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Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae) from Guyana

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Abstract: Dominance of primary rain forests by the ectomycorrhizal, leguminous canopy tree *Dicymbe corymbosa* (Caesalpiniaceae) was investigated in the Pakaraima Mountains of western Guyana. In five 1-ha forest inventory plots in the Upper Ireng and Upper Potaro River drainages basal areas of *D. corymbosa* ranged from 38.4–52.8 m^2 ha^{-1} (63–85% of total) among all trees ⩾10 cm diameter at breast height (dbh), values in the upper range for tropical moist forests worldwide. The high basal areas for *D. corymbosa* were due to the prevalence of large (>150 cm dbh), multi-stemmed individuals. Stem densities in *Dicymbe* plots ranged from 276–433 ha^{-1}, with *D. corymbosa* contributing 24.6–59.8%. In three 1-ha mixed forest plots adjacent to the *Dicymbe* plots, *D. corymbosa* was absent. In the mixed forests, stem densities were higher (480–585 ha^{-1}), basal areas were lower (36.7–39.8 m^2 ha^{-1}), species diversity was higher, and canopy tree species were more equitably distributed than in the *Dicymbe* plots. Tree community composition was not qualitatively different between *Dicymbe* and mixed forests. In the *Dicymbe* plots, mean sapling and seedling densities of *D. corymbosa* were significantly higher than most other canopy species, indicating persistent monodominance. Edaphic variation did not account for variation in forest composition. Life history traits are discussed which may contribute to clumping in *D. corymbosa*, including coppicing and mast-fruiting, and the potential role of litter-trapping physiognomy and ectomycorrhiza-mediated nutrient dynamics in promoting monodominance is noted.

Key Words: Caesalpiniaceae, ectomycorrhiza, forest ecology, Guyana, monodominance, Neotropics

INTRODUCTION

Early accounts of forest dominance by tropical tree species were given 50 years ago by P. W. Richards in his landmark book on rain-forest ecology (Richards 1952). In subsequent decades more examples have come to light in which a single, late-successional canopy tree species strongly dominated significant areas of forest in both the Palaeotropics and Neotropics (for reviews see Connell & Lowman 1989, Hart 1990, Richards 1996*a*). If the dominant species comprises ~60% or more of the number of canopy individuals or basal area (or both) of a given stand that species can be considered *monodominant* (*sensu* Connell & Lowman 1989). Some tropical monodominant forests are on sites with impeded drainage and are explained by adaptations of the dominant species to soil inundation, or are non-persistent successional seres (Richards 1996*a*). Of particular ecological interest are old-growth monodominant forests on well-drained upland sites, often occurring in close proximity to species-rich mixed forests. Such forests are persistently monodominant when the dominant species successfully recruits and replaces itself under its own canopy (Connell & Lowman 1989). Well-known persistent dominants in the Asian tropics are in the family Dipterocarpaceae (e.g. *Dryobalanops aromatica*, Whitmore 1984) while those in the African tropics and the Neotropics are primarily in the leguminous family Caesalpiniaceae (e.g. *Gilbertiodendron dewevrei* in Africa, Hart *et al*. 1989; *Mora excelsa* in Trinidad, Beard 1946; and *Peltogyne gracilipes* in Brazil, Nascimento *et al*. 1997; for examples in other families see Connell & Lowman 1989).

Monodominant forests contrast sharply with the otherwise extraordinarily high tree species richness in the tropics, and in attempts to explain tropical diversity they have traditionally been ignored or predicted not to exist (Connell 1971, Janzen 1970, MacArthur 1970). Monodominant forests present one of the more intriguing enigmas in tropical ecology (Schluter & Ricklefs 1993), and a growing number of studies have attempted to unravel the mechanisms contributing to the origin and maintenance of tropical monodominance (Gross *et al*. 2000, Hart 1995, Hart *et al*. 1989, Kachi & Okuda 1993, Martijena 1998, Nascimento & Proctor 1997*a*, Nascimento *et al*. 1997, Torti & Coley 1999, Torti *et al*. 2001). Proposed causal factors range from a single life history

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trait of the dominant species (e.g. the ectomycorrhizal habit; Connell & Lowman 1989) to a suite of traits (e.g. mast fruiting, low seed predation, shade tolerance, etc.; Hart *et al*. 1989, Torti *et al*. 2001) but a consensus has yet to be reached (Henkel *et al*. 2002, ter Steege & Hammond 2000).

The forests of Guyana provide important examples of neotropical forest dominance and studies of their ecology may further elucidate mechanisms leading to monodominance. The Guiana Shield region of north-eastern South America possesses lower overall tree species richness than equivalent areas of western or central Amazonia (Terborgh & Andresen 1998, ter Steege *et al*. 2000). Within this matrix of lower tree diversity (by Amazonian standards) local sites may be dominated by one or a few canopy species. Early examples documented in Guyana by Davis & Richards (1933, 1934) and corroborated by later studies included stands where > 40% of canopy trees comprised either *Mora excelsa*, *Mora gonggrijpii*, *Eperua falcata* (Caesalpiniaceae) or *Chlorocardium rodiei* (Lauraceae) separated locally along gradients of soil chemistry and drainage, while occasionally interspersed with mixed rain forests having no clear dominants (Clarke *et al*. 2001, Fanshawe 1952, ter Steege *et al*. 1993). Such patterns of local tree dominance characterize much of Guyana's near interior and explanations have centred around environmental stability and low disturbance regimes leading to competitive exclusion (Davis 1941, Hammond & Brown 1995, ter Steege & Hammond 2000).

Striking but poorly documented examples of monodominance in Guyana are found in species of *Dicymbe* Spruce ex Benth. (Caesalpiniaceae, tribe Amherstieae). *Dicymbe* is endemic to the greater Guiana Shield region and most of the 19 described species are small trees found in xeromorphic woodlands of eastern Venezuela (Steyermark *et al*. 1998). However, *Dicymbe altsonii* Sandw. and *Dicymbe corymbosa* Spruce ex Benth. are canopy trees which form extensive stands at lower elevations of the Pakaraima Mountains and outlying regions of west-central Guyana. *Dicymbe altsonii*-dominated forests were first referred to by Fanshawe (1952) and later shown to achieve moderate dominance levels (40–50% of stand basal area) (Isaacs *et al*. 1996, Zagt 1997*a*). Forests dominated by *D. corymbosa* were first noted by Myers (1936) but dominance levels have not been adequately quantified (Richards 1952, 1996*a*). Field observations from the interior Pakaraima Mountains have suggested that *D. corymbosa* reaches very high levels of dominance, and has unusual traits which might contribute to its dominance, including coppice shoot formation, mast-fruiting and an ectomycorrhizal habit (Henkel *et al*. 1993, 2002; Hoffman & Henkel 1992, Myers 1936, Richards 1952).

Many of these life history traits of *Dicymbe* characterize the caesalpinioid tribe Amherstieae, species of which form the majority of monodominant forests in Guinea-Congolian Africa (Alexander 1989). The best-known Amherstieae monodominant, *Gilbertiodendron dewevrei*, reaches extreme monodominance (> 90% of canopy trees) with abundant recruitment of seedlings and saplings (Hart *et al*. 1989). Other Amherstieae monodominant forests in Africa exhibit these patterns, and generally lack edaphic specificity (Conway & Alexander 1992, Newbery *et al*. 1988). These features have led to the suggestion that biotic interactions control the occurrence and distribution of African monodominant forests (Hart *et al*. 1989, Torti *et al*. 2001). Intriguingly, *Dicymbe* is the only genus of Amherstieae known to form monodominant forests in the New World. These facts, along with the role of *Dicymbe* forests as exclusive habitats for endemic ectomycorrhizal fungi (Henkel 1999, 2001; Henkel *et al*. 2000, 2002; Miller *et al*. 2001), argue for detailed investigation into the composition and structure of these unusual forests.

This study explored monodominance in *D. corymbosa* through an extensive dataset compiled from eight 1-ha forest inventory plots in the Pakaraima Mountains of Guyana. Specific questions addressed were: (1) To what degree does *D. corymbosa* dominate forests? (2) Is *D. corymbosa* dominance persistent? (3) Are *D. corymbosa* forests compositionally and structurally different from adjacent mixed forests? (4) Do edaphic factors influence forest composition in *D. corymbosa* stands and adjacent mixed forests? (5) What above- and below-ground characteristics could potentially contribute to *D. corymbosa* dominance?

STUDY AREA

The current study was conducted during 1999–2000 in the central Pakaraima Mountains of western Guyana (general area: 5°05′N; 59°58′W; Figure 1). Two sites previously observed to have co-occurring *Dicymbe* forests and mixed forests were chosen for the establishment of study plots: (1) The Upper Ireng River basin in the vicinity of Mt Wokomung; and (2) the Upper Potaro River basin in the vicinity of Mt Ayanganna (Figure 1). These two sites are separated by a linear distance of ~35 km across a regional watershed divide, with the Potaro N–NE of the Ireng site. Details of the geology, soils, climate and vegetation of the Ireng site can be found in Henkel *et al*. (1993, 2002). Both sites are situated in intermountain valleys at 700–800 m elevation on hilly terrain adjacent to main river courses, and are densely forested with a mosaic of mature *Dicymbe*-dominated and mixed forest stands. Obvious signs of prior anthropogenic disturbance were absent from both sites. Upland soils at both sites are grey and brown sands derived from sandstone parent materials, with occasional ridges of lateritic red clays and loams derived from igneous intrusions (Henkel *et al*., *pers. obs*.). Precipitation is estimated at 3500–4000 mm annually for both sites, with peaks during May–July and December–January; no

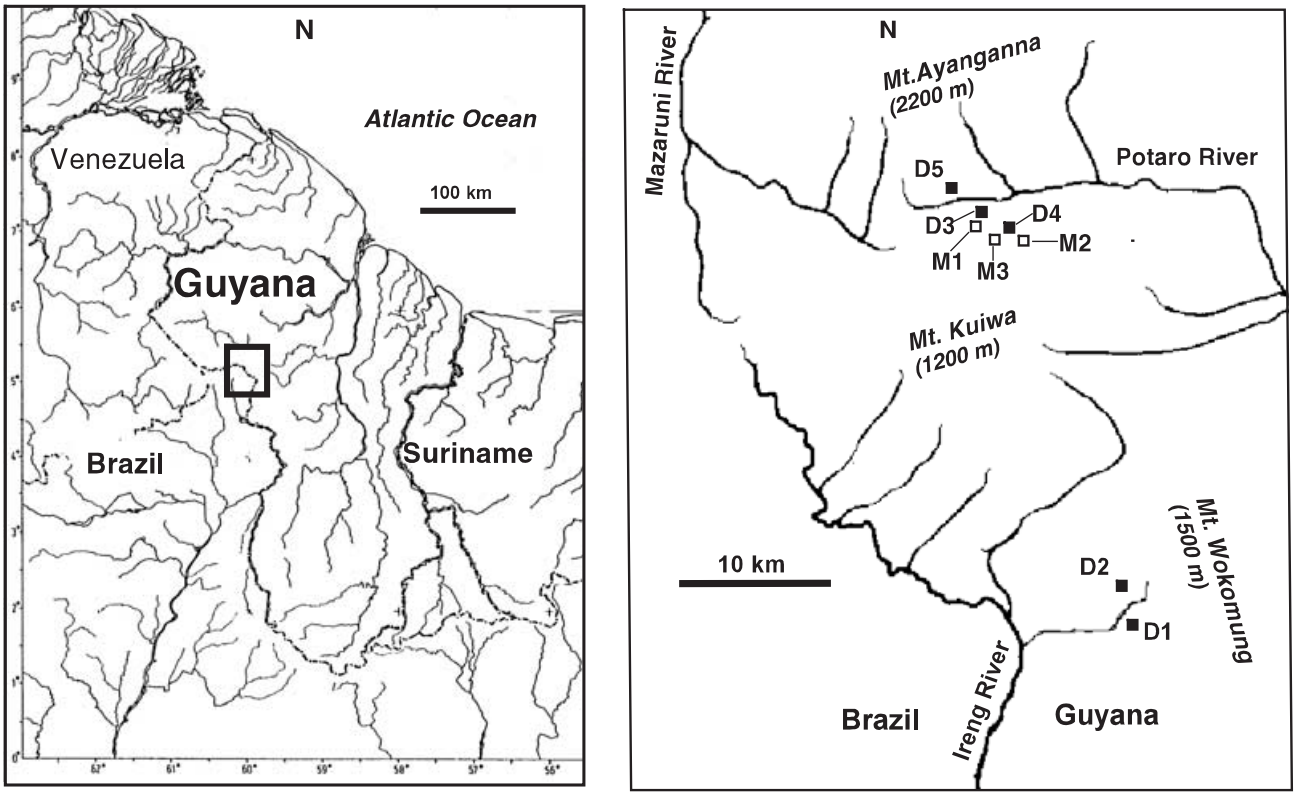

Figure 1. Maps of the research location in the Pakaraima Mountains of western Guyana, and location of study plots in the Upper Ireng and Upper Potaro River drainages. Squares denote 1-ha plots (not to scale). Plot designations are: D1–D2: Ireng *Dicymbe* forests; D3–D5: Potaro *Dicymbe* forests; M1–M3: Potaro mixed forests.

months experience less than 100 mm precipitation (Fanshawe 1952, Henkel *et al*. 2002).

