mature stems, dead stem turnover, and large pseudotrunk composed of anastamosed stem bases and descending woody roots.
Figure 2. Adventitious roots and pseudotrunk development of *Dicymbe corymbosa* in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. (a, b) aerial adventitious roots with secondary thickening upon contact with the ground; (c) hanging adventitious root mat at 4 m; (d) large pseudotrunk formed from anastamosis and secondary thickening of adventitious roots.
Table 1. Proportion of multi-stemmed trees and stem diameter distribution of *Dicymbe corymbosa* in small, medium, and large tree basal diameter classes in two 1-ha study plots in the Upper Potaro River Basin, Pakaraima Mountains, Guyana.

<table>
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<tr>
<th>Diameter class&lt;sup&gt;a&lt;/sup&gt;</th>
<th># of Individuals</th>
<th>Single-stemmed</th>
<th>Multi-stemmed</th>
<th>Stems&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Stems ≥ 10 &lt; 20</th>
<th>Stems ≥ 20 &lt; 50</th>
<th>Stems ≥ 50</th>
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<td>102</td>
<td>55</td>
<td>47</td>
<td>243</td>
<td>64</td>
<td>38</td>
<td>0</td>
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<td>2</td>
<td>102</td>
<td>7</td>
<td>95</td>
<td>993</td>
<td>55</td>
<td>88</td>
<td>17</td>
</tr>
<tr>
<td>3</td>
<td>103</td>
<td>2</td>
<td>101</td>
<td>1760</td>
<td>167</td>
<td>126</td>
<td>77</td>
</tr>
<tr>
<td>Total</td>
<td>307</td>
<td>64</td>
<td>243</td>
<td>2996</td>
<td>286</td>
<td>252</td>
<td>94</td>
</tr>
</tbody>
</table>

<sup>a</sup> Diameter class; 1, basal diam ≥ 10 cm ≤ 47 cm; 2, basal diam > 47 cm < 105 cm; 3, basal diam ≥ 105 cm.

<sup>b</sup> Stem diameter in cm measured immediately above point of implantation.

For the total sample of 307 trees basal diameter was positively correlated with the number ($P < 0.0001$) and basal area ($P < 0.0001$) of live and live + dead stems, suggesting that reiteration was cumulative over time (Table 2; Figure 3). Pseudotrunk and root mound volume were each positively correlated ($P < 0.0001$) with both the number and basal area of stems, implying increased production of adventitious roots with the presence of more and larger stems (Table 2). Self-thinning of stems was inevident due to the positive correlation between the number of live stems and the basal area of the largest live stem ($P < 0.0001$; Table 2). The number of live stems and the coefficient of variation for the basal area of live stems were positively correlated, implying a size hierarchy among the live stems, possibly indicating cohorts of stems arising through time ($R^2 = 0.56$, $P < 0.0001$, $N = 307$; the number of live stems was square root transformed). The number of dead stems was positively correlated with the number of live stems ($R^2 = 0.54$, $P < 0.05$, $N = 307$; both variables were square root transformed), indicating that
stem turnover may have stimulated epicormic sprouting. From the six trees subsampled for crown dimensions, mean individual shoot length, shoot crown volume, and top distance increased with shoot diameter (Table 3). As tree basal diameter increased, total crown volume increased ($R^2 = 0.64, P = 0.057, N = 6$; Figure 4).

Table 2. Coefficients of determination ($R^2$) for correlations among *Dicymbe corymbosa* tree structure variables ($N = 307$ trees) in two 1-ha study plots in the Upper Potaro River Basin, Pakaraima Mountains, Guyana$^a$.

