Reiteration in the Monodominant Tropical Tree *Dicymbe corymbosa* (Caesalpiniaceae) and its Potential Adaptive Significance

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ABSTRACT

The tropical monodominant tree *Dicymbe corymbosa* reiterates via epicormic shoots and roots, resulting in multistemmed trees with complex pseudotrunks and root mounds. In 2 ha of primary forest on the Guiana Shield, we quantified the reiterative structure and aboveground soil development of 307 *D. corymbosa* individuals ≥ 10 cm dbh and investigated the potential adaptive significance of reiteration in terms of genet persistence and root exploitation of aboveground soil accumulations. We also investigated the incidence of the heart rot fungus *Phellinus robustus* in *D. corymbosa* and examined its relationship to the reiteration process. Large trees contained more and larger reiterations, greater trunk, root mound, and organic soil volumes, and a higher incidence of *Phellinus* than smaller trees. Roots and ectomycorrhizas were abundant in aboveground soils on the trees, occurred at higher densities than those of the surrounding forest floor, and may be important in recycling mineral nutrients. Stem turnover and reiteration were associated with *Phellinus* heart rot and appeared to be cumulative over time, resulting in persistent, structurally complex trees of indeterminate lifespan. *Dicymbe corymbosa* provides a rare example of a tree species that exploits both persistence and recruitment niches, as it successfully recruits through mast fruiting.

Key words: arboreal soil; ectomycorrhiza; Guiana Shield; Guyana; heart rot; Neotropics; *Phellinus;* tropical rain forest.

REITERATION IN WOODY PLANTS CAN BE DEFINED AS THE PRODUCTION OF SHOOTS AND ROOTS from the activation and growth of apical meristems outside their normal temporal sequence due to advancing age or physical disturbance (Hallé *et al.* 1978, Jeník 1994). Reiteration may enable persistence of established individuals and influence plant population structure over time. Despite the potential importance of reiteration, particularly in disturbance-prone environments, most studies involving woody plant population dynamics have focused on the 'recruitment niche' (*e.g.*, seed dispersal, germination, and seedbanks) and ignored the impact of reiteration and resulting individual persistence (*i.e.*, the 'persistence niche' *sensu* Paciorek *et al.* 2000, Bond & Midgley 2001, Douhovnikoff *et al.* 2004). In tropical systems, understanding of forest dynamics may be enhanced by documenting and interpreting the various patterns of reiteration exhibited by individual trees (Putz & Brokaw 1989, Bellingham *et al.* 1994, Zagt 1997, Paciorek *et al.* 2000).

Here we examine reiteration and its potential adaptive significance in the Neotropical monodominant tree *Dicymbe corymbosa* Spruce *ex* Benth. (Caesalpiniaceae; Richards 1996a, Henkel 2003). Single-species dominance such as that exhibited by *D. corymbosa* may result from life-history traits of the dominant species that alter the understory environment, promote self-recruitment, and lead to 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 known that combines the aforementioned traits with intensive reiteration via epicormic shoots and roots, apparently in the absence of damage (Henkel 2003). Reiteration through spontaneous trunk sprouting as documented in temperate forests (Koop 1987, Sillett 1999) may

be less common in tropical rain forests (Zagt 1997). In Guyana, the majority of *D. corymbosa* trees have numerous stems of various sizes, suggesting that cumulative reiteration may result in persistent, stand-dominating individuals.

The reiterative shoot and root structure exhibited by *D. corymbosa* may enhance persistence of individual trees and subsequently influence forest dynamics. Reiteration in *D. corymbosa* yields large, structurally complex individuals consisting of woody stems of various diameters and heights (*i.e.*, reiterated trunks *sensu* Sillett & Van Pelt, 2007), some of which are dead, dying, or hollow, an intricate common trunk composed of anastamosed stem bases and descending woody roots (hereafter 'pseudotrunk' *sensu* Jeník 1994), and decaying stumps from turnover of previous iterations. Additionally, large conical root mounds form through anastamosis of adventitious roots arising from the developing pseudotrunk (*e.g.*, Fig. 1; Henkel 2003).

Potential advantages afforded to *D. corymbosa* by a multistemmed physiognomy include spreading the risk of parent tree mortality among many stem units (Eriksson & Jerling 1990, Lacey & Johnston 1990) and buffering individual stems from mechanical damage (Peterson & Jones 1997). Additionally, stabilizing effects of the pseudotrunk and root mound may enhance tree longevity, reduce population turnover (Peterson & Jones 1997, Bond & Midgley 2001), and serve to limit recruitment opportunities for competing species, resulting in increased monodominance (Henkel 2003). From an evolutionary standpoint, each additional stem may enhance the fitness of the genet through increased survivorship, prolonged seed production, and production of ensuing generations (Fischer & van Kleunen 2002, Pan & Price 2002, Douhovnikoff *et al.* 2004).