METHODS

Study plots

Ireng site. Two 1-ha plots were established in *Dicymbe* forest at the Ireng site during May–June of 1999 (Figure 1). Logistical limitations prevented the establishment of more than two plots at the Ireng site. Both plots were located in an upland area previously determined to have a high proportion of homogeneously distributed *D. corymbosa* (Henkel *et al*. 1993). Plot positions were randomly chosen and adjusted somewhat to account for landscape irregularities (e.g. larger creek beds, rock outcrops). *Dicymbe* plot 1 (hereafter referred to as D1) was situated on a gently NW–SW slope 200 m west of Suruwabaru Creek. D1 was delimited as a square, 100 m on a side. D1 was divided and marked into one hundred 10×10-m subplots. All trees $\geqslant$ 10 cm diameter at breast height (dbh; 1.3 m above the ground) were marked and measured for dbh. Trees with buttresses at 1.3 m were measured immediately above the buttresses. For individuals of *D. corymbosa* that exhibited multiple shoots below the 1.3 m level, diameter of each shoot was measured and assigned as a series of diameters for that individual. *Dicymbe corymbosa* trees that were not coppiced or had coppiced above the 1.3 m level were measured as a single trunk. Coppice shoots are here defined as epicormic stem sprouts arising from the tree trunk, not in response to damage or cutting. Trees were assigned to families and identified to genus and species when possible, or otherwise assigned to morphospecies according to the guidelines of Richards (1996*b*). Basal area and number of stems were calculated for each tree species in the subplots. For coppiced individuals of *D. corymbosa*, basal area was calculated for each shoot and summed to give basal area per individual. For these individuals the number of coppice shoots of all diameters was recorded.

Dicymbe plot 2 (D2) was located ~1 km north of D1 on an upland, gentle E–W slope adjacent Yuarka Creek. This plot was also delimited as a square in an area of homogeneous *Dicymbe* forest, and divided into 100 equal subplots. No rock exposures were present in the plot and drainage was uniformly good. Trees were sampled as described for D1.

Potaro site. In order to allow comparison of Dicymbe with mixed forest, an array of six 1-ha plots (three *Dicymbe*, three mixed) was established in May–June 2000 within a

5-km radius of a base camp along the Upper Potaro River (Figure 1). Plot positions for both *Dicymbe* and mixed forests were randomly chosen within larger areas (> 3 ha) perceived as having homogeneous coverage of the respective primary forest type, away from sharp transitional edges to other forests (see Henkel *et al.* 2002). *Dicymbe* plot 3 (D3) was located on a ridge top (800 m elevation) 2 km south-east of the base camp and was delimited as a rectangle 250 × 40 m. D3 had frequent exposures of small sandstone boulders interspersed with lateritic ironstone. Soils were relatively thin. *Dicymbe* plot 4 (D4) was located ~1 km east of D3 on a gentle W–E slope, and was delimited as a 200 × 50-m rectangle. Soils at D4 were red clay-loams with no rock exposures. *Dicymbe* plot 5 (D5) was at an outlying position across the west bank of the Potaro River ~5 km W–SW of the base camp. D5, also 200 × 50 m, was on a gentle W–SW slope with frequent small lateritic exposures and abundant ironstone gravel present in the otherwise red silty-loam soils.

Mixed-forest plot 1 (M1) was located on the same ridge as D3 adjacent to a sharp N–S transition between *Dicymbe* and mixed forest (Figure 1). M1 was 250 × 40 m, with red, loamy soils and infrequent rock exposures. Mixed-forest plot 2 (M2) was located 0.5 km further east from D4 beyond an extensive, sharp transition between the two forest types. M2 contained numerous sandstone boulders but no lateritic exposures, with uniformly reddish loamy soils. M2 was delimited in two adjacent units; the first a 150 × 50-m unit on a gentle W–E slope, and the second 50 × 50-m unit immediately to the north of the first; the plot was split in this manner to account for the presence of a large sandstone outcrop which resulted in discontinuities in the vegetation. Mixed plot 3 (M3) was located 0.5 km southwest of M2 on a gentle N–S slope. M3, 200 × 50 m, was bisected by a small, intermittent stream with small sandstone exposures, with red loamy soils lacking laterite.

Soils in all Potaro plots had no signs of impeded drainage. Potaro plots were subdivided into 10 × 10-m subplots, woody vegetation was enumerated, and voucher specimens collected in the manner described above.

Family and generic taxonomy for woody taxa followed that based on vegetative characters of Gentry (1996) except for Caesalpiniaceae (Cowan & Lindeman 1989). Vernacular names applied by Amerindian tree spotters were used in consultation with published lists by Fanshawe & Mennega (Mennega *et al.* 1988). Further identification of primarily sterile voucher collections was facilitated by comparison with herbarium specimens at the University of Guyana and the US National Herbarium, and consultation with the *Flora of the Guianas* series, the *Flora of the Venezuelan Guayana* and Boggan *et al.* (1997). Voucher specimens for all species and morphospecies were deposited at the University of Guyana (BRG) and the US National Herbarium (US). A list of all species/morphospecies with voucher collection numbers is available upon request from the author.

Coppicing structure of *Dicymbe corymbosa*

Additional data were obtained to provide a more exact picture of coppicing structure of mature *D. corymbosa* than that obtained on the plots. In a 5-ha area of old-growth *Dicymbe* forest surrounding the Potaro base camp, 20 *D. corymbosa* trees ⩾ 100 cm in basal diameter (i.e. diameter immediately below the first coppice split) were randomly chosen using the point-quarter method (Greig-Smith 1983). For these trees, basal diameter, height above ground level where the first split in the trunk occurred and diameter of all coppice shoots were obtained. Diameter of coppice shoots was measured immediately above the point of attachment to the trunk. Shoots were counted as 'canopy' shoots if some portion of their leaf-bearing column reached the upper stratum ~15–30 m in height. 'Non-canopy' shoots were those that did not reach the upper stratum.

Seedlings and saplings

Seedlings and saplings of woody vegetation were sampled in each 1-ha plot at the Ireng and Potaro sites. Saplings were defined as woody individuals ⩾ 1 m in height but < 10 cm dbh (= small saplings plus poles). For each plot ten 10 × 10-m subplots were randomly chosen (total sampling area = 0.1 ha per plot) and saplings of all individuals occurring in each subplot were identified to species/morphospecies and counted. Seedlings were defined as woody individuals of mid-storey and canopy species < 1 m in height. For each of the six Potaro plots seedlings of all species/morphospecies were indentified and enumerated for each of the 10 × 10-m subplots used for sapling enumeration. Due to extremely high seedling densities on the two Ireng *Dicymbe* plots, seedlings were enumerated in 5 × 5-m subplots randomly nested within the ten 10 × 10-m subplots used for sapling counts (total sampling area = 0.025 ha per plot).

Soil sampling

Edaphic variability among the *Dicymbe* and mixed forests was assessed with soil samples taken from each of the eight plots. For each Ireng *Dicymbe* plot A-horizon subsamples were collected at a 10 cm depth in the mineral soil beneath the leaf litter at four randomly chosen points within each of ten randomly positioned 10 × 10-m subplots. These subsamples were bulked, air-dried and passed through a 2-mm sieve to produce a final 100-g sample per subplot, n = 10 per plot. Depth of the litter layer (= O horizon humic layer + recently fallen leaves) above the

mineral soil was measured at each soil collection point to yield n = 20 per plot. On the Potaro plots, soil was sampled with the same technique but sample size was reduced to five per plot due to logistical and cost considerations. Upon returning from the field all soils were stored at 5 °C until analysed.

Soil texture was determined using standard particle size analysis (ASTM 1998); extractable P, Al, Ca, K, Mg and Na using the Mehlich III extraction (Mehlich 1984); soluble NO_3-N and NH_4-N using a 2N KCL extraction (Dahnke 1990); pH using the methods of McLean (1982), organic matter using ashing procedures (Storer 1984) and cation exchange capacity (CEC) using a modified summation of the Mehlich III-extracted cations and hydrogen (Sumner & Miller 1996).

Data analyses

Basal area, stem density and frequency (% of subplots occurring in) per plot were calculated for woody species $\geqslant$ 10 cm dbh. Relative density and frequency of saplings and seedling species were calculated for their subsampled areas. Means for normally distributed soil parameters were compared between plots using ANOVA and Tukey–Kramer's multiple comparison; for those non-normally distributed the Kruskal–Wallis test was used (Sokal & Rohlf 1995). Litter-depth data were log-transformed and analysed with ANOVA followed by Tukey–Kramer's. Diameter class distributions for trees $\geqslant$ 10 cm dbh were plotted for all plots. Dominance and equitability among tree species in *Dicymbe* and mixed forests were plotted with dominance–diversity curves based on basal area and stem number, which rank the 'most important' (i.e. species with the highest parameter value) to the 'least important' species in each plot (Greig-Smith 1983). Density–diversity curves were plotted for seedlings and saplings. Linear regression was employed to examine relationships among trunk and coppice shoot structure in *D. corymbosa*.

Similarity of tree community compositions for two plot combinations were assessed using Jaccard's index of similarity, *J*, which is calculated as: $J = a/(a + b + c)$, where *a* is the number of species common to both plots, *b* is the number of species restricted to the first plot and *c* is the number of species restricted to the second plot (Pielou 1984). In addition, the similarity of tree species compositions of Potaro *Dicymbe* forests was compared with that of Potaro mixed forests using a simple Mantel test (Mantel 1967). The Mantel test involves measuring the association between the elements present in two data matrices by a suitable statistic, then assessing the significance of this statistic by comparison with the distribution found by randomly reallocating the order of the elements in one of the matrices (Douglas & Endler 1982). Data matrices for *Dicymbe* and mixed forests were based on presence/absence of each of the 150 trees species that occurred in plots of the respective forest types. For the Mantel test, Jaccard's coefficient was chosen as a distance measure, and an asymptotic approximation algorithm was employed (Douglas & Endler 1982). The Ireng *Dicymbe* plots (n = 2) were not included in the Mantel test because equal sample sizes are required in the similarity matrices.