<table>
<thead>
<tr>
<th></th>
<th># live stems</th>
<th># live + dead stems</th>
<th>Live stem basal area ($m^2$)</th>
<th>Live + dead stem basal area ($m^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diameter (cm)</td>
<td>0.42*</td>
<td>0.47*</td>
<td>0.80*</td>
<td>0.83*</td>
</tr>
<tr>
<td>Pseudotrunk volume ($m^3$)</td>
<td>0.30*</td>
<td>0.33*</td>
<td>0.64*</td>
<td>0.66*</td>
</tr>
<tr>
<td>Root mound volume ($m^3$)</td>
<td>0.31*</td>
<td>0.33*</td>
<td>0.59*</td>
<td>0.64*</td>
</tr>
<tr>
<td>Basal area of largest stem ($m^2$)</td>
<td>0.42*</td>
<td>0.44*</td>
<td>0.96*</td>
<td>0.76*</td>
</tr>
</tbody>
</table>

$^a$ Asterisks indicate significant positive correlations ($P \leq 0.0001$). Number of live stems and number of live + dead stems were square root transformed. All other variables were log transformed.
Figure 3. Relationship between basal diameter (cm) of trunk/pseudotrunk and number and basal area of live stems for the 307 *Dicymbe corymbosa* trees ≥ 10 cm dbh in two 1-ha study plots in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. Values are untransformed.

Table 3. Mean stem and crown dimensions of six *Dicymbe corymbosa* trees\(^a\) in two 1-ha study plots in the Upper Potaro River Basin, Pakaraima Mountains, Guyana\(^b\).

<table>
<thead>
<tr>
<th>Stem diameter class (cm)</th>
<th>&lt; 5</th>
<th>≥ 5 &lt; 10</th>
<th>≥ 10 &lt; 20</th>
<th>≥ 20 &lt; 50</th>
<th>≥ 50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem length (m)(^c)</td>
<td>2.1</td>
<td>7.6</td>
<td>15.6</td>
<td>25.0</td>
<td>32.0</td>
</tr>
<tr>
<td>(0.26)</td>
<td></td>
<td>(0.66)</td>
<td>(2.6)</td>
<td>(2.5)</td>
<td>(1.4)</td>
</tr>
<tr>
<td>Crown Volume (m(^3))</td>
<td>0.41</td>
<td>8.2</td>
<td>26.0</td>
<td>139.0</td>
<td>317.0</td>
</tr>
<tr>
<td>(0.11)</td>
<td></td>
<td>(2.8)</td>
<td>(4.9)</td>
<td>(40.1)</td>
<td>(46.5)</td>
</tr>
<tr>
<td>Top Distance (m)(^d)</td>
<td>0.8</td>
<td>1.3</td>
<td>2.0</td>
<td>4.5</td>
<td>8.7</td>
</tr>
<tr>
<td>(0.1)</td>
<td></td>
<td>(0.2)</td>
<td>(0.4)</td>
<td>(1.0)</td>
<td>(4.0)</td>
</tr>
</tbody>
</table>

\(^a\) Pseudotrunk basal diameters of the six trees ranged from 75.8 - 178.4 cm (mean = 131.9 cm).
\(^b\) Values are mean (SEM).
\(^c\) Length of stem from implantation point on pseudotrunk to top of stem axis.
\(^d\) Horizontal distance from stem apex to the central longitudinal axis of the pseudotrunk.
Stem turnover and incidence of *Phellinus* heart rot

One-hundred-twenty-five dead stems ≥ 10 cm in diameter (included fallen, standing dead, and stumps attached to pseudotrunks) were recorded from 84/307 (27%) of the trees. Of the 125 dead stems, 99 were recorded from trees ≥ 105 cm basal diameter, 25 were from trees > 47 cm < 105 cm, and one from a tree ≤ 47 cm. In P1, 18 trees contained at least two dead stems ≥ 10 cm diameter. Of these trees, six contained dead stems in the same decay class, and 12 contained from 2-7 dead stems in different stages of decay, indicating a temporal sequence of stem death (Table 4). Additionally, 22 hollow bases of pseudotrunks were recorded, of which 17 were from trees ≥ 105 cm basal diameter and five were from trees > 47 cm < 105 cm. Signs and/or indications of *P.*
robustus were recorded from 78 (62%) of the dead stems and 22 (100%) of the hollow pseudotrunk bases (Figure 5a-f). Twenty-one percent of the 307 D. corymbosa trees had signs and/or indications of P. robustus. Within the basal diameter classes, 46 percent of trees ≥ 105 cm, 13 percent of trees > 47 cm < 105 cm, and 3 percent of trees ≤ 47 cm had signs and/or indications of P. robustus. Phellinus robustus incidence was positively correlated with the volume of soil occurring in decaying shoot cavities and the cavities of hollow trunks (r = 0.31, P < 0.05, N = 118); the volume of cavity soil was log transformed).