Large reiterated *D. corymbosa* individuals may command a major share of aboveground and belowground resources. Reiteration by *D. corymbosa* expands and maintains crowns, yielding a sun-exposed

FIGURE 1.   *Dicymbe corymbosa* physiognomy in the Upper Potaro River Basin, Guyana, as indicated by (A) young *D. corymbosa* with developing epicormic shoots; (B) adventitious root development prior to root mound formation; (C) aerial adventitious roots with secondary thickening upon contact with the ground; (D) mature *D. corymbosa* with well-developed root mound; (E) large pseudotrunk formed from anastamosis and secondary thickening of adventitious roots.

overstory and stratified understory of woody stems (Richards 1996a, Henkel 2003). Following windthrow of upper canopy stems, pre-existing understory stems may rapidly exploit the resulting gaps (Ohkubo *et al.* 1996, Zagt 1997, Paciorek *et al.* 2000, Henkel 2003). *Dicymbe corymbosa* may also obtain mineral nutrients from 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 high 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. W. Henkel, pers. obs., Bakshi & Singh

1970, Sunhede & Vasiliauskas 2002). Such aboveground soil accumulations may create favorable substrata for adventitious root development and mineral nutrient recycling (Jeník 1978, 1994; Longman & Jeník 1987; Sanford 1987; Nadkarni 1994). Overall, the reiteration exhibited by *D. corymbosa* may result in high levels of productivity, competitive advantage for conspecific seedling recruitment and self-replacement, and a greater ability to survive disturbances, ultimately promoting the persistence of monodominant stands.

The purpose of this study was to quantify the degree of reiteration in a large sample of *D. corymbosa* trees and explore its potential adaptive significance in tree, soil, and stand structural development.

We asked: (1) Are the effects of reiteration cumulative over time, indicating potential for risk spreading, gap exploitation, and resource acquisition? (2) Does reiteration promote soil accumulation and, if so, are these soils exploited by adventitious roots and ectomycorrhizas? and (3) What is the incidence of *P. robustus* in *D. corymbosa* trees, and how may its wood decay affect reiteration?

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) at elevations of 700–2200 m. In the intermountain valleys of the Upper Potaro River Basin, 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). For further details of the climate, geology, and soils of the area see Henkel (2003), Henkel *et al.* (2005), and Mayor and Henkel (2006).

STUDY AREA.—To quantify reiteration in *D. corymbosa*, 2 ha (two 50 × 200 m plots) of forest was randomly delimited within a larger homogenous area of primary *D. corymbosa*-dominated forest on lateritic clay soil, 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, at 710–750 m asl. Prior anthropogenic disturbance was not evident within the 2 ha of forest. 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 occurring in the 2 ha of forest were numbered and their dbh was measured. Each tree was identified to genus and species or otherwise assigned to morphospecies (Richards 1996b).

REITERATIVE STRUCTURE OF *DICYMBE CORYMBOSA*.—Each *D. corymbosa* tree ≥ 10 cm dbh in the 2-ha sampling area of forest was measured for basal diameter (*i.e.*, ground-level diameter of trunk, or pseudotrunk if original trunk was obscured by regenerative growth), pseudotrunk diameter (*i.e.*, diameter immediately below the first major reiteration), and pseudotrunk height (*i.e.*, vertical distance from ground level to the first major reiteration). Each live stem ≥ 5 cm diameter was measured for basal diameter and height of origin (*i.e.*, vertical distance from ground level to point of origin on the trunk or pseudotrunk) as well as distance and compass angle relative to the center of the trunk or pseudotrunk. Basal diameter was also measured for dead stems occurring as standing dead or fallen stem traces emanating from the pseudotrunk. Dead stems ≥ 10 cm diameter were classified by state of decay in four categories as follows: (1) solid wood with some leaves and/or fine twigs still attached; (2) moderately decayed wood, with rotten sloughing bark; (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 (Triska & Cromack 1980, Harmon *et al.* 1995). Decay

classes were presumed to represent increasing periods of time since stem death. Live and dead stems < 5 cm in diameter were summed for each tree.

Root mound radial length was measured in four cardinal directions from the base of the pseudotrunk to average ground level. Using a probe, root mound depth from the suspended litter horizon to the mineral soil was measured along each of the cardinal directions immediately adjacent to the pseudotrunk (*i.e.*, root mound height), at 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 × π/3 × [lower radius^2 + (lower radius × upper radius) + 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 percent air space. Consequently, calculated root mound volumes were halved to more accurately represent the internal volume of soil and roots.

To characterize three-dimensional crown structure of multistemmed trees, six trees over a range of basal diameters were randomly selected, 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, CO, U.S.A.).

SOIL ACCUMULATIONS.—Location, number, and dimensions of organic soil accumulations occurring up to 4 m height on each of the 307 *D. corymbosa* trees were recorded. Soil accumulations were divided into two types based on parent material and location: (1) aerial soil occurring in crotches between stems, which was composed of freshly fallen litter and humus derived from abscised leaves, bark, twigs, and invertebrate frass; or (2) cavity soil occurring in stem cavities and the interior of pseudotrunks, which was composed mainly of decayed wood and invertebrate frass. Length, width, and depth of each soil accumulation were measured using a metal 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.*, π × [length/2] × [width/2]) and mean depth (Sillett & Bailey 2003).