Species richness was listed for each plot. Diversity indices incorporating species richness and equitability were employed to compare tree species diversity among the plots (Peet 1974). These included H', the Shannon–Weaver Diversity Index, using the equation $H' = -\Sigma\ p_i \log p_i$, where p_i corresponds to the probability of sampling the *i*th species among all species in a sample, i.e. the *i*th species' proportion of a total for some importance value, which can be number of individuals or basal area (Pielou 1977). *D*, the Simpson's Index, uses $D = 1 - [\Sigma n_i(n_i-1)/N(N-1)]$, where n_i equals the number of individuals of the i^{th} species in a sample, and N equals the total number of individuals (all species) in the sample. D allows estimation of sample heterogeneity by determining the probability that any two individuals drawn randomly from the sample will belong to different species (Greig-Smith 1983). In general, H' is more affected by rare species and D is more sensitive to changes in the most common species (Peet 1974).

RESULTS

General description of *Dicymbe* forests

Forest physiognomy. In all of the *Dicymbe* study plots forest physiognomy was similar. The upper canopy reached 25–30 m, generally of even height due to the abundance of mature *D. corymbosa* trees (Figure 2). Isolated mature trees of co-occurring canopy species were occasionally emergent to 35–40 m. Epiphytes were sparse due to the vertical branching patterns of *D. corymbosa*; those present were primarily bole-attached *Tillandsia* spp. (Bromeliaceae). Large lianas of *Doliocarpus brevipedicellatus* Garcke (Dilleniaceae) were occasionally observed. The midstorey at 10–25 m was quite open, composed largely of younger-generation coppice shoots from the mature *D. corymbosa* trees, with scattered younger individuals of *D. corymbosa* interspersed with *Licania* spp. (Chrysobalanaceae), *Eschweilera sagotiana* Miers (Lecythidaceae) and other associates. The understorey below 10 m was sparsely stocked, aside from *D. corymbosa* saplings, with understorey associates such as *Duguetia* and *Guatteria* spp. (Annonaceae), *Duroia hirsuta* K. Schum. (Rubiaceae) and various Melastomataceae. Ground cover consisted of frequently dense concentrations of *D. corymbosa* seedlings interspersed with scattered seedlings of other woody species. True ground herbs were wanting except for *Calathea* spp.

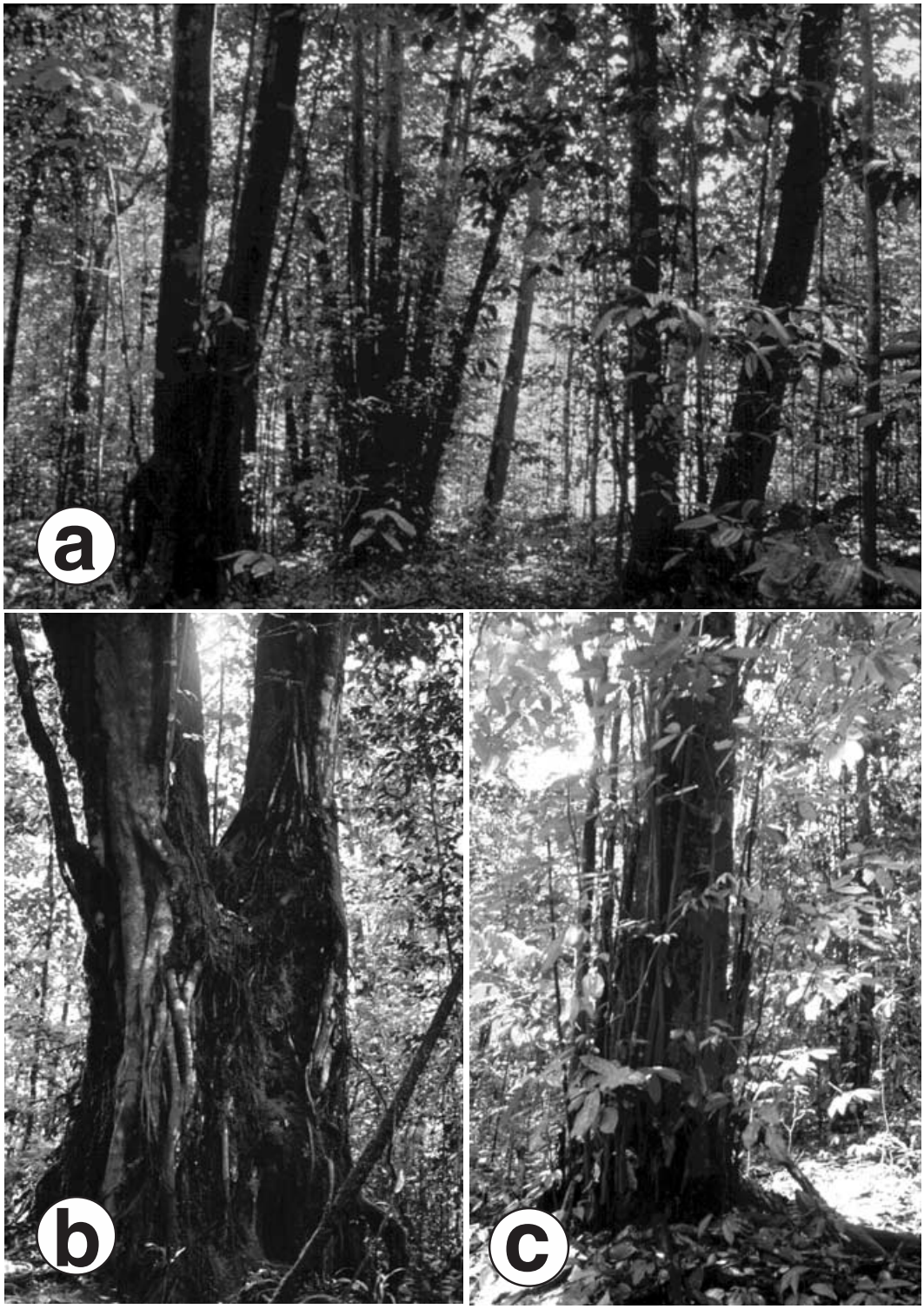

Figure 2. Physiognomy of *Dicymbe* monodominant forests. (a) Forest aspect; Upper Ireng River, Guyana. (b) Mature *Dicymbe corymbosa* with well-developed canopy shoots and large basal trunk, ~2.0 m dbh; Upper Potaro River. (c) Immature *Dicymbe corymbosa* with young coppice shoots emerging from base; Upper Ireng River.

(Marantaceae) and *Rapatea* spp. (Rapateaceae) along small watercourses.

Physiognomy of Dicymbe corymbosa. Mature *D. corymbosa* trees exhibited a 'candelabra' physiognomy consisting of multiple large, outward-spreading shoots emerging from a large basal trunk (~0.75–2.0+ m diameter). These large canopy shoots were roughly 0.2–0.6 m in diameter and bore reiterating, vertically arranged branches above the midpoint, the sum effect being a leaf-bearing crown 15–20 m in diameter (vertically and horizontally; Figure 2). Crown and midstorey shoots were subtended by a usually dense concentration of shoots < 5 cm in diameter which functioned as a perfunctory 'understorey'. Instances where these basal shoots had grown upwards into gaps created by fallen canopy shoots were regularly observed. In the largest and presumably oldest individuals the original generation of canopy shoots had apparently all died, as evidenced by fallen, decomposed shoots, succeeding coppice generations had reached canopy levels, and the basal trunk had been maintained by the grafting and expansion of shoot bases. The interior trunk of these ancient individuals was often hollow.

Crotches formed between the iterating shoots accumulated large amounts of leaf litter and thick humic masses, these being invaded by adventitious roots derived from the adjacent cambium up to 5 m above ground level. These humic mats were also invaded by vertically ascending roots from neighbouring conspecific trees.

In mature *D. corymbosa* trees a large basal root mound was formed by the development of adventitious secondary and tertiary roots from the trunk base, which through anastomosis and thickening ultimately yielded a mound 1–2 m in height (Figure 3). The basal root mound appeared to function as a litter trap. Accumulations of mor-like humus in the mounds were 0.5–1 m thick and permeated by dense concentrations of ectomycorrhizal rootlets (Figure 3). Outward from the basal root mound, root systems of large *D. corymbosa* trees spread along the soil surface and comingled with those of surrounding conspecifics to create a springy root mat throughout the forest, with humic accumulations present but less thick than those near the tree bases.

Physiognomy of young Dicymbe. *Dicymbe corymbosa* seedlings developed vertically into single-stemmed saplings and poles. Coppice shoot formation appeared to initiate when trees reached the subcanopy at about 15 m height (10–30 cm dbh). At this stage basal suckers emerged and grew upwards, tightly arranged around the main stem. The onset of root-mound formation was evident at this stage by the emergence of thick masses of geotropic adventitious roots from the basal cambium (Figure 3).

Floristic diversity

A total of 3293 trees ⩾ 10 cm dbh comprising 150 species, 89 genera and 39 families was found in the 8 ha of forest sampled at the Ireng and Potaro sites (Table 1).

Dicymbe *forest.* In the 5 ha of *Dicymbe* forest a total of 1689 trees was recorded, comprising 81 species, 65 genera and 33 families (Table 1). Due to the high densities of *D. corymbosa*, Caesalpiniaceae contributed the greatest number of individuals on all *Dicymbe* plots (38–59.9% of total).

Mixed forest. In the 3 ha of mixed forest sampled a total of 1604 trees were recorded, comprising 120 species, 75 genera and 34 families (Table 1). Species were considerably more equitable than in the *Dicymbe* forests, with eight families contributing at least 4% of individuals. The most abundant families were Chrysobalanaceae (primarily *Licania* spp.), contributing 12–18% of individuals per ha, and Lecythidaceae (*Eschweilera sagotiana*), contributing 4–20.4% of individuals per ha.

Species richness and diversity

Tree species richness ranged from 37–56 species per ha in *Dicymbe* forests and 70–91 species per ha in the mixed forests (Table 1). Among the *Dicymbe* forests species richness was lowest for the Ireng plots, although these plots were not compared statistically with the Potaro plots due to the inadequate sample size (n = 2). Mean species richness and H′ diversity indices were significantly lower for Potaro *Dicymbe* plots compared with the mixed forests; mean Simpson's D values were not significantly different (Table 2).

Tree community similarity

Jaccard's similarity values for interplot comparisons ranged from 0.17 (D2 vs. M2) to 0.54 (M2 vs. M3). Interplot comparisons involving D1 and D2, the least diverse plots, yielded the lowest Jaccard values (0.17–0.33). Values were generally lower for comparisons between forest types, and higher within forest types. Relative high between-forest values were seen in two comparisons, D4 vs. M2 (0.43) and D4 vs. M3 (0.48).

The Mantel test indicated that tree community compositions (based on species presence or absence) of the Potaro *Dicymbe* and mixed forests were significantly similar (standardized Mantel statistic $r = 0.983$; $P < 0.003$).