Table 4. Structural characteristics of 12 Dicymbe corymbosa with at least two dead stems ≥ 10 cm diameter in study plot P1 in the Upper Potaro River Basin, Pakaraima Mountains, Guyana.

<table>
<thead>
<tr>
<th>Tree</th>
<th>Basal diameter (cm)</th>
<th>Stems&lt; 10</th>
<th>Stems ≥ 10 &lt; 20</th>
<th>Stems ≥ 20 &lt; 50</th>
<th>Stems ≥ 50</th>
<th>Deadb ≥10</th>
<th>Decay class</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>116.0</td>
<td>8</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>2, 3, 3</td>
</tr>
<tr>
<td>2</td>
<td>129.4</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>2, 2, 3</td>
</tr>
<tr>
<td>3</td>
<td>165.4</td>
<td>16</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>2, 3</td>
</tr>
<tr>
<td>4</td>
<td>169.9</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>2, 4</td>
</tr>
<tr>
<td>5</td>
<td>191.9</td>
<td>39</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2, 3</td>
</tr>
<tr>
<td>6</td>
<td>193.4</td>
<td>8</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>3, 4, 4</td>
</tr>
<tr>
<td>7</td>
<td>195.8</td>
<td>6</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>1, 3, 3</td>
</tr>
<tr>
<td>8</td>
<td>224.9</td>
<td>33</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2, 3</td>
</tr>
<tr>
<td>9</td>
<td>247.0</td>
<td>17</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1, 4</td>
</tr>
<tr>
<td>10</td>
<td>287.5</td>
<td>10</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>3, 3, 4</td>
</tr>
<tr>
<td>11</td>
<td>293.5</td>
<td>27</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>2, 4, 4</td>
</tr>
<tr>
<td>12</td>
<td>335.9</td>
<td>11</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>7</td>
<td>1, 1, 1, 3, 3, 4, 4</td>
</tr>
</tbody>
</table>

a Number of live stems in each diameter size class (cm).
b Number of dead stems ≥ 10 cm diameter.
Figure 5. Incidence of *Phellinus robustus* on *Dicymbe corymbosa* in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. (a) *P. robustus* basidiomata on pseudotrunk of *D. corymbosa*; (b) white pocket rot with brown setal hyphae; (c) white pocket rot in sapwood; (d) fallen stem with well developed internal decay column and external basidiomata; (e) soil-filled heart rot column; (f) stem snapped off at base, with heart rot column.
Organic soil accumulations

Root mound volume for the total sample of 307 *D. corymbosa* trees was 199 m$^3$ with a mean of 0.6 m$^3$ (range 0.001-24.0 m$^3$). Of the 245 soil accumulations recorded for the 307 trees, 193 (79%) occurred on trees ≥ 105 cm basal diameter. The total volume of the 245 soil accumulations was 26.1 m$^3$, with aerial soil comprising 7.7 m$^3$ (30%) and pseudotrunk and shoot cavities combining for 18.4 m$^3$ (70%). Aerial, pseudotrunk cavity, and shoot cavity soil accumulations are illustrated in Figure 6a-c.