ORGANIC SOIL ROOT DENSITY.—To assess root activity of *D. corymbosa* in aboveground soils, root density was estimated in 3.8 L cores extracted from aerial, cavity, and root mound soils of 12 randomly selected 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 with volume ≥ 3.8 L. 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 soil sampling the 3.8 L core was extracted from the central portion of the soil accumulation. In total, 12 root mound, six aerial, and six cavity accumulations were sampled. *Dicymbe corymbosa* roots were separated from non-*Dicymbe* roots based on gross morphology, non-*Dicymbe* roots were discarded, and the *D. corymbosa* roots were cleaned of

debris, field dried over a constant low heat for 72 h, packaged in air tight containers, and stored at 5°C upon returning from the field. Roots were then separated into ≤ 2 mm diameter (fine roots; Vance & Nadkarni 1992) and > 2 mm diameter classes, dried further at 60°C until a constant weight was obtained, and weighed.

To compare aboveground rooting activity with that of the forest floor (*i.e.*, away from root mounds), 24 randomly positioned 3.8-L cores were excavated from the organic rich surface layer, 10–15 cm deep in our case (Van Breeman & Buurman 2002). The samples were processed for root density as described above.

Mycorrhization of fine root tips.—To assess development of functional ectomycorrhizas in the various soils, from each fine root sample three 1-g subsamples were randomly selected, cut into 1-cm lengths, suspended in a Petri dish containing water, and randomized (Brundrett *et al.* 1994). The percentage of ectomycorrhizal (EM) rootlets was quantified by scoring each rootlet that intersected the lines of a 1-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).

Incidence of *Phellinus robustus*.—Each *D. corymbosa* individual, including dead and fallen stems ≥ 10 cm diameter, was inspected for the presence of *P. robustus*. Incidence was assessed in two ways: (1) the presence of basidiomata (hereafter 'signs'); and/or (2) the presence of decayed wood (hereafter 'indications') typical of many *Phellinus* spp., a white pocket rot with brown setal hyphae (Sunhede & Vasiliauskas 2002). The 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 maximum diameter, as well as incidence of a *P. robustus* decay column were recorded. Voucher specimens for *P. robustus* basidiomata and decayed wood are housed at Humboldt State University.

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, number of live + dead stems, pseudotrunk volume, and root mound volume (NCSS 2004). Stem numbers were square-root transformed, and all other variables were log transformed prior to analysis.

To 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; $N = 102$), and ≥ 105 cm (diameter class 3; $N = 103$). In each of these basal diameter classes the proportion of multistemmed individuals was determined, and the number of stems occurring in each of the following diameter classes was recorded: < 10 cm, ≥ 10 cm < 20 cm, ≥ 20 cm < 50 cm, and ≥ 50 cm.

Relationships between total soil volume (*i.e.*, aerial soil + cavity soil) and tree structural variables were analyzed with a stepwise multiple regression (SAS 2001). Total soil volume was designated as the dependent variable. Root mound soil volume was excluded due to excessive intertree variability. Multicollinearity among tree structural variables was eliminated prior to regression by principal components analysis using PC-ORD (McCune & Mefford 1999). The primary matrix consisted of 11 tree-level structural variables (*i.e.*, pseudotrunk basal diameter, pseudotrunk volume, basal area of live stems, basal area of dead stems, number of live stems, number of dead stems, maximum stem diameter, average stem diameter, coefficient of variation of stem diameter, average stem basal area, and coefficient of variation of stem basal area). Analysis was restricted to trees with two or more reiterated stems ≥ 5 cm diameter and one or more soil accumulations ($N = 118$). Multivariate normality among the structural variables was improved by square-root transforming (*i.e.*, basal areas of stems) or cube-root transforming (*i.e.*, pseudotrunk volume) those variables exhibiting excessive skewness or kurtosis. In the final matrix, skewness of the variables ranged from 0.10 to 1.95 and kurtosis ranged from –0.16 to 6.78. The cross-products matrix consisted of Pearson correlation coefficients among the structural variables. The resulting principal components, which represented orthogonal dimensions of tree structure, were interpreted by inspecting correlations between significant components (*i.e.*, actual > broken-stick Eigenvalues) and individual structural variables. Tree scores along these dimensions were then regressed against total soil volume.

The relationship between cavity soil volume and incidence of *P. robustus* in randomly selected trees was assessed with Pearson's correlation.

Differences in total and fine root density and fine root percent mycorrhization among forest floor, root mound, aerial, and cavity soils from randomly selected trees were analyzed with a one-way ANOVA (NCSS 2004).

RESULTS

Forest structure.—*Dicymbe* forest was similar in structure and composition to other *D. corymbosa*-dominated forests in the area (Henkel *et al.* 2002, 2005; Henkel 2003). In the 2 ha of forest, *D. corymbosa* accounted for 51.6 percent of the 595 individual trees and 78.5 percent of the total basal area (41.9 m²/ha). Tree species richness averaged 35 spp./ha. The most common co-occurring canopy species was *Eschweilera sagotiana* (Lecythidaceae), representing 14 percent of trees. For a list of additional commonly occurring canopy trees see Henkel (2003).