Forest composition and structure

Dicymbe *forests.* Of the 1689 trees ⩾ 10 cm dbh recorded on the five 1-ha Ireng and Potaro *Dicymbe* plots, 737

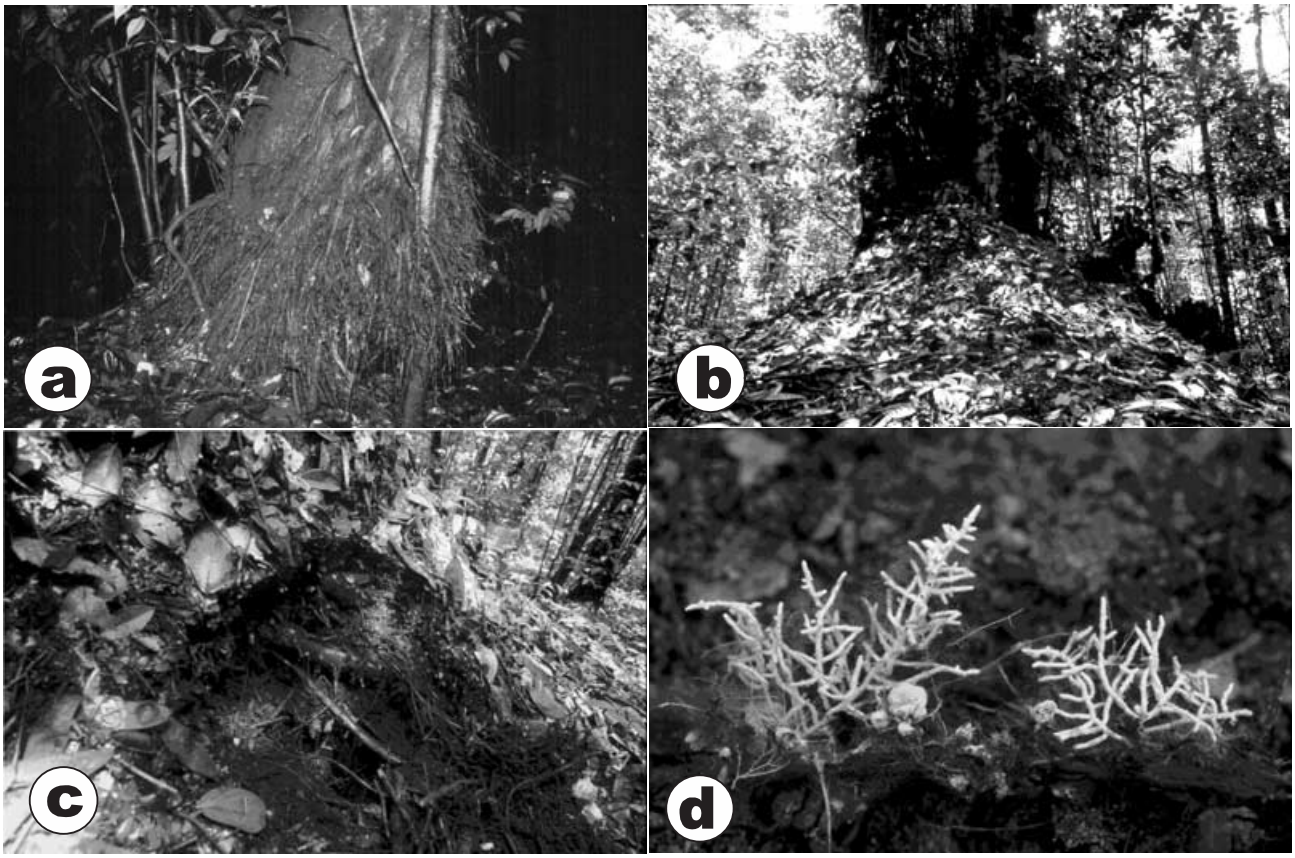

Figure 3. Root mound formation and ectomycorrhizae in *Dicymbe corymbosa*. (a) Geotropic adventitious roots emerging from base of immature *Dicymbe corymbosa*; Upper Ireng River. (b) Large conical root mound subtending base of mature *Dicymbe corymbosa*; Upper Ireng River. (c) Excavation of root mound pictured in b, revealing thick accumulations of mor humus; Upper Ireng River. (d) Ectomycorrhizal rootlets of *Dicymbe corymbosa*, × 2.5; Upper Potaro River.

Table 1. Number of individuals, basal area and taxonomic diversity of woody plants ⩾ 10 cm dbh on eight 1-ha plots[1] at the Ireng and Potaro sites, Pakaraima Mountains, Guyana.

Site	Plot	Number of trees		Basal area (m^2)		Species[2]	Genera[3]	Families[3]
		All spp.	*Dicymbe corymbosa*	All spp.	*Dicymbe corymbosa*			
Ireng	D1	276	152	62.1	52.8	37	25	22
	D2	284	170	54.1	45.0	44	32	24
Potaro	D3	325	175	61.6	51.3	50	37	26
	D4	371	91	61.6	46.1	56	38	23
	D5	433	149	61.2	38.4	51	37	24
	M1	585	–	36.7	–	91	58	30
	M2	480	–	39.8	–	70	48	25
	M3	539	–	39.4	–	74	48	28
	Total	3293	737	416.5	233.6	150	89	39

[1] Plot designations are: D1–D2: Ireng *Dicymbe* forest; D3–D5: Potaro *Dicymbe* forest; M1–M3: Potaro mixed forest.
[2] Identified at the species/morphospecies level, including family indets.
[3] Does not include family indets.

(43.6%) were *D. corymbosa*. Of the 301 m^2 of total basal area occurring on these five plots, *D. corymbosa* contributed 234 m^2 (77.7%). Basal area values for *D. corymbosa* were consistently high among the plots (38.4–52.8 m^2 ha^{-1}; 62.9–85% of total) although the number of individuals was variable (91–175 ha^{-1}) (Table 1). The most abundant co-occurring canopy species varied somewhat between the plots but usually included *Miconia* aff. *guianensis* (Melastomataceae), *Licania laxiflora* (Chrysobalanaceae), *Eschweilera sagotiana* (Lecythidaceae) and *Macrolobium* sp. 1 (Caesalpiniaceae) (Table 3). Major canopy species co-occurring with *D. corymbosa* were

Table 2. Tree species diversity of *Dicymbe* forests and mixed forests[1] at the Ireng and Potaro sites, Pakaraima Mountains, Guyana.

Forest	Species ha^{-1} Mean (SEM)	H'(ind.) Mean (SEM)	H'(ba) Mean (SEM)	D_s Mean (SEM)
Dicymbe forest (Ireng)	40.5 (3.5)	0.87 (0.03)	0.26 (0.02)	0.65 (0.03)
Dicymbe forest (Potaro)	52.3 (1.9)	1.17 (0.08)	0.58 0.09)	0.82 (0.06)
Mixed forest (Potaro)	78.3 (6.4)	1.53 (0.03)	1.47 (0.1)	0.94 (0.009)
P[3]	< 0.02	< 0.02	< 0.002	NS

[1] Values shown are mean and standard error of the mean (SEM) calculated from two 1-ha plots at the Ireng site, and three 1-ha plots each of *Dicymbe* forest and mixed forest at the Potaro site.
[2] Calculated diversity indices are the Shannon–Weaver diversity index (H'), $-\Sigma(n_i/N)\log(n_i/N)$, and Simpson's diversity index (D_s), $1-\Sigma[n_i(n_i-1)/N(N-1)]$ where n_i is the number of individuals of species i and N is the total number of individuals; H' (ba) was calculated using basal area in place of number of individuals. Only stems ⩾ 10 cm diameter at breast height were included.
[3] Differences between *Dicymbe* and mixed forests were compared for plots (n = 3 for each forest type) at the Potaro site, using Student's t-test, df = 2.

more abundant and equitably distributed in D4 and D5 compared to other *Dicymbe* plots (Table 3). Dominance–diversity curves for the five combined *Dicymbe* plots demonstrated a clear prevalence of *D. corymbosa*, in terms of number of trees and basal area (Figure 4a, b).

Diameter class structure for trees ⩾ 10 cm dbh for *D. corymbosa* contrasted with that of the combined individuals of co-occurring species (Figure 5a). In *Dicymbe* forest the smaller diameter classes exhibited higher proportions of non-*Dicymbe* species, but as diameter class increased *D. corymbosa* became prevalent. Large (> 100 cm dbh) and extremely large (> 150 cm dbh) *D. corymbosa* trees were numerous on all plots. The largest *D. corymbosa* found on the plots had a dbh of 255 cm, on D3.

Coppicing was abundant on *D. corymbosa* trees in all plots (Table 4). Of the 737 *D. corymbosa* trees occurring on the Ireng and Potaro plots, 540 (73.3%) had at least two epicormic shoots at the 1.3 m height level. These values were an underestimate as coppice shoots arising above the 1.3 m level were not recorded. On the 540 coppiced individuals, 2990 shoots < 10 cm diameter and 1080 ⩾ 10 cm diameter were recorded. The proportion of individuals coppiced at the 1.3 m height level was higher for the Potaro plots. The number of coppice shoots ⩾ 100 cm diameter ranged from 12–18 per plot. The random sample of 20 large *D. corymbosa* trees outside of the plots showed that the average number of shoots per tree reaching the canopy was 4.1 with an average diameter per shoot of 38.8 cm; average number of non-canopy shoots was 20.2 (Table 5). Two standing-dead canopy shoots were recorded on these 20 trees. Average trunk diameter for these trees was 154.5 cm with an average height of trunk split of 114.8 cm. Basal diameter was positively correlated with the number of canopy shoots ($r = 0.53$, $P < 0.02$).

Mixed forests. A total of 1604 individual trees were recorded in the three 1-ha mixed-forest plots. Stem densities/ha were higher and basal areas/ha lower compared with the *Dicymbe* plots (Table 1). Mixed forests exhibited more equitable densities and basal areas among the prevalent canopy species, without pronounced dominance by any species (Table 3, Figure 4). Prevalent canopy species included many of the common associates of *Dicymbe* forests such as *L. laxiflora*, *E. sagotiana*, *Protium decandrum* (Burseraceae) and *Macrolobium* sp. 1 (Table 3). *Swartzia* cf. *jenmanii* was prevalent on M2 and M3. Certain rare species (e.g. *Mora excelsa* and *Tachigali* sp. 1) contributed significant basal areas due to the presence of a few large individuals. Rare species comprised from 57–81% of all species in the mixed forest plots.

Diameter class distributions for the combined mixed-forest plots exhibited the negative exponential curve characteristic of most forests (Figure 5). Large trees were less common than in the *Dicymbe* plots. Only 11 individuals ⩾ 70 cm dbh occurred in M1, 19 in M2 and 15 in M3. Only one tree among the three plots had a dbh greater than 150 cm.

Seedlings and saplings

Dicymbe *forests.* *Dicymbe corymbosa* dominated the seedling and sapling classes in all plots (Table 3, Figure 6). Mean sapling densities for *D. corymbosa* ranged from 19.6–35.5 per 0.001 ha (all plots), and mean seedling densities from 144.6 per 0.001 ha (Potaro plots) to 337.3 per 0.0025 ha (Ireng plots). Frequency of *D. corymbosa* seedlings and saplings was 100% among all subplots sampled, indicating that recruitment of the dominant canopy species was spread throughout the plots, while recruitment of co-occurring canopy species was more patchy (Table 3). Dominance of seedling and sapling classes by *D. corymbosa* was most pronounced in D1, D2 and D3 (Table 3) and high overall for the combined plots (Figure 6). In general, patterns of recruitment among co-occurring canopy species varied among plots similar to patterns in the adult trees. In D4 and D5, where canopy dominance by *D. corymbosa* was more moderate, seedlings and saplings, while still dominated by *D. corymbosa*, were more equitably distributed among co-occurring

Table 3. Density, basal area, frequency and recruitment of the most abundant canopy tree species in *Dicymbe* forest and mixed forest at the Ireng and Potaro sites, Pakaraima Mountains, Guyana.