Principal components analysis extracted three significant components (PC1, PC2, PC3; eigenvalues = 4.59, 2.59, 1.70), accounting for 80% of the total variation in the 11 original variables (Table 5). PC1 represented the overall size of a tree, PC2 represented tree vigor, and PC3 represented the amount of dead wood on a tree. The best equation for estimating total soil volume (aerial and trunk cavity soil volume) was the following:

$$\text{total volume} = 0.5 + 0.08 \times \text{PC1} - 0.04 \times \text{PC2} + 0.1 \times \text{PC3} \quad (R^2 = 0.82, \ P < 0.0001, \ N = 118; \ \text{Figure 7}).$$

The negative correlation of tree vigor (PC2) with total soil volume may reflect an influence of advanced reiteration on the accumulation of plant debris. The strong positive correlation between the number of live stems < 5 cm diameter and PC2 ($r = 0.60, \ P < 0.0001, \ N = 118$) may indicate that an abundance of small stems acts as a barrier to the accumulation of debris, thereby creating a negative correlation of tree vigor (PC2) with total soil volume. Overall, larger, more complex trees, with large amounts of dead wood contained more and larger soil accumulations.
Table 5. Correlation coefficients between 11 tree structure variables and their significant principal components for 118 *Dicymbe corymbosa* trees in two 1-ha study plots in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. Asterisks indicate significant correlations (*P* < 0.001).

<table>
<thead>
<tr>
<th>Tree structure variables</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area live stems (m²)</td>
<td>0.94*</td>
<td>0.06</td>
<td>-0.8</td>
</tr>
<tr>
<td>Diameter largest stem (cm)</td>
<td>0.93*</td>
<td>0.14</td>
<td>-0.29</td>
</tr>
<tr>
<td>Average live stem basal area (m²)</td>
<td>0.79*</td>
<td>-0.3</td>
<td>-0.49</td>
</tr>
<tr>
<td>Pseudotrunk volume (m³)</td>
<td>0.78*</td>
<td>-0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>Tree basal diameter (cm)</td>
<td>0.72*</td>
<td>-0.2</td>
<td>0.52</td>
</tr>
<tr>
<td>Average stem diameter (cm)</td>
<td>0.65</td>
<td>-0.5</td>
<td>-0.48</td>
</tr>
<tr>
<td>Number dead stems</td>
<td>0.49</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>CV stem diameter</td>
<td>0.40</td>
<td>0.76*</td>
<td>-0.15</td>
</tr>
<tr>
<td>CV stem basal area</td>
<td>0.33</td>
<td>0.85*</td>
<td>0.04</td>
</tr>
<tr>
<td>Number live stems</td>
<td>0.32</td>
<td>0.64</td>
<td>0.31</td>
</tr>
<tr>
<td>Dead stem basal area (m²)</td>
<td>0.20</td>
<td>-0.5</td>
<td>0.71*</td>
</tr>
</tbody>
</table>

*a* Pseudotrunk volume was cube root transformed.

*b* Live stem basal area, average live stem basal area, and dead stem basal area were square root transformed.

**Root density**

Roots were abundant in all three types of soil accumulations (*i.e.*, root mounds, cavity, and aerial; Figure 6c-d). Total root density of the forest floor H horizon was 138.5 mg/cm³. Root mound and aboveground soil accumulations combined was 328.4 mg/cm³. Density of the fine root fraction was 31.7 mg/cm³ (23%) for the forest floor and 97.4 mg/cm³ (30.0%) for the combined soil accumulations. Although fine root density of the soil accumulations tended to be greater than that found in the forest floor H horizon, the difference was not statistically significant.
Figure 6. Soil accumulations and root development of *Dicymbe corymbosa* in the Upper Potaro River Basin, Pakaraima Mountains, Guyana. (a) aerial soil in shoot/shoot junctions; (b) soil accumulation inside a pseudotrunk cavity with large woody roots; (c) shoot cavity soil accumulation; (d) adventitious roots permeating a soil accumulation; (e) white tomentose ectomycorrhizas; (f) thelephoroid and black strigose ectomycorrhizas.
Mycorrhization of fine root tips

Ectomycorrhizas were present in all soil accumulations as well as the forest floor. Mean ectomycorrhization of fine root tips was 46 percent (range 33-55%), with the highest percentage (though not statistically significant) of ectomycorrhizal root tips occurring in the root mounds. The thelephoroid morphotype was the most abundant, occurring in > 89 percent of all soil accumulations. Conversely, the white tomentose and black strigose morphotypes were rarer but had their highest occurrences in aerial and cavity soil accumulations, respectively (see Figure 6e-f).
DISCUSSION