Reiterative structure of *D. corymbosa*.—*Dicymbe corymbosa* trees exhibited abundant reiteration through epicormic shoot and root production (Fig. 1). Overall, 243 of 307 (79%) *Dicymbe* trees ≥ 10 cm dbh had at least two stems. On the 243 multistemmed trees, 2996 stems < 10 cm in diameter and 628 stems ≥ 10 cm in diameter were recorded. The mean number of living stems per

TABLE 1.   *Number of multistemmed trees and stem diameter distribution of* Dicymbe corymbosa *in small, medium, and large tree basal diameter classes in 2 ha of primary forest in the Upper Potaro River Basin, Guyana.*

Diameter class[a]	No. of individuals	Single-stemmed	Multi-stemmed	Stems[b] < 10	Stems ≥ 10 < 20	Stems ≥ 20 < 50	Stems ≥ 50
1	102	55	47	243	64	38	0
2	102	7	95	993	55	88	17
3	103	2	101	1760	167	126	77
Total	307	64	243	2996	286	252	94

[a]Diameter class; 1, basal diameter ≥ 10 cm ≤ 47 cm; 2, basal diameter > 47 cm < 105 cm; 3, basal diameter ≥ 105 cm.

[b]Stem diameter in cm measured immediately above point of implantation.

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 multistemmed and highly reiterated (Table 1).

For the total sample of 307 trees, basal diameter was positively correlated with the number of live ($R^2 = 0.42$, $P < 0.0001$; Fig. 2) and live + dead ($R^2 = 0.47$, $P < 0.0001$) stems, and basal area of live ($R^2 = 0.80$, $P < 0.0001$; Fig. 2) and live + dead ($R^2 = 0.83$, $P < 0.0001$) stems, suggesting that stem reiteration was cumulative over time. Pseudotrunk and root mound volume were each positively correlated with both the number (pseudotrunk $R^2 = 0.30$, $P < 0.0001$; root mound $R^2 = 0.31$, $P < 0.0001$) and basal area (pseudotrunk $R^2 = 0.64$, $P < 0.0001$; root mound $R^2 = 0.59$, $P < 0.0001$) of live stems, implying increased production of adventitious roots with the presence of more and larger stems. Self-thinning of stems was obscured by the positive correlation between the number of live stems and the basal area of the largest live stem ($R^2 = 0.42$, $P < 0.0001$). The number of live stems and the coefficient of variation of basal area of live stems were positively correlated ($R^2 = 0.56$, $P < 0.0001$), implying a size hierarchy among the live stems, possibly indicating cohorts of stems arising through time. The number of dead stems was positively correlated

with the number of live stems ($R^2 = 0.54$, $P < 0.05$), indicating that stem turnover may stimulate epicormic sprouting. From the six trees subsampled for crown dimensions, mean individual stem length, stem crown volume, and top distance increased with stem diameter (Table 2). As tree basal diameter increased, total crown volume increased ($R^2 = 0.64$, $P = 0.057$, $N = 6$) such that trees of 80 and 160 cm basal diameter had crown volumes of approximately 150 and 550 m³, respectively.

STEM TURNOVER AND INCIDENCE OF *PHELLINUS* HEART ROT.—One hundred and twenty-five dead stems ≥ 10 cm in diameter (included fallen, standing dead, and stumps attached to pseudotrunks) were recorded from 84 of 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. Eighteen 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 two to seven dead stems in different stages of decay, indicating a temporal sequence of stem death (Table 3). 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 (Fig. 3). Twenty-one percent of the 307 *D. corymbosa* trees had incidence of *P. robustus*. Within the basal
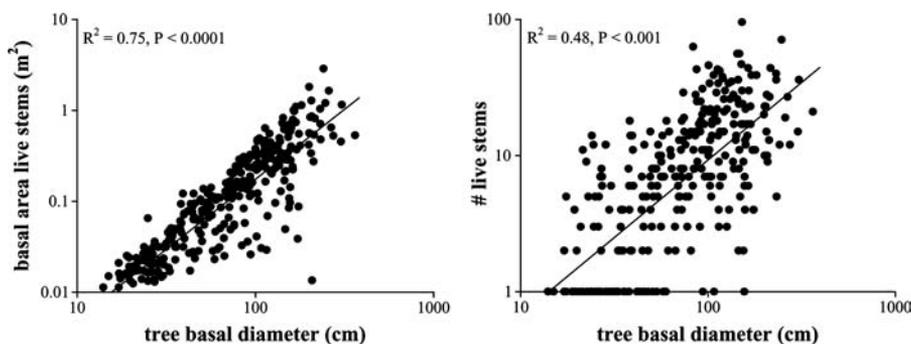

FIGURE 2.   Relationships between basal diameter (cm) of trunk/pseudotrunk and number and basal area of live stems for 307 *Dicymbe corymbosa* trees ≥ 10 cm dbh in 2 ha of primary forest in the Upper Potaro River Basin, Guyana. Note that axes are on a logarithmic scale.

TABLE 2. *Mean (SE) stem and crown dimensions of six* Dicymbe corymbosa *trees*[a] *in the Upper Potaro River Basin, Guyana.*

	Stem diameter class (cm)				
	< 5	≥ 5 < 10	≥ 10 < 20	≥ 20 < 50	≥ 50
Stem length (m)[b]	2.1 (0.3)	7.6 (0.7)	15.6 (2.6)	25.0 (2.5)	32.0 (1.4)
Crown volume (m^3)	0.4 (0.1)	8.2 (2.8)	26.0 (4.9)	139.0 (40.1)	317.0 (46.5)
Top distance (m)[c]	0.8 (0.1)	1.3 (0.2)	2.0 (0.4)	4.5 (1.0)	8.7 (4.0)

[a]Pseudotrunk basal diameters of the six trees ranged from 75.8 to 178.4 cm (mean = 131.9 cm).