Plot[1]	Species	Family[2]	Trees[3]	Basal area (m^2)	Sapling[4]	Seedlings[5]	Frequency (trees)	Frequency (saplings)	Frequency (seedlings)
D1	*Dicymbe corymbosa*	CAE	152	52.8	381	3373	78	100	100
	Eschweilera sagotiana	LEC	15	0.9	7	7	14	20	20
	Licania laxiflora	CHR	15	0.4	10	0	15	50	0
	Eperua falcata	CAE	12	0.5	4	0	11	30	0
	Diospyros dichroa	EBE	10	0.4	22	1	10	60	10
	Miconia aff. *guianensis*	MEL	9	0.2	7	4	9	50	10
	Dicymbe altsonii	CAE	8	1.5	8	9	7	30	10
	Carapa guianensis	MELI	5	0.4	0	3	5	0	10
D2	*Dicymbe corymbosa*	CAE	170	45.0	353	1710	75	100	100
	Licania laxiflora	CHR	19	0.8	10	11	16	70	60
	Miconia aff. *guianensis*	MEL	13	0.3	7	24	10	50	40
	Homalium sp. 1	FLA	9	0.1	3	37	8	30	10
	Eperua falcata	CAE	8	1.0	0	2	8	0	10
	Dicymbe altsonii	CAE	4	0.4	22	14	2	40	30
	Catostemma cf. *fragrans*	BOM	4	0.2	2	0	4	20	0
	Inga alba	MIM	3	0.6	0	0	3	0	0
D3	*Dicymbe corymbosa*	CAE	175	51.3	355	2806	86	100	100
	Miconia aff. *guianensis*	MEL	15	0.5	5	14	14	30	60
	Eschweilera sagotiana	LEC	13	0.4	20	13	12	70	60
	Licania laxifora	CHR	10	0.3	3	13	9	20	60
	Macrolobium sp. 1	CAE	8	1.2	31	512	8	50	90
	Inga cf. *thibaudiana*	MIM	6	0.2	0	3	6	0	10
	Catostemma cf. *fragrans*	BOM	5	0.2	3	0	5	20	0
	Unonopsis aff. *glaucopetala*	ANN	5	0.1	11	66	5	50	60
	Tachigali sp. 1	CAE	0	0	5	315	0	10	90
D4	*Dicymbe corymbosa*	CAE	91	46.1	196	1446	66	100	100
	Eschweilera sagotiana	LEC	43	2.1	8	86	35	60	90
	Mora gonggrijpii	CAE	35	3.5	33	674	12	40	40
	Miconia aff. *guianensis*	MEL	34	1.0	12	8	30	40	60
	Licania laxiflora	CHR	14	0.7	9	21	14	50	70
	Pentaclethra macroloba	MIM	11	0.2	4	11	8	20	30
	Byrsonima cf. *stipulacea*	MAL	9	0.1	1	5	8	10	40
	Macrolobium sp. 1	CAE	7	1.0	4	51	6	40	50
	Tachigali sp. 1	CAE	6	1.4	3	934	6	20	100
D5	*Dicymbe corymbosa*	CAE	149	38.4	245	2009	79	100	100
	Macrolobium sp. 1	CAE	41	5.3	15	1382	30	50	100
	Licania heteromorpha	CHR	38	0.9	40	75	30	90	90
	Miconia aff. *guianensis*	MEL	22	0.7	11	10	20	60	60
	Licania laxiflora	CHR	19	0.7	3	15	18	20	50
	Eschweilera sagotiana	LEC	16	0.8	13	109	13	60	70
	Eschweilera decolorans	LEC	11	1.4	5	50	11	20	30
	Inga sp. 1	MIM	9	3.6	16	92	9	60	60
	Tachigali sp. 1	CAE	0	0	0	3	0	0	10
M1	*Licania laxiflora*	CHR	96	3.8	16	65	63	80	90
	Marliera cf. schomburgkiana	MYR	81	2.7	11	322	49	60	90
	Sapium sp. 1	EUP	47	2.6	9	50	37	80	80
	Protium decandrum	BUR	30	1.4	35	176	27	100	100
	Eschweilera sagotiana	LEC	24	0.8	5	9	20	30	30
	Iriartea exorrhiza	ARE	22	0.4	3	6	17	20	20
	Miconia aff. *guianensis*	MEL	20	0.4	5	4	18	30	30
	Pouteria sp. 1	SAP	15	0.5	2	0	15	20	0
	Tachigali sp. 1	CAE	2	2.0	5	1198	2	30	0
M2	*Eschweilera sagotiana*	LEC	98	4.1	61	239	61	90	100
	Licania laxiflora	CHR	46	1.8	20	73	35	80	100
	Swartzia cf. *jenmanii*	FAB	30	6.3	55	243	26	80	100
	Protium decandrum	BUR	27	2.9	40	211	24	90	100
	Iriartea exorrhiza	ARE	16	0.4	1	4	14	10	30
	Marliera cf. *schomburgkiana*	MYR	15	0.5	7	26	15	40	50
	Macrolobium sp. 1	CAE	11	2.4	2	110	11	20	90
	Sapium sp. 1	EUP	11	1.2	6	76	10	50	80
	Tachigali sp. 1	CAE	7	2.6	0	3102	7	100	100

Table 3. Density, basal area, frequency and recruitment of the most abundant canopy tree species in *Dicymbe* forest and mixed forest at the Ireng and Potaro sites, Pakaraima Mountains, Guyana—*Continued*

Plot[1]	Species	Family[2]	Trees[3]	Basal area (m^2)	Sapling[4]	Seedlings[5]	Frequency (trees)	Frequency (saplings)	Frequency (seedlings)
M3	*Eschweilera sagotiana*	LEC	58	3.7	110	198	50	100	100
	Swartzia cf. *jenmanii*	FAB	42	6.1	110	222	32	100	100
	Protium decandrum	BUR	42	4.0	42	385	34	90	100
	Licania laxiflora	CHR	36	1.4	28	69	32	90	100
	Iriartea exorrhiza	ARE	19	0.4	5	14	16	30	50
	Marliera cf. *schomburgkiana*	MYR	18	0.6	22	355	15	60	80
	Licania heteromorpha	CHR	18	0.4	23	50	15	80	80
	Pentaclethra macroloba	MIM	17	1.1	17	51	16	80	70
	Tachigali sp. 1	CAE	7	2.0	5	246	7	40	100

[1] 1-hectare plot designations are: D1–D2: *Dicymbe* forest, Ireng; D3–D4: *Dicymbe* forest, Potaro; M1–M3: mixed forest, Potaro.
[2] Family designations are: ANN–Annonaceae; ARE–Arecaceae; BUR–Burseraceae; CAE–Caesalpiniaceae; CHR–Chrysobalanaceae; BOM–Bombacaceae; EBE–Ebenaceae; EUP–Euphorbiaceae; FLA–Flacourtiaceae; LEC–Lecythidaceae; MAL–Malpighiaceae; MEL–Melastomataceae; MELI–Meliaceae; MIM–Mimosaceae; MYR–Myrtaceae; FAB–Fabaceae; SAP–Sapotaceae.
[3] Trees are individuals $\geqslant$ 10 cm diameter at breast height (dbh); values are on a per hectare basis for each plot; frequency of trees calculated as the percentage of one hundred 10 × 10-m subsamples per plot in which a species occurred.
[4] Saplings are individuals $\geqslant$ 1 m in height but < 10 cm dbh; values are on a 0.1 ha basis for each plot; frequency of saplings calculated as the percentage of ten 10 × 10-m subsamples per plot in which a species occurred.
[5] Seedlings are individuals < 1 m in height; values are on a 0.025 ha basis for plots D1–D2, and on a 0.1 ha basis for all other plots; frequency of seedlings calculated as the percentage of ten 5 × 5-m subsamples per plot (D1–D2) or ten 10 × 10-m subsamples per plot (D3–D5, M1–M3) in which a species occurred.

canopy species (Table 4). Most species occurring as seedlings and saplings were rare (Figure 6).

Mixed forests. In the Potaro mixed forests seedling and sapling densities were more equitable among canopy tree species than in the *Dicymbe* forests (Table 3; Figure 6). Mean sapling densities for combined species ranged from 38.9–58.9 per 0.001 ha and mean seedling densities from 280.2–512.5 per 0.001 ha. In general, species most abundant as trees were well represented as seedlings and saplings (Table 3). Absolute seedling and sapling densities of common canopy species such as *L. laxiflora*, *E. sagotiana*, *Swartzia* cf. *jenmanii* and *Marliera* cf. *schomburgkiana* were higher in the mixed forests than the *Dicymbe* forests, reflecting the greater abundance of these species as trees.

An exception to this equitability was seen on *Tachigali* sp. 1 which contributed an inordinate amount of seedlings to M1, M2 and to a lesser extent M3 (Table 3). In each of these plots *Tachigali* sp. 1 was present as scattered, infrequent large individuals, a few large, standing-dead individuals, and was poorly represented in the sapling class. These patterns are consistent with monocarpic reproduction, a feature documented in other neotropical *Tachigali* species (Foster 1977, Kitajima & Augspurger 1989).

Soils

Soil textures varied considerably among the plots (Table 6). In general soils of the Ireng *Dicymbe* forests were more sandy, whereas the Potaro soils had higher proportions of silt. D1–D2 soils also had significantly lower pH, per cent organic matter, Ca, Mg and Na concentrations, and significantly higher NO_3-N concentrations than most of the Potaro plots. Clay fractions were relatively equivalent among the plots except for the significantly higher proportion in D4. The high sand fraction of D5 was qualitatively different from that of D1 and D2. The 'sand' fraction of D5 was composed of fine-grained (<2 mm diameter) erosionates of ironstone, while those of D1–D2 were true quartz silicates derived from sandstone parent materials. Among the Potaro plots, soils were generally uniform with statistically significant differences occurring with a few variables associated with M3 (% organic matter, pH and NH_4-N). All soils were low in extractable P (8.8–11.3 mg kg^{-1}) and high in soluble Al (848–1508 mg kg^{-1}), features consistent with most tropical soils. Litter depth was greatest for the Ireng *Dicymbe* plots and in general was higher in all *Dicymbe* plots compared with the mixed forests.

DISCUSSION

Forest dominance by *Dicymbe corymbosa*

Dicymbe corymbosa exhibited remarkable levels of dominance of tree and recruitment classes at the Ireng and Potaro sites. The percentages of stand basal area ranging from 63–85% in this study would unequivocally classify these *Dicymbe* forests as monodominant (Connell & Lowman 1989). Even on plots where co-occurring canopy trees were more dense (e.g. D4, D5) *Dicymbe corymbosa* dominated the largest size classes and contributed 63–74% of the basal area while maintaining a large seedling and sapling pool.