Adaptive significance of vegetative regeneration

Epicormic stem and root production is a basic trait of *D. corymbosa*, and the majority if individuals are stable, multi-stemmed trees. As individual *D. corymbosa* trees mature, evidenced by increasing size of the pseudotrunk, the number and diameter of stems increases, without dependence on external damage to older stems, although death of stems ≥ 10 cm diameter is associated with greater epicormic stem production. New stems were usually initiated around the periphery of the largest and presumably oldest stems, resulting in clusters of stems of various sizes emerging from the expanding pseudotrunk, in total yielding a leaf-bearing crown with upper-, mid-, and lower strata components. As tree basal diameter increases, the number and size of sprout stems, crown volume, pseudotrunk volume, and root mound volume increase, indicating the intrinsic cumulative nature of the regenerative process (this study, Henkel 2003, for *Dicymbe altsonii* see Zagt 1997). In this context, the vegetative regeneration of *Dicymbe* contrasts sharply with the more commonly observed sprouting of tropical trees in response to relaxation of apical dominance through wind and treefall damage (Uhl et al. 1981, Putz et al. 1983, Putz & Brokaw 1989, Clark & Clark 1991, Walker 1991, Bellingham et al. 1994, Jenik 1994, Vandermeer et al. 1995, Guáiru, Paciorek et al. 2000, Bond & Midgley 2001, Van Bloem et al. 2005). Cumulative stem production in *D. corymbosa* is analogous to spontaneous root or trunk suckering seen in

Vegetative regeneration likely facilitates persistent monodominance in *D. corymbosa*. Large, long-lived, regenerating individuals produce large quantities of poorly-dispersed seeds during mast fruiting events, resulting in large recruitment banks. This process ultimately results in high densities of uneven-aged conspecific trees (Henkel *et al.* 2005). Clumping may enhance the fitness of the species by increasing its competitive ability and subsequent success within the community (Henkel 2003).

Vegetative regeneration of *D. corymbosa* may thus have a number of important ecological and evolutionary implications.

**Individual persistence**

Compared to single-trunked trees, multi-stemmed *D. corymbosa* individuals may have enhanced capacity for *in situ* persistence. Increased stability of mature *D. corymbosa* afforded by their large pseudotrunks and root mounds appears to reduce whole-tree turnover. In two hectares of forest only one recent tip-up of *D. corymbosa* was recorded, and no new *D. corymbosa* tip-ups occurred during the two-year study, a much lower rate than that perceived in surrounding mixed rain forest at the Potaro site (T. Henkel pers. obs.). In other primary tropical forests the rate of whole tree tip-ups and
resulting mortality is considerably higher; (e.g., Barro Colorado Island, Panama, 0.5 tip-ups/ha/yr (Putz & Milton 1982); La Selva, Costa Rica, 2.5 tip-ups/ha/yr (Lieberman et al. 1985); and Saul, French Guiana, 2.7 tip-ups/ha/yr (van der Meer & Bongers 1996).

*Dicymbe corymbosa* tip-ups, when observed elsewhere, readily sprout from the horizontal boles on the ground, indicating lack of genet death (L. Woolley & T. Henkel pers. obs.; Lacey & Johnston 1990). With each successive round of ramet production, the lifespan of the genet may be increased, as the risk of genet mortality can be spread among its many ramets, reinforced by stabilizing effects of the pseudotrunk and root mound (Eriksson & Jerling 1990).