[b]Length from origin on pseudotrunk to stem apex.

[c]Horizontal distance from stem apex to trunk center at ground level.

diameter classes, 46 percent of trees ≥ 105 cm, 13 percent of trees > 47 cm < 105 cm, and 3 percent of trees ≤ 47 cm had incidence of *P. robustus*. *Phellinus robustus* incidence was positively correlated with log-transformed volume of soil occurring in decaying stem cavities and cavities within pseudotrunks ($r = 0.31$, $P < 0.05$, $N = 118$).

SOIL ACCUMULATIONS.—Total root mound soil volume of the 307 *D. corymbosa* trees was 199 m^3 with a mean of 0.6 m^3/tree (range 0.001–24.0 m^3). Of the 245 soil accumulations (aerial + cavity) recorded for the 307 trees, 193 (79%) occurred on trees ≥ 105 cm basal diameter. The total soil accumulation volume was 26.1 m^3, with cavity soil comprising 18.4 m^3 (70%) and aerial soil 7.7 m^3 (30%) (Fig. 3).

Principal components analysis extracted three significant components (PC1, PC2, and PC3; eigenvalues = 4.59, 2.59, and 1.70) accounting for 80.7 percent of the total variation in the 11 original variables among the 118 trees with at least two stems and one soil accumulation (Table 4). 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 predicting aerial + trunk cavity soil volume was the following: soil volume = 0.463 + 0.084 × PC1 − 0.037 × PC2 + 0.100 × PC3 ($R^2 = 0.82$, $P < 0.0001$, $N = 118$; Fig. 4). Overall, larger, more complex trees, with large amounts of dead wood contained more and larger soil accumulations. The negative correlation between tree vigor (PC2) and total soil volume may reflect a negative influence of advanced reiteration on the accumulation of plant debris. The positive correlation between the number of live stems < 5 cm diameter and PC2 ($r = 0.60$, $P < 0.0001$, $N = 118$) suggests that an abundance of small stems acts as a barrier to debris accumulation.

ROOT DENSITY.—*Dicymbe corymbosa* roots were abundant in root mounds, trunk cavities, and aerial litter of randomly selected trees. For *D. corymbosa*, mean total root density (fine + coarse) of the forest floor was 11.5 (±1.5) mg/cm^3 and mean fine root density was 2.6 (±0.35) mg/cm^3. Mean total root density for root mound soil was 14.0 (±5.3) mg/cm^3, 14.8 (±4.2) mg/cm^3 for cavity soil, and 12.0 (±0.6) mg/cm^3 for aerial soil. Mean fine root density for root mound soil was 3.6 (±2.0) mg/cm^3, 4.7 (±3.6) mg/cm^3 for

TABLE 3. *Stem structure, number of live and dead stems, and decay classes of 12* Dicymbe corymbosa *with at least two dead stems* ≥ 10 *cm diameter in the Upper Potaro River Basin, Guyana.*

		No. live stems in diameter classes (cm)					
Tree	Basal diameter (cm)	< 10	≥ 10 < 20	≥ 20 < 50	≥ 50	No. dead ≥ 10 cm	Decay class
1	116.0	8	1	3	0	3	2, 3, 3
2	129.4	2	0	1	0	3	2, 2, 3
3	165.4	16	3	3	0	2	2, 3
4	169.9	3	0	1	0	2	2, 4
5	191.9	39	1	3	1	2	2, 3
6	193.4	8	1	3	0	3	3, 4, 4
7	195.8	6	2	3	1	3	1, 3, 3
8	224.9	33	3	1	2	2	2, 3
9	247.0	17	2	2	1	2	1, 4
10	287.5	10	3	2	1	3	3, 3, 4
11	293.5	27	7	4	1	3	2, 4, 4
12	335.9	11	4	6	0	7	1, 1, 1, 3, 3, 4, 4

FIGURE 3.   Incidence of *Phellinus robustus* and organic soil on *Dicymbe corymbosa* in the Upper Potaro River Basin, Guyana, as indicated by (A) fallen stem with well-developed internal decay column and external basidiomata; (B) stem snapped off at base, with heart rot column; (C) soil inside a stem cavity with root exploration, with *P. robustus* basidiomata on left-hand side; (D) aerial soil in crotches between stems.

cavity soil, and 4.3 ($\pm$1.3) mg/cm^3 for aerial soil. Fine root densities of the organic soils tended to be greater (though not statistically so) than those found in the forest floor.

MYCORRHIZATION OF FINE ROOT TIPS.—Ectomycorrhizas were present in all soil accumulations and the forest floor. Mean ectomycorrhization of fine root tips among all soils was 46 percent (range 33–55%), with the highest percentage (though not statistically significant) of ectomycorrhizal root tips occurring in the root mounds. Among the three morphotypes encountered, a brown tomentose morphotype was the most abundant, occurring in

> 89 percent of the soil accumulations. Conversely, white tomentose and black strigose morphotypes were rarer but had their highest percent occurrence in aerial soils (21%) and cavity soils (32%), respectively.