The dominance levels for *D. corymbosa* were among

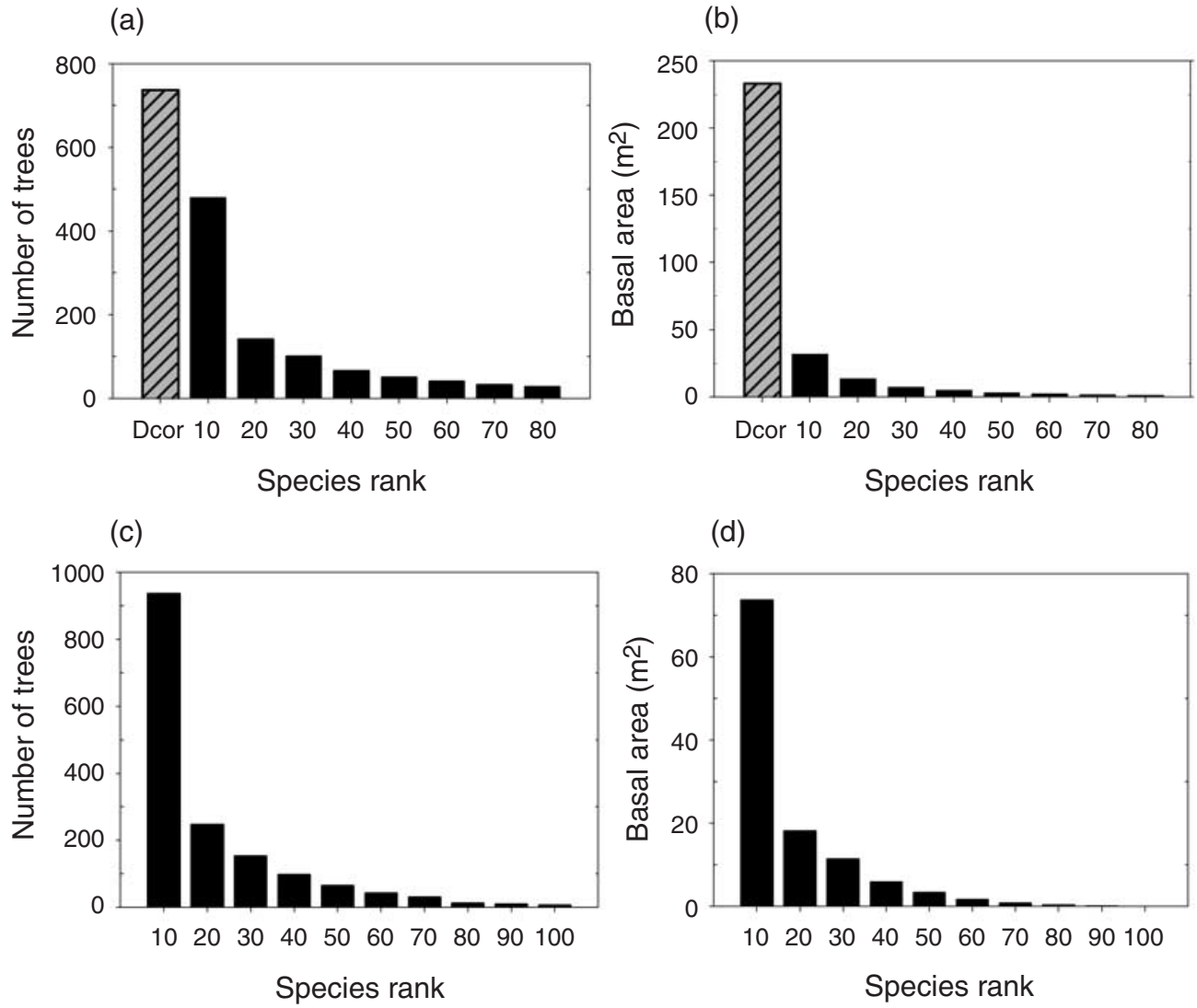

Figure 4. Dominance–diversity curves for tree species in *Dicymbe* and mixed forests at the Ireng and Potaro sites, Pakaraima Mountains, Guyana. Graphs are based on combined abundance and basal-area data for five 1-ha plots for *Dicymbe* forest, and three 1-ha plots for mixed forest. (a, b) *Dicymbe* forests. First-ranked species is *Dicymbe corymbosa* (Dcor). Data for remaining species were combined for groups of 10 ranked from most to least important. (c, d) Mixed forests. Data for species were combined for groups of 10 ranked from most to least important.

the highest recorded for upland monodominant species in the Neotropics. The highest levels of neotropical monodominance previously recorded are for the caesalpinioid *Mora excelsa* in Trinidad, which formed 85–95% of all trees ⩾ 30 cm dbh over several contiguous hectares (Beard 1946) and 67% of trees ⩾ 40 cm dbh at Moraballi Creek, Guyana (Davis & Richards 1933). Whereas *M. excelsa* occurred on terra firma soils in Trinidad (Rankin 1978, Torti *et al*. 1997) it is widely recognized in Guyana that dominance by *M. excelsa* is restricted to alluvial floodplains; where the species occurs above the flood level it is much less dominant and restricted to rocky slopes with shallow, impermeable clay soils (Clarke *et al*. 2001, Davis & Richards 1933, 1934; ter Steege *et al*. 1993, Henkel *pers. obs*.). Monodominance by *M. excelsa* in Guyana may be achieved by adaptation to periodic inundation similar to that observed in *Pentaclethra macroloba* and *Prioria copaifera* in Central America (Condit *et al*. 1993, Hartshorn 1972, Lopez & Kursar 1999). In the present study *D. corymbosa* comprised 78.5% of trees ⩾ 60 cm dbh, which is higher than values recorded for other truly upland neotropical monodominants such as *Eperua falcata* and *Mora gonggrijpii* in Guyana (Davis & Richards 1933) and *Peltogyne gracilipes* in Brazil (Nascimento *et al*. 1997).

The high *Dicymbe* basal areas resulted from the preponderance of *D. corymbosa* trees in the largest size classes. As all of the study stands were old growth it was surprising to note that, at Potaro, 62 *D. corymbosa* trees ⩾ 100 cm dbh (including 14 ⩾ 150 cm) were recorded in 3 ha,

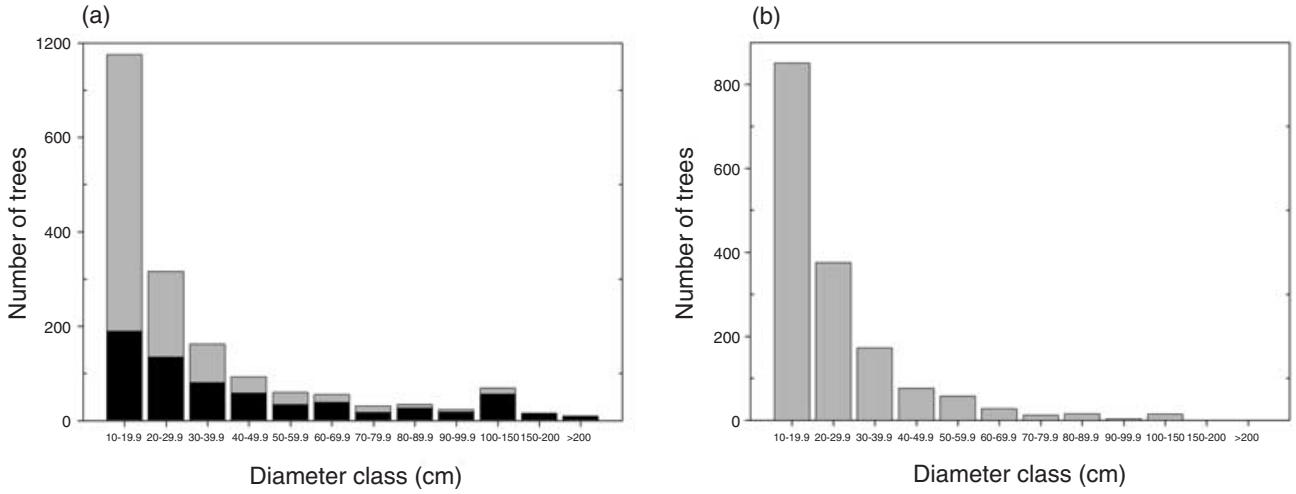

Figure 5. Diameter class distribution of trees for five combined 1-ha *Dicymbe* plots and three combined 1-ha mixed forest plots at the Ireng and Potaro sites, Pakaraima Mountains, Guyana. (a) *Dicymbe* forest. Black bars = *Dicymbe corymbosa*; grey bars = combined mixed forest species. (b) Mixed forest.

Table 4. Coppicing structure of *Dicymbe corymbosa* on five 1-ha plots at the Ireng and Potaro River sites, Pakaraima Mountains, Guyana.[1]

Plot	Number of individuals	Non-coppiced[2]	Coppiced	Stems[3] < 10	Stems ⩾ 10 < 20	Stems ⩾ 20 < 50	Stems ⩾ 50 < 100	Stems ⩾ 100
D1	152	78	72	397	75	83	27	12
D2	170	68	102	715	121	107	26	15
D3	175	8	167	842	131	82	42	17
D4	91	21	70	424	43	44	24	15
D5	149	20	129	612	104	81	14	18
Total	737	195	540	2990	474	397	133	77

[1] Plot designations are: D1–D2: Ireng *Dicymbe* forests; D3–D5: Potaro *Dicymbe* forests.
[2] Coppice shoots not present at 1.3 m above ground level.
[3] Stem measurements in cm.

Table 5. Coppicing structure of mature *Dicymbe corymbosa* trees[1] at the Potaro site, Pakaraima Mountains, Guyana.

	Basal diameter (cm)	Height of trunk split (cm)	Number of canopy shoots	Diameter of canopy shoots (cm)	Number of non-canopy shoots
Mean (range)	154.5 (100–262)	114.8 (39–280)	4.1 (1–7)	38.8 (13–84)	20.2 (6–48)

[1] Means are calculated from 20 trees with basal diameters ⩾ 100 cm randomly chosen from an area of *Dicymbe* forest of approximately 4 ha.

while the equivalent area of mixed forest contained only 14 trees ⩾ 100 cm dbh. Basal area values recorded for *D. corymbosa* alone were exceptional for tropical moist forests worldwide. The range for *D. corymbosa* of 38.4–52.5 m^2 ha^{-1} compared favourably with basal areas in a recent study by Pitman *et al.* (2001), who found an average basal area of ~30 m^2 ha^{-1} over an array of 24 primary terra firme plots in Upper Amazonia. The values for *Dicymbe* generally exceed the figure of 30–40 m^2 ha^{-1} for lowland forests in northern South America given by Lamprecht (1972) and fall into the category of ⩾ 40 m^2 ha^{-1} given for 'exceptionally large' Amazonian forests by Pires & Prance (1985). In a comprehensive survey of mature, biomass-rich Asian tropical forests, Brown *et al.* (1991) recorded only 6% of forests with basal area values above 30 m^2 ha^{-1}; the highest value in the study was ~ 48 m^2 ha^{-1}. Dawkins (1959) reported a range of 23–37 m^2 ha^{-1} for lowland forests of Africa. On a worldwide basis, mean stand basal areas for mature tropical moist forests average ~ 25 m^2 ha^{-1} (Brown & Iverson 1992). Even among tropical monodominant forests, *Dicymbe* basal areas were considerably higher. Whole-forest basal areas (i.e. monodominant species plus associates) for *Gilbertiodendron* forests in the Congo averaged 34 m^2 ha^{-1} (~ 29 m^2 ha^{-1} for the dominant; Hart *et al.* 1989), and for *Peltogyne* forests in northern Brazil ranged from 25–43 m^2 ha^{-1} (Nascimento *et al.* 1997). In both of these studies, basal areas of monodominant forests were much more equitable with those of adjacent mixed forests than those observed in the present study.