In *D. corymbosa*, death of larger ramets appeared to be caused by snap-off above the pseudotrunk. The majority of these downed ramets contained a well developed decay column of *P. robustus*; the resulting loss of heartwood may have reduced stem strength, increasing the risk of snap-off due to wind or falling debris (Bakshi & Singh 1970, Clark & Clark 1991, Hennon 1995, Richards 1996a). A number of live ramets had hollow cores and *Phellinus* rot as detectable through probing via basal cavities. Trees that consist of many ramets are more likely to have some ramets escaping heart rot infection and surviving to maturity than trees consisting of a single stem (Peterson & Jones 1997). Additionally, ramet clustering may “buffer” interior ramets from damage or death due from force agents (Peterson & Jones 1997). Ramet clustering exhibited by the clonal palm *Oenocarpus mapora* in Panama reduced mortality from falling debris for smaller stems and from falling trees and windthrow for larger stems (De Steven 1989). The maximum number of ramets recorded on a *D. corymbosa* genet was 96, although there
may be no limit to the number of ramets produced over a genet’s lifetime. A successfully regenerating genet would be spatially and temporally persistent and may approach immortality. In many large *D. corymbosa*, the original ortet was undetectable, having been replaced with multiple ensuing ramet generations. Determining the age of *D. corymbosa* may be impossible due to stem turnover, decay, and coexistence of multi-generational stems. We can only speculate that large genets may be many centuries old given their structural complexity and the rarity of whole tree tip-ups. Some insight may be provided by ongoing studies which are addressing increment growth rates of trees of various sizes and stem complexities.

The persistence of large *D. corymbosa* genets may reduce recruitment opportunities of other tree species by mitigating gap phase dynamics (Hartshorn 1989) and ultimately depressing tree species diversity over time (Bond & Midgley 2001, Henkel 2003). The scarcity of whole-tree turnover in *D. corymbosa* likely decreases the area of disturbance and number of sites available for successful establishment (*e.g.*, less disruption of mineral soil and minimal reduction in root competition) compared to surrounding mixed forests (Henkel 2003). This process may ultimately decrease the opportunities for light-demanding tree species to reach maturity (Hartshorn 1978, Putz 1983, Brokaw 1985, Schaetzl *et al.* 1989). Furthermore, when canopy gaps occur due to turnover of upper stratum stems, the lower story stems of *D. corymbosa*, connected to an extensive pre-established root system, may quickly fill canopy gaps, as exhibited by other coppicing species (Lacey & Johnston 1990, Ohkubo *et al.* 1996, Zagt 1997, Bond & Midgley 2001, Henkel 2003). This process was apparent in individual *D. corymbosa*
trees given the coexistence of stems in multiple size classes, including fallen stems and those in various stages of decay. The positive correlation between live and dead stem basal area and tree basal diameter implied that a substantial internal portion of pseudotrunks were composed of dead stems, with ensuing stem generations filling the gaps created by dead stems and contributing to pseudotrunk expansion. Enhanced stability and circumvention of gap phase dynamics may contribute to the extremely low tree species richness recorded in *D. corymbosa* forests (this study, Henkel et al. 2002, 2005, Henkel 2003).

**Resource acquisition**

Carbon and mineral acquisition are most likely skewed towards the larger, more structurally complex *D. corymbosa* genets. Effective photosynthesis may be achieved by large genets that have upper, middle, and lower crown stems. The increase in stem length, crown volume, and horizontal distance of stem apex to pseudotrunk axis with increasing stem diameter, creates a multi-tiered method of three-dimensional crown enlargement and replacement, allowing *D. corymbosa* to control stand light resources. As a result stratified *D. corymbosa* crowns often exceed 100% of the stand area (Henkel et al. 2005).

The large root mounds and presumably large root systems, appear to effectively fill above- and belowground resource space. The elevated, sloping, lattice-like structure of the root mounds, which is best developed on the largest trees, acts as an effective litter trap, accounting for the greatest volume of soil. Multi-stemmed *D. corymbosa* trees are also effective at aerial litter trapping and subsequent root exploration, and may increase
the surface area available for downward funneling of nutrient-rich stemflow (Bruijnzeel 1989). Aboveground soil accumulations had similar macronutrient concentrations but lower nitrification rates compared to those of the forest floor H horizon (Nadkarni, 1984, Vance & Nadkarni 1990, 1992, Lesica & Antibus 1991, Nadkarni et al. 2002). The strong positive correlation between *P. robustus* and trunk cavities, and the large contribution of soil in these cavities to total aboveground soil, lends support to Janzen's hypothesis that rotten tree cores are adaptive, becoming sources of nitrogen and other minerals which can be recycled via adventitious roots of the host tree (Janzen 1976).