DISCUSSION

CUMULATIVE REITERATION AND ITS POTENTIAL ADAPTIVE SIGNIFICANCE.—Epicormic shoot and root production is a basic trait of *D. corymbosa*, and the majority of individuals are stable,

TABLE 4.   *Correlation coefficients between 11 tree structure variables and their significant principal components for 118* Dicymbe corymbosa *trees*[a] *in the Upper Potaro River Basin, Guyana. Significant correlations are indicated in bold text (*P < 0.001*).*

Tree structure variable[b]	PC1	PC2	PC3
Basal area live stems (m^2)	**0.94**	0.06	**−0.80**
Diameter largest stem (cm)	**0.93**	0.14	−0.29
Average live stem basal area (m^2)	**0.79**	−0.30	−0.49
Pseudotrunk volume (m^3)	**0.78**	−0.30	0.40
Tree basal diameter (cm)	**0.72**	−0.20	0.52
Average stem diameter (cm)	0.65	−0.50	−0.48
Number dead stems	0.49	0.32	0.32
CV[c] stem diameter (cm)	0.40	**0.76**	−0.15
CV stem basal area (m^2)	0.33	**0.85**	0.04
Number live stems	0.32	0.64	0.31
Dead stem basal area (m^2)	0.20	−0.50	**0.71**

[a]Analysis was restricted to trees with at least two stems ≥ 5 cm diameter and one humic accumulation ($N = 118$).

[b]Pseudotrunk volume was cube-root transformed; live stem basal area, average live stem basal area, and dead stem basal area were square-root transformed.

[c]CV = coefficient of variation.

multistemmed trees. As the overall size of individual *D. corymbosa* trees increases over time, the number and diameter of stems increase without dependence on external damage to older stems, although stem death is associated with greater epicormic shoot production. New shoots are initiated around the periphery of the largest and presumably oldest stems, resulting in clusters of stems of various sizes emerging from the expanding pseudotrunk and yielding a highly
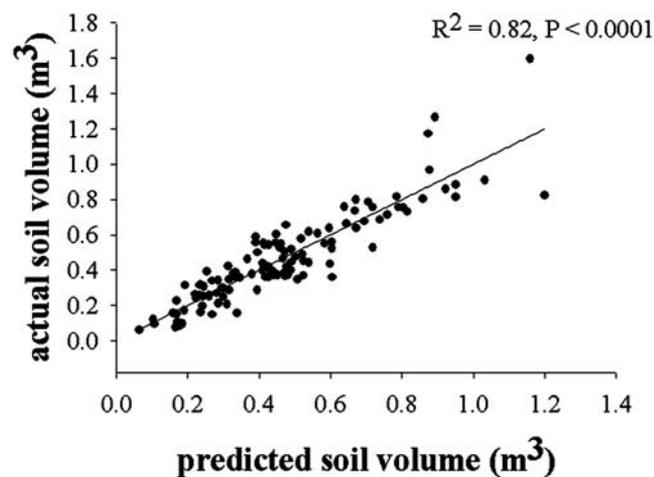

FIGURE 4.   Predicted versus actual soil volume for 118 *Dicymbe corymbosa* trees in the Upper Potaro River Basin, Guyana. Soil volume was predicted by a stepwise regression of the first three principal components derived from an analysis of tree-level structure.

stratified leaf-bearing crown. As tree basal diameter increases, the number and size of stems, crown volume, pseudotrunk volume, and root mound volume increase, indicating the intrinsic cumulative nature of the regenerative process. Reiteration of *Dicymbe* contrasts sharply with the more commonly observed sprouting of tropical trees in response to relaxation of apical control (*sensu* Wilson 2000) 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, Jeník 1994, Vandermeer *et al.* 1995, Guariguata 1998, Paciorek *et al.* 2000, Bond & Midgley 2001, Van Bloem *et. al.* 2005). Cumulative reiteration in *D. corymbosa* is analogous to, but more extreme than, spontaneous root or trunk suckering seen in some temperate trees (*e.g.*, *Alnus, Betula, Doryphora, Eucryphia, Fagus, Salix, Tilia, Ulmus*; Johnston & Lacey 1983, Kim *et al.* 1986, Koop 1987, Peters & Ohkubo 1990, Cao & Peters 1998), and *Trigonobalanus verticillata* in Southeast Asia (Corner 1990).

Dicymbe corymbosa is one of the few Neotropical trees known to combine cumulative reiteration with ample sexual reproduction (for *D. altsonii* see Zagt 1997). Large, long-lived, reiterating individuals produce large quantities of poorly dispersed seeds during mast fruiting events, resulting in large recruitment banks. This process ultimately leads to high densities of uneven-aged conspecific trees (Henkel *et al.* 2005). Clumping may enhance the fitness of the species by increasing its within-community competitive ability (Henkel 2003).