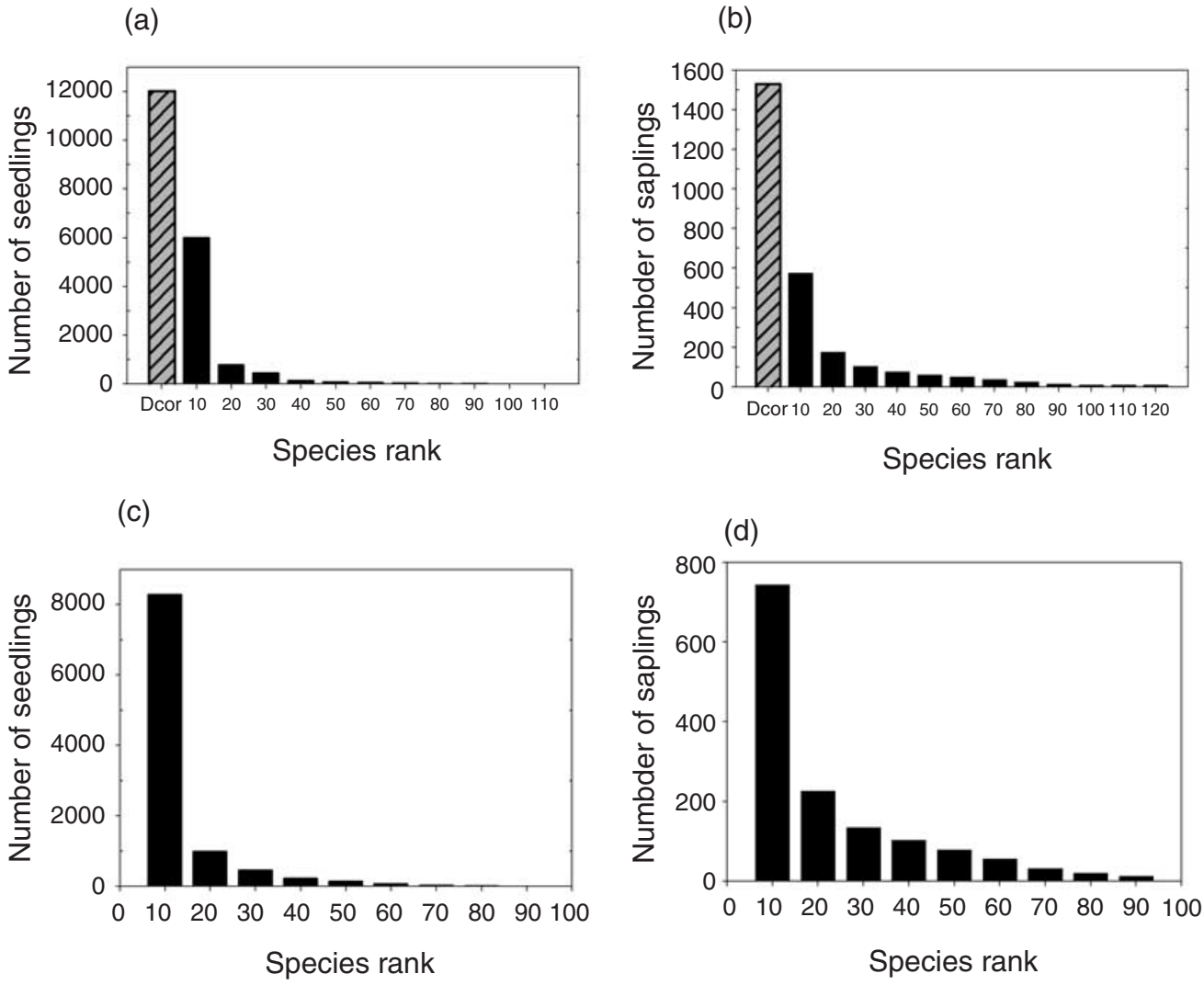

Figure 6. Dominance–diversity curves for seedlings and saplings of woody species in *Dicymbe* and mixed forests at the Ireng and Potaro sites, Pakaraima Mountains, Guyana. Graphs are based on combined abundance data for five subsampled 1-ha plots for *Dicymbe* forest, and three subsampled 1-ha plots for mixed forest. Total area sampled in *Dicymbe* forest was 0.5 ha for saplings and 0.35 ha for seedlings. In mixed forest, 0.3 ha was sampled for both saplings and seedlings. (a, b) *Dicymbe* forests. First-ranked species is *Dicymbe corymbosa* (Dcor). Data for remaining species were combined for groups of 10 ranked from most to least important. (c, d) Mixed forests. Data for species were combined for groups of 10 ranked from most to least important.

Due to atypical allometric relationships in multiple-stemmed trees, regression equations derived to calculate above-ground biomass from diameter measurements could not be accurately applied to these *Dicymbe* stands (Brown 1997). For the Potaro mixed forests above-ground biomass estimates ranged from 442–512 t ha^{-1}, within the upper range for tropical moist forests (Brown 1997). Given the much greater number of large trees in the *Dicymbe* forests, true above-ground biomass must be exceedingly high (Brown & Iverson 1992, Brown & Lugo 1992). Regarding below-ground biomass, *D. corymbosa* allocated substantial resources to the production of extensive root mounds throughout the forest. Studies in tropical and temperate forests have shown that root biomass density of trees is inversely related to soil fertility, particularly in extremely nutrient-poor podzols and white sands (Vitousek & Sanford 1986, Vogt *et al.* 1995, Waring & Schlesinger 1985), and that above-ground biomass is a good indicator of below-ground biomass (Cairns *et al.* 1997). Given these relationships and the poor nature of soils under *Dicymbe* stands it seems safe to assume that high above-ground productivity in *D. corymbosa* was coupled with exceptional productivity below ground.

What factors could lead to the large basal areas seen in *D. corymbosa*? While the age of large *Dicymbe* trees is unknown, such individuals must be ancient. Successive rounds of coppicing are evident on the large trees, as well as standing dead and fallen coppice shoots in various

Table 6. Physical and chemical characteristics of the upper 10 cm of mineral soil and litter depth in eight 1-ha study plots at the Ireng and Potaro sites, Pakaraima Mountains, Guyana.[1,2]

Plot	Clay (%)	Silt (%)	Sand (%)	Organic matter (%)	Litter depth (cm)	pH	CEC (meq 100 g^{-1})
D1	12.2 ^{a} (2.0)	17.3 ^{a} (5.3)	70.5 ^{a} (6.2)	3.5 ^{a} (0.7)	7.3 ^{a} (0.9)	4.2 ^{a} (0.1)	11.0 ^{ac} (1.4)
D2	14.6 ^{a} (2.0)	17.8 ^{a} (2.7)	67.6 ^{ab} (4.1)	5.8 ^{a} (1.0)	13.0 ^{b} (1.3)	3.9 ^{ac} (0.1)	19.9 ^{b} (2.0)
D3	10.6 ^{a} (2.2)	33.8 ^{abc} (1.5)	55.6 ^{abcd} (2.2)	17.7 ^{bd} (0.7)	8.0 ^{a} (0.9)	4.9 ^{be} (0.2)	17.3 ^{bc} (0.9)
D4	35.4 ^{b} (4.8)	24.4 ^{ac} (4.3)	40.2 ^{cd} (1.8)	12.6 ^{cde} (1.3)	5.3 ^{ac} (0.4)	5.3 ^{bd} (0.2)	12.1 ^{c} (0.9)
D5	9.8 ^{a} (2.0)	18.6 ^{a} (2.9)	71.6 ^{ac} (1.9)	12.3 ^{ce} (0.8)	6.8 ^{a} (0.6)	4.8 ^{be} (0.03)	13.4 ^{abc} (0.8)
M1	5.8 ^{a} (2.0)	45.2 ^{b} (3.2)	49.0 ^{bcd} (2.7)	17.0 ^{d} (0.8)	3.6 ^{d} (0.3)	4.5 ^{cde} (0.1)	18.5 ^{bcd} (0.6)
M2	29.1 ^{b} (2.2)	32.4 ^{abc} (2.3)	38.5 ^{d} (1.3)	12.1 ^{ce} (0.5)	3.9 ^{cd} (0.3)	4.8 ^{be} (0.1)	19.2 ^{bd} (1.1)
M3	13.4 ^{a} (2.0)	42.0 ^{bc} (1.4)	44.6 ^{d} (2.7)	10.0 ^{e} (0.9)	3.6 ^{d} (0.2)	4.7 ^{e} (0.1)	14.4 ^{abcd} (1.3)

Plot	extr. P (mg kg^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})	K (mg kg^{-1})	NO_3-N (mg kg^{-1})	NH_4-N (mg kg^{-1})	Al (mg kg^{-1})
D1	7.7 ^{a} (0.7)	25.8 ^{a} (5.0)	16.2 ^{a} (1.4)	23.5 ^{a} (2.8)	36.5 ^{a} (2.9)	13.5 ^{ab} (2.3)	1086 ^{a} (122)
D2	11.3 ^{b} (1.0)	63.6 ^{ab} (24.1)	12.9 ^{a} (1.2)	22.8 ^{a} (1.8)	51.4 ^{b} (6.9)	18.2 ^{ab} (3.7)	1508 ^{a} (224)
D3	10.8 ^{b} (0.8)	134.8 ^{bc} (13.6)	41.2 ^{b} (2.6)	32.8 ^{a} (4.7)	12.0 ^{c} (7.3)	24.4 ^{a} (3.4)	848 ^{a} (57)
D4	10.4 ^{b} (0.8)	172.8 ^{c} (40.3)	41.0 ^{b} (1.1)	24.4 ^{a} (1.2)	8.0 ^{c} (0.3)	11.0 ^{ab} (1.7)	1102 ^{a} (93)
D5	11.2 ^{b} (1.0)	188.0 ^{c} (36.6)	40.0 ^{b} (1.2)	29.6 ^{a} (1.2)	2.4 ^{c} (0.4)	11.0 ^{ab} (1.4)	1052 ^{a} (30)
M1	9.4 ^{b} (0.5)	126.0 ^{bc} (6.3)	45.0 ^{b} (1.4)	29.0 ^{a} (0.6)	13.1 ^{c} (0.5)	10.3 ^{ab} (0.7)	1102 ^{a} (67)
M2	13.6 ^{c} (0.7)	299.8 ^{d} (85.9)	33.6 ^{c} (1.7)	29.6 ^{a} (2.2)	7.6 ^{c} (1.2)	18.8 ^{ab} (2.0)	1273 ^{a} (23)
M3	8.8 ^{b} (0.4)	152.8 ^{bc} (25.4)	42.2 ^{b} (2.2)	28.6 ^{a} (1.6)	3.6 ^{c} (0.6)	7.7 ^{b} (0.7)	1392 ^{a} (30)

[1] Values are mean (standard error of the mean). For each parameter, means followed by the same letter are not significantly different at $P \leq 0.05$. Sample size was n = 10 for all plots except for litter depth, where n = 10 for D1 and D2, and n = 20 for D3–D5 and M1–M3. Plot designations are: D1–D2: Ireng *Dicymbe* forests; D3–D5: Potaro *Dicymbe* forests; M1–M3: Potaro mixed forests.
[2] Non-normally distributed data (clay, silt, organic matter, P, Ca, Mg, NO_3–N, NH_4) were analysed with the Kruskal–Wallis test followed by Tukey–Kramer's means comparison; litter depth data were log-transformed and analysed with one-way ANOVA followed by Tukey–Kramer's; all other data were untransformed and analysed with one-way ANOVA followed by Tukey–Kramer's.

stages of decay. Tip-ups of entire *Dicymbe* trees were rarely observed, while treefalls in mixed forests appeared to occur at a more typical rate for tropical forests (Henkel *pers. obs.*, also see Zagt 1997*b*). Gaps produced by death of *Dicymbe* canopy shoots were filled by lower coppice shoots already in place, circumventing the gap phase dynamics and recruitment of light-demanding species characterizing other tropical forests (Hartshorn 1978). This apparent freedom from significant disturbance points to great stability and persistence of canopy individuals of *D. corymbosa* resulting, in the long term, in high sequestration of biomass (Brown *et al.* 1991, 1997; Carey *et al.* 1994, Phillips *et al.* 1998, ter Steege & Hammond 2000).

Persistence of monodominance

Dicymbe forests clearly qualified as persistently monodominant. The high density and frequency of seedlings and saplings of *D. corymbosa* indicated ample sexual reproduction. Large seed crops are produced by *D. corymbosa* on an irregular supra-annual basis (Henkel unpubl. data; for *D. altsonii* see Zagt 1997*a*). A masting event was observed by the author during May–June of 1998 at the Ireng site. The large (3–4 cm diameter) seeds were explosively dehisced from mature pods during the height of the rainy season and fell in the immediate vicinity of the parent tree. Germination was immediate and erect, greening cotyledons were present on the seedlings within 1–2 wk. Levels of seed and seedling predation are unknown but the dense carpets of seedlings present at many sampling sites suggested a high rate of early survival. While lower sapling densities indicated considerable mortality among post-establishment seedlings, *D. corymbosa* continued to strongly dominate the sapling stages. Recruitment proceeds in the deep shade cast by parent trees with no indication that high light levels are necessary for establishment. Such reproductive features characterize other tropical monodominants (e.g. *Gilbertiodendron dewevrei*; Hart 1995, Torti *et al.* 2001) and in a low-disturbance environment should allow convergence on monodominance (Huston 1994, ter Steege & Hammond 2000). What sets *D. corymbosa* apart from other tropical monodominants is that the sexual reproductive features consistent with monodominance were accentuated by the coppicing habit which allowed mature individuals to continually refill their own light gaps. This unusual combination of features surely contributes to *D. corymbosa* dominance through time.