*Dicymbe corymbosa* adventitious roots were abundant in all soil accumulations, and were derived from the cambia of adjacent stems and from apogeotropic roots of conspecific neighbors, suggesting that soil accumulations are mineral nutrient sources and perhaps recipients of stemflow nutrients, as demonstrated elsewhere (Jeník 1978, Longman & Jeník 1987, Sanford 1987, Herwitz 1991, Jeník 1994, Nadkarni 1994). Additionally, decaying heartwood may be a site for nitrogen fixation by free-living bacteria, increasing its value as a nitrogen source (Harvey et al. 1989).

While forest floor root density of *D. corymbosa* was lower than that recorded for other tropical tree species (Vance & Nadkarni 1992), aboveground total and fine root densities were much greater, indicating prioritization of root exploration to the aboveground soil. Adventitious roots exploring aboveground litter and soil are functional organs in other tree species, similar in structure and absorptive capacity to their belowground counterparts (Sanford 1987, Nadkarni & Primack 1989). In our study, aggregations of fine roots in the aboveground soil accumulations may reflect sites of
nutrient release from decomposition (Jordan 1985, Turner 2001). The ubiquitous presence of ectomycorrhizas in the soil accumulations may implicate a direct pathway of nutrients from decomposing organic matter to the roots (Janzen 1976, Jordan 1985), possibly contributing to a closed mineral nutrient cycle (Henkel 2003, Mayor & Henkel 2006).

Seed output and increased genetic representation

During the 2003 masting event *D. corymbosa* seed production ranged from 66,056-161,056 seeds/ha. The resulting seedlings contributed to an enormous standing recruitment bank of 41,000-92,000 seedlings and 1,800-4,500 saplings/ha (Henkel et al. 2005). Larger multi-stemmed trees contributed most to the seed rain, with higher genetic representation in the subsequent seedling populations. Persistent vegetative regeneration and high levels of sexual recruitment may be a unique combination of life history traits. Several temperate tree species with similar forms of vegetative regeneration either lack or have severely limited seedling recruitment (*e. g.*, *Fagus grandifolia*, Held 1983; *Doryphora sassafras*, *Eucryphia moorei*, Johnston & Lacey 1983; *Populus alba*, *Ulmus laevis*, *Ulmus minor*, Koop 1987; *Fagus japonica*, Peters & Ohkubo 1990; *Tilia cordata*, Bond & Midgley 2001). Clonal persistence in addition to high sexual recruitment could ensure *D. corymbosa* dominance in space and time (*sensu* Hallé 1978).

Evolutionary considerations

In woody plants, the propensity for vegetative regeneration increases with increasing frequency of disturbance (Bond & Midgley 2003). For example, in the fire prone shrublands of South Africa selection for vegetative sprouting among sprouting and
non-sprouting species is strongly tied to the frequency, severity, and consistency of the fires (Bond & Midgley 2003). In Puerto Rico, basal sprouting of trees following a hurricane is proportional to the amount of structural damage incurred in a stand (Van Bloem et al. 2005). Regarding the Guianas, where large-scale disturbances are rare and climatic conditions stable (Davis 1941, Hammond & Brown 1995, Henkel 2003), the driving forces for the evolution of ubiquitous vegetative regeneration observed in *D. corymbosa* are less clear.