INDIVIDUAL PERSISTENCE.—Compared to single-stemmed trees, multistemmed *D. corymbosa* trees may have a prolonged lifespan. Increased stability of mature trees afforded by their large pseudotrunks and root mounds might reduce whole-tree turnover. In the 2 ha of forest reported here, only one recent *D. corymbosa* tip-up was recorded, and no new tip-ups occurred during the 2-yr study, a lower rate than that perceived in surrounding mixed rain forest at the Potaro site (L. P. Woolley and T. W. Henkel, pers. obs.). In other mature Neotropical forests, the rate of whole tree tip-ups and resulting mortality appears to be higher, ranging from 0.5–2.7 tip-ups/ha/yr (Putz & Milton 1982, Lieberman *et al.* 1985, van der Meer & Bongers 1996). *Dicymbe corymbosa* tip-ups readily sprout from horizontal trunks on the ground, indicating lack of genet death (L. P. Woolley & T. W. Henkel, pers. obs.; Lacey & Johnston 1990). With each successive reiteration, the lifespan of the genet may be increased because the risk of genet mortality is spread among its many reiterated stems, a process reinforced by stabilizing effects of the pseudotrunk and root mound (Eriksson & Jerling 1990).

Risk spreading may be extended to the impacts of *P. robustus* and windthrow of stems. In *D. corymbosa*, fallen stems snap off above the pseudotrunk. The majority of these downed stems contain a well-developed decay column of *P. robustus*; the resulting loss of heartwood likely reduces stem strength, increasing the risk of breakage due to wind or falling debris (Bakshi & Singh 1970, Clark & Clark 1991, Hennon 1995, Richards 1996a). Probing of basal cavities revealed that a number of live stems had hollow cores and *Phellinus* rot. Trees consisting of many stems are more likely to have some stems escaping heart rot infection and surviving

to maturity than single-stemmed trees (Peterson & Jones 1997). Stem clustering may also buffer interior stems from windthrow and falling debris (De Steven 1989, Peterson & Jones 1997). In many large *D. corymbosa*, the original trunk is undetectable due to stem turnover, decay, and coexistence of multigenerational stems. Such successively reiterating genets would be spatially and temporally persistent during a long lifespan. We suspect that large genets may approach a millennium in age given their structural complexity and the rarity of whole tree tip-ups.

Gap dynamics.—The persistence of large *D. corymbosa* genets may reduce recruitment opportunities of other tree species by circumventing gap dynamics (Hartshorn 1989, Bond & Midgley 2001, Henkel 2003). The scarcity of whole-tree turnover in *D. corymbosa* likely minimizes the area of disturbance and number of available recruitment sites compared to surrounding mixed forests. Consequently, opportunities for light-demanding tree species to establish and reach maturity may be diminished (Hartshorn 1978, Putz 1983, Brokaw 1985, Schaetzl *et al.* 1989). The extensive and long-established root systems of mature *D. corymbosa* individuals may facilitate rapid growth of connected understory stems into crown gaps created by overstory turnover (Lacey & Johnston 1990, Ohkubo *et al.* 1996, Zagt 1997, Bond & Midgley 2001, Henkel 2003). This process is apparent in the largest *D. corymbosa* trees, which possess stems in all size classes, including fallen stems and those in various stages of decay. A substantial internal portion of their pseudotrunks is composed of dead stem volume, with multiple generations of reiteration filling crown gaps created by dead stems and contributing to sustained pseudotrunk expansion. Circumvention of gap dynamics may contribute to the extremely low tree species richness recorded in *D. corymbosa* forests (Henkel *et al.* 2002, 2005; Henkel 2003).

Resource acquisition.—Carbon acquisition is most likely skewed toward the larger, more structurally complex trees that have woody stems of multiple heights. The increase in stem length, crown volume, and horizontal distance of stem apex to pseudotrunk center with increasing stem basal diameter creates broad, multitiered crowns up to 40-m tall. Overlapping *D. corymbosa* crowns may exceed 100 percent cover of stand ground area, yielding overwhelming control of the stand-level light environment, and, presumably, photosynthesis (Henkel *et al.* 2005).

Effective water and mineral acquisition may be facilitated by large root mounds and extensive root systems that fill belowground resource space. The elevated, sloping, lattice-like root mounds, which are best developed in the largest trees, accumulate litter and account for the greatest volumes of organic soil. Highly reiterated trees with large amounts of dead wood are also effective at accumulating aboveground soil and sustaining root exploration of this resource, and their high stem surface areas may promote the downward funneling of nutrient-rich stemflow (Bruijnzeel 1989), some of which may be retained in the soil (Jeník 1978, Longman & Jeník 1987, Sanford 1987, Herwitz 1991, Jeník 1994, Nadkarni 1994, Nadkarni *et al.* 2002, Enloe *et al.* 2006). While data are currently lacking for *D. corymbosa*, in other studies aboveground soils have exhibited similar macronutrient concentrations and cation ex-

change capacities but lower nitrification rates compared to those of the forest floor (Nadkarni 1984; Vance & Nadkarni 1990, 1992; Lesica & Antibus 1991; Nadkarni *et al.* 2002; Enloe *et al.* 2006). The positive correlation between *P. robustus* and soil volume in stem and pseudotrunk cavities lends support to Janzen's hypothesis that rotten tree cores are adaptive, becoming sources of nitrogen and other minerals that can be recycled via adventitious roots of the host tree (Janzen 1976). 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* is lower than that recorded for other tropical tree species (Vance & Nadkarni 1992), aboveground root densities are much higher, suggesting an intensification of root exploration in the aboveground soils. In other tree species, adventitious roots exploring aboveground soils are similar in structure and absorptive capacity to their belowground counterparts (Sanford 1987, Nadkarni & Primack 1989). Aggregations of fine roots in aboveground organic soils may reflect sites of nutrient release from decomposition (Jordan 1985, Turner 2001, Enloe *et al.* 2006). The ubiquitous presence of ectomycorrhizas in aboveground soils may indicate a direct pathway of nutrients from decomposing organic matter to *D. corymbosa* roots (Janzen 1976, Jordan 1985, Mayor & Henkel 2006).