The higher seedling and sapling densities of non-*Dicymbe* species in D4 and D5 suggested that *Dicymbe* dominance in those plots may be in decline. Indeed, widely distributed canopy species such as *L. laxiflora*, *E. sagotiana* and *Miconia* aff. *guianensis* were better represented as trees, seedlings and saplings than in the other *Dicymbe* plots. Nonetheless, in D4 and D5 *D. corymbosa* maintained a much higher proportion of larger trees, greatly dominated stand basal area and maintained much higher absolute density of seedlings and saplings than any other co-occurring species. Canopy displacement by non-

Dicymbe species cannot therefore be projected as the ultimate fate of these stands.

Coppicing dynamics

Natural coppice shoot formation was an integral life history component of *D. corymbosa*. In the present study the majority of trees ⩾ 10 cm dbh exhibited sprouting from the lower trunk. As individual *Dicymbe* trees matured the number and diameter of shoots reaching the canopy increased without dependence on death or damage to older shoots, indicating that sprouting was an intrinsic phenomenon occurring in a cumulative fashion throughout the life of the tree (for *D. altsonii* see Zagt 1997*b*). In this respect trunk sprout formation in *Dicymbe* differed greatly from the more frequently observed occurrence of sprouts on broken, cut or otherwise damaged trees (Bellingham *et al.* 1994, Clark & Clark 1991, Jenik 1994, Khan & Tripathi 1989, Putz & Brokaw 1989, Uhl *et al.* 1981, Vandermeer *et al.* 1995, Walker 1991). The cumulative nature of shoot production in *D. corymbosa* is more akin to root suckering seen in some temperate trees (e.g. *Fagus*) and the neotropical *Dimorphandra conjugata* (Fanshawe 1952, Koop 1987). Cumulative trunk sprouting has been recorded in a few south-east Asian Fagaceae, e.g. *Trigonobalanus verticillata* (Corner 1990). *Dicymbe corymbosa* appears to be the only tropical tree known that combines the trunk-sprouting habit with extreme monodominance.

Dicymbe corymbosa retains the 'best of both worlds' by merging ample generative and vegetative reproduction. Coppicing can contribute to long-term site dominance by allowing sexually mature individuals to persist for long periods of time without whole-tree death resulting from tip-ups. Given the apparent shade tolerance of *Dicymbe* seedlings and saplings (Isaacs *et al.* 1996, Zagt 1997*a*) clonal reproduction of mature individuals should, in the long run, contribute to successful recruitment by providing continual canopy coverage, light harvesting capacity and seed production. Trunk sprouts, lined up in succession, are in place and ready to respond quickly to light gaps produced by attrition of the larger canopy shoots. These sprouts would benefit from the large root system of the parent tree. As this process proceeds trunk diameter gets ever larger, and is further stabilized by an increasingly large basal root mound, reducing further the possibility of tip-up. In this manner ancient *D. corymbosa* stands may be relatively free from the destabilizing effects of gap-phase dynamics (Hartshorn 1989).

Species richness and diversity

While tree species richness was less in *Dicymbe* than in mixed forest, the most common canopy species co-occurring with *Dicymbe* were generally the same as the common species of the mixed forest. These included species of *Eschweilera*, *Licania*, *Protium* and *Swartzia*, genera which are highly characteristic of mixed forest associations in the Guianas (Terborgh & Andresen 1998, ter Steege *et al.* 2000). The Mantel test for association indicated that qualitative tree community composition was positively associated between *Dicymbe* and mixed forest at the Potaro site. These data demonstrated that the tree species pool was the same for both forest types. Quantitative differences in stand composition were largely determined by the presence or absence of *D. corymbosa*. Similar congruence in species has been found between mixed forests and adjacent monodominant forests of *Gilbertiodendron dewevrei* (Hart *et al.* 1989) and *Tetraberlinia* spp. in Africa (Newbery *et al.* 1988), and appears to be a feature of tropical monodominant forests worldwide (Hart 1990).

Monodominance by *D. corymbosa* depressed tree alpha-diversity at the stand level. Species richness values ranging from 37–51 species ha^{-1} were among the lowest, if not *the* lowest, recorded for high-canopy moist forests in the neotropics (Gentry 1988, Nascimento *et al.* 1997). As *D. corymbosa* proceeds toward extreme monodominance, less resources and space are available for other species, rare species become rarer, and the net effect is reduced tree alpha-diversity. Species equitability was further depressed as *D. corymbosa* came to dominate the larger size classes. Mixed forest species were persistent in some of the *Dicymbe* stands reported here (e.g. D4 and D5). Species-area curves indicated that the pool of species regionally available was larger than sampling had recorded (Henkel, unpubl. data). The lack of unique species composition makes *Dicymbe* forests difficult to classify floristically, but reinforces the idea that monodominance in rain forests is achieved by biotic interactions that enhance the competitive abilities of the dominant species (Hart *et al.* 1989, Torti *et al.* 2001).

Influence of soils

Dicymbe corymbosa stands occurred on soils varying considerably in texture and macronutrients. While the sandy, more oligotrophic Ireng *Dicymbe* soils differed markedly in several parameters from those of both Potaro *Dicymbe* and mixed forests, *D. corymbosa* was able to achieve dominance at both sites. In general, soils were the same under *Dicymbe* stands and mixed forests at the Potaro site. These results support the previous findings of Henkel *et al.* (2002) in which ordinations of transect data showed no influence of edaphic factors on the local distribution of *D. corymbosa* or *D. altsonii* in the Upper Ireng Basin. A similar lack of edaphic specificity has been repeatedly shown for *Gilbertiodendron dewevrei*-dominated forests in the Congo (Conway & Alexander 1992, Hart *et al.* 1989) and also for *Peltogyne gracilipes* monodominant

forests in Roraima, Brazil (Nascimento & Proctor 1997*b*) and points to biological factors driving the occurrence and distributions of these forests.

Below-ground components of monodominance

Dicymbe corymbosa exhibited below-ground features which possibly contributed to its monodominance. These included the development of extensive root mounds at the base of large trees, which extended outward between conspecifics and formed a forest-wide litter trap. Litter depths averaged 5–13 cm in *Dicymbe* forests and often exceeded 50 cm in the basal root mounds. Ectomycorrhizal rootlets and extramatrical mycelia perfused the fermentation horizon, especially between compressed layers of partially decomposed *Dicymbe* leaves. Additionally, thick humic mats suspended among coppice shoots were permeated by EM rootlets and mycelia, and yielded abundant fruitbodies of EM fungi (Henkel 1999, Henkel *et al*. 2000). Such observations seem to suggest that mechanisms have been evolved for litter trapping, and, presumably, nutrient recycling, in *D. corymbosa*.

If litter trapping is indeed an adaptive trait in *D. corymbosa*, how might it facilitate monodominance? One hypothesis is that EM mycelium enables the direct cycling of organic nutrients from the litter to the host trees (Herrera *et al*. 1978). Reports have suggested that direct cycling of phosphorus from litter may occur in grove-forming, EM African caesalpinioids (Moyersoen *et al*. 1998, Newbery *et al*. 1988, 1997). Laboratory experiments have demonstrated that selected EM fungi have the enzymatic capacity to utilize organic N and P from litter sources and translocate the derived nutrients directly to host plants, leaving high C/N residues behind (Abuzinadah *et al*. 1986, Bending & Read 1995, Perez-Moreno & Read 2000). Direct EM uptake of organic nitrogen and phosphorus compounds could promote dominance in EM trees by reducing the pools of N and P available for mobilization by saprotrophic microorganisms, and might ultimately inhibit the establishment of arbuscular-mycorrhizal plants not able to benefit from the EM network (Allen 1991). Accumulations of acidic mor humus might be expected to occur under these conditions and were in fact observed in central Amazonian campinarana forests containing EM trees (Singer 1984, Singer & Araujo 1979, Singer & Araujo-Aguiar 1986), Guinea-Congolian groves of EM *Microberlinia* and *Tetraberlinia* spp. (Newbery *et al*. 1988) and *Gilbertiodendron dewevrei* (Torti *et al*. 2001), as well as EM-dominated temperate forests (Alexander 1983). Additionally, some evidence exists for the antagonistic suppression of litter saprotrophic organisms by EM fungi, contributing to a reduction in litter breakdown in EM forests of the neotropics (Singer & Araujo 1979, Singer & Araujo-Aguiar 1986) and New Zealand (Gadgil & Gadgil 1971, 1975). Conversely, deep litter layers occur in Guyanese forests dominated by the non-EM *Dimorphandra conjugata* (Fanshawe 1952) and in Amazon caatinga forest dominated by non-EM *Eperua* spp. (Moyersoen 1993). While the hypothesis of EM-mediated direct cycling under natural conditions in the tropics remains unsubstantiated, the ectomycorrhizal *D. corymbosa* forests, with their highly suggestive litter-trapping physiognomy, may provide an ideal system within which to test it.

Another avenue for further research regards the potential role of EM networks in promoting putative shade tolerance in *Dicymbe* seedlings. Shade tolerance has been proposed as a key feature of persistent tropical monodominants, allowing persistence of their seedlings in heavily shaded understoreys (Hart 1990). Tolerance of low light levels has been demonstrated in seedlings and saplings of the monodominants *Gilbertiodendron dewevrei* in the Congo (Hart 1995) and *Dryobalanops aromatica* in Malaysia (Kachi & Okuda 1993). It is tantalizing to speculate that seedlings of monodominant EM species may receive carbon directly from conspecific overstorey trees via shared EM networks, thereby promoting shade tolerance and survival (Newman 1988, Read 1992). Interplant carbon transfer via common EM mycelium has been demonstrated in laboratory experiments (Duddridge *et al*. 1988, Ek *et al*. 1996, Finlay & Read 1986*a*, Soderstrom *et al*. 1988) and from overstorey to understorey conspecifics in temperate coniferous forests (Simard *et al*. 1997*a*, *b*; but see Robinson & Fitter 1999), although Newbery *et al*. (2000) found few benefits of proximity to conspecific adults to the establishment of tropical EM seedlings. One might hypothesize that in a monospecifically dominant system such as that of *D. corymbosa*, a putative EM network shared by conspecifics could potentially reinforce the competitive abilities of the dominant, not only by promoting shade tolerance through carbon flow to understorey members, but possibly through interplant translocation of phosphorus and nitrogen (Arnebrandt *et al*. 1993, Finlay & Read 1986*b*). If such below-ground processes are indeed occurring in *D. corymbosa*, they may complement stability-promoting above-ground features such as coppicing and mast-fruiting in enhancing the success of this extraordinary species.

SUMMARY

Dicymbe corymbosa exhibited persistent monodominance in the Pakaraima Mountains of Guyana. Canopy dominance was universal on all *Dicymbe* study plots, and, while mixed forest species occasionally dominated smaller size classes, *D. corymbosa* maintained ample seedling and sapling pools on all plots. *Dicymbe corymbosa* dominance was not restricted by soil type. Coppicing occurred on the majority of *D. corymbosa* trees and may contribute to site stability in the species. Basal areas of *D. corymbosa* were

in the upper range for tropical forests worldwide and, coupled with extensive root mound development, indicated exceptional above- and below-ground biomass allocation for the species. Tree species diversity was depressed in *Dicymbe* stands although co-occurring species were drawn from the same pool as adjacent mixed forests. Life history traits of *D. corymbosa* such as mast-fruiting, putative shade tolerance, and the ectomycorrhizal habit are shared with members of the Amherstieae which form monodominant forests in Africa. Litter-trapping physiognomy and ectomycorrhiza-mediated nutrient dynamics may complement above-ground traits in fostering extreme monodominance in *D. corymbosa*.

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