

Mast fruiting and seedling survival of the ectomycorrhizal, monodominant *Dicymbe corymbosa* (Caesalpiaceae) in Guyana

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Summary

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- In Guyana, we investigated seed output, and resulting seedling establishment and survival, during a 'mast' year, by the ectomycorrhizal, monodominant rainforest canopy tree *Dicymbe corymbosa* (Caesalpiaceae), a species with high, synchronous seed production at intermittent years.
- By utilizing seed traps, the mast seed output, predation, carbon and mineral investment, and masting synchrony were quantified in 2003 in primary *D. corymbosa* forests. Establishment of seedling cohorts was monitored, and climatic conditions associated with masting were assessed.
- During 2003, *D. corymbosa* in the Pakaraima Mountains exhibited high, synchronous seed production with low dispersal and predation. Investment in reproductive biomass was large relative to that in other tropical forests. Recent *D. corymbosa* reproductive events followed El Niño-induced droughts, with little intervening seed production. Over 12 months, 40% of the 2003 seedling cohort survived.
- Our results suggest that *D. corymbosa* has a strongly bimodal fruiting pattern that allows the establishment of a large seedling bank, facilitating persistent monodominance. Resource investment in large seed crops may depend on mineral recycling via ectomycorrhizas, coupled with the reallocation of carbon from vegetative maintenance.

Key words: *Dicymbe corymbosa* (Caesalpiaceae), ectomycorrhizas, forest ecology, Guiana Shield, mast fruiting, monodominance, Neotropics.

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Introduction

Mast fruiting is the synchronous heavy fruiting of a plant species at intervals greater than 1 year (Kelly & Sork, 2002). Mast fruiting is exhibited primarily by iteroparous perennial woody plants and is best known to occur in plants from temperate ecosystems (e.g. many Fagaceae, Pinaceae; Sork *et al.* 1993; Herrera *et al.*, 1998; Koenig & Knops, 2000; Kelly & Sork, 2002), although significant examples are known from the tropics (e.g. Dipterocarpaceae; Janzen, 1974). Herrera *et al.* (1998) noted that the wide variety of patterns of mast fruiting (i.e. in timing and extent) are probably the result of several factors interacting at different sites for different

species. Nonetheless, two main nonexclusive hypotheses may explain mast fruiting: first, the intermast period allows the accumulation of resources (carbohydrates and mineral nutrients) to threshold levels necessary for the next fruiting event, followed by resource depletion and renewed resource accumulation (Van Schaik *et al.*, 1993; Isagi *et al.*, 1997; Newbery *et al.*, 1998); and, second, mast fruiting is an evolved predator-avoidance strategy, with seed/seedling predators periodically satiated and unable to maintain effective populations in the intermast period, which shows enhanced seedling establishment following masting events (Janzen, 1974; Silvertown, 1980; Sork, 1993; Kelly, 1994). Additionally, synchronous masting in both temperate and tropical tree

populations appears to be cued by environmental factors, although much variability exists among these (e.g. drought, solar radiation, threshold high or low daily temperatures; Kelly & Sork, 2002), and the impact of environmental factors on resource relations relative to masting remains unclear (Newbery *et al.*, 1