Sprouting in response to disease, which has been documented for some temperate trees (Koop 1987, Del Tredici 2001), may have selected for *D. corymbosa*'s habit. In the absence of frequent disturbance, forests may persist in an old-growth state, allowing fungi to cause their persistent, but slow, heart rot decay (Hennon 1995). In the present study, the incidence of *P. robustus* in *D. corymbosa* was high, infecting the vast majority of fallen stems, with basidiomata also observed on living components of the pseudotrunk. Signs or indications of *P. robustus* were recorded from trees in all size classes, most preponderantly in those ≥ 105 cm basal diameter. This finding suggests that there may be a long period of internal decay until outward signs and indications of *P. robustus* are evident. It is likely that many more *D. corymbosa* individuals contain *Phellinus* decay columns than are detectable. The high density of *D. corymbosa* individuals in monodominant stands could provide ample resources for *P. robustus*, which appears to have a “bottom-up” advance pattern in the trees, possibly spreading through root-to-root contact (L. Woolley & T. Henkel pers. obs.).
The original concept of heart rot as a purely saprotrophic process, with fungi entering through wounds or dead branches and subsequently invading the dead heartwood, with little or no invasion of the functional, living sapwood, is inaccurate (Pearce 2000). It is more likely that infections by heart rot fungi are initiated in the cambium and subsequently compartmentalized to the center of the tree (Shigo & Marx 1977). Moreover, several species of *Phellinus* (*e.g.*, *P. hartigii*, *P. pini*, and *P. chrysoloma*) do not confine their decay activity to heartwood and may grow into sapwood and phloem, killing these tissues and possibly the entire tree (Hennon 1995). Such parasitism has also been demonstrated for northern races of *P. robustus* on *Quercus robur* (Sunhede & Vasiliauskas 2002). If *P. robustus* has been ubiquitous in monospecific *D. corymbosa* stands, could it have driven the evolution of vegetative regeneration in *D. corymbosa*? A type of evolutionary arms race may have developed between *P. robustus* as the “frequent disturbance factor” and the high density of *D. corymbosa* hosts. One method to increase tree survivorship and evolutionary fitness under these circumstances would be to invest heavily in the “persistence niche,” by vegetatively sprouting and spreading the risk of infection and genet mortality among many ramets.

Given the ubiquity of heart rot in tropical trees (Janzen 1976), why do other tropical trees apparently lack such a strategy? The ability to vegetatively regenerate varies not only with the type and frequency of disturbance but also with the age or size of the plant. Many tropical and temperate trees retain the ability to sprout from the seedling to sapling stage, but lose this ability as adults (Del Tredici 2001, Bond & Midgley 2003).
*Dicymbe corymbosa* retains the ability to sprout into adulthood, likely from suppressed epicormic buds, making it well-suited to overcome the destabilizing effects of heart rot decay in the original ramets.

From a mechanistic standpoint, the number of suppressed epicormic buds produced by a tree species is genetically determined (Ashton *et al.* 1990), and the degree of epicormic sprouting is directly related to the number of epicormic buds present (Krajicek 1959, Kormanick & Brown 1964, Bachelard 1969, Lacey & Johnston 1990). Release of suppressed epicormic buds is inhibited by auxin, a phytohormone basipetaly transported by the phloem in trees undergoing apical dominance (Zimmermann & Brown 1971). Suppressed buds may be released when the plant's internal ethylene to auxin ratio increases (Wood 1985, Sanyal & Bangerth 1998). Ethylene production may increase due to stress, mechanical damage, or from diseased plant tissue (Bird and Cutting 1971, Abeles 1992, Kozlowski & Pollardy 1997).

In *D. corymbosa* the release of epicormic buds and subsequent stem development may be induced by increased production of ethylene resulting from tissue damage by *P. robustus*. This mechanism is particularly likely if the fungus is able to exploit functional sapwood, which contains higher baseline concentrations of ethylene than heartwood (Kozlowski & Pollardy 1997). Increased ethylene derived from fungal or host tissues has been observed in many plants infected with fungi (Byrde & Cutting 1973, Abeles 1992, Kozlowski & Pollardy 1997, Hudgins & Franceschi 2004).

In *D. corymbosa* ethylene levels may rise with the presence of *P. robustus* decay, stimulating the release of suppressed epicormic buds. While we have no direct evidence
of such a mechanism, this model could explain the ubiquitous epicormic sprouting in otherwise healthy appearing individuals of *D. corymbosa.*
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