Seed output and recruitment.—During the 2003 masting event, *D. corymbosa* seed production ranged from 66,000 to 161,000 seeds/ha, the majority contributed by large, multistemmed trees. The resulting seedlings contributed to an enormous standing recruitment bank of 41,000 to 92,000 seedlings and 1800–4500 saplings/ha one year post-mast (Henkel *et al.* 2005). The high level of sexual recruitment and cumulative reiteration exhibited by *D. corymbosa* may be a unique combination of life-history traits. Several temperate tree species that regularly reiterate 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; *Sequoia sempervirens*, S. Sillett, pers. obs.). Individual persistence and high sexual recruitment clearly reinforce *D. corymbosa* dominance in space and time (*sensu* Hallé 1978).

Evolutionary considerations.—In woody plants, the propensity for reiteration increases with increasing frequency of disturbance (Bond & Midgley 2003). For example, selection for vegetative sprouting in shrublands of South Africa is strongly tied to the frequency, severity, and consistency of fires (Bond & Midgley 2003). In Puerto Rico, basal sprouting of trees following hurricanes is proportional to the frequency or intensity of structural damage incurred in a stand (Van Bloem *et al.* 2005). Regarding the Guianas, where large-scale disturbances are rare and climatic conditions are stable (Davis 1941, Hammond & Brown 1998, Henkel 2003), the driving forces for the evolution of the reiterative habit of *D. corymbosa* are less clear.

Persistent infections with *P. robustus* may have provided a selective force for the evolution of sprouting in *D. corymbosa*. Sprouting in response to disease has been documented for some temperate trees (Koop 1987, Del Tredici 2001). The incidence of *P. robustus* in *D. corymbosa* is high; the majority of dead stems are infected and basidiomata also occur on living components of the trees. *Phellinus robustus* occurs on trees in all size classes, especially ≥ 105 cm basal diameter. There may thus be a long period of internal decay before signs and indications of *P. robustus* are evident (Hennon 1995). It is likely that many more *D. corymbosa* individuals contain *Phellinus* decay columns than are detectable without destructive sampling. 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 and may even spread through root-to-root contact (L. P. Woolley & T. W. Henkel, pers. obs.).

If *P. robustus* has been ubiquitous in monodominant *D. corymbosa* stands, could it have driven the evolution of reiteration in *D. corymbosa*? Given the presumed competitive advantage to *D. corymbosa* of growing in monodominant stands, perhaps an evolutionary arms race has developed with *P. robustus* in which the fungus acts as a 'frequent disturbance factor' within dense stands of susceptible hosts. One method for the tree to increase survivorship and evolutionary fitness under these circumstances would be to invest heavily in sprouting and thus spreading the risk of infection and genet mortality among many stems. In this adaptive response scenario trees with sprouting genotypes would be more likely to sexually reproduce over time.

Given the apparent ubiquity of heart rot in tropical trees (Janzen 1976) why might other tropical trees lack such a reiterative strategy? The ability to reiterate varies not only with the type and frequency of disturbance but also with the age or size of the plant. From a mechanistic standpoint, the number of epicormic buds produced by a tree species is genetically determined (Ashton *et al.* 1990) and the degree of sprouting is related to the number of epicormic buds present (Krajicek 1959, Kormanick & Brown 1964, Bachelard 1969, Lacey & Johnston 1990). Many tropical and temperate trees retain the ability to sprout from the seedling to sapling stage but lose this ability as adults, perhaps due to a decline of epicormic buds (Del Tredici 2001, Bond & Midgley 2003). *Dicymbe corymbosa* retains the ability to sprout into adulthood, likely from persistence and possibly *de novo* synthesis of epicormic buds, making it well suited to overcome the destabilizing effects of heart rot decay in older stems.

The release of epicormic buds in *D. corymbosa* may be induced by increased production of ethylene resulting from tissue damage by *P. robustus*. Epicormic buds are suppressed by auxin, a phytohormone basipetaly transported in trees exhibiting apical control (Zimmermann & Brown 1971). Increased ethylene levels reduce the influence of auxin and suppress apical control in plants infected with fungi (Byrde & Cutting 1973, Wood 1985, Abeles *et al.* 1992, Kozlowski & Pollardy 1997, Sanyal & Bangerth 1998, Hudgins & Franceschi 2004). While we have no direct evidence of such a mechanism in *D. corymbosa*, given the ubiquity of *P. robustus* infec-

tions this model could explain the regular epicormic sprouting seen in otherwise undamaged individuals of the species.

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CORRECTION

The following reference: Sillett, S.C., Van Pelt, R. 2007. has been updated in the Literature Cited.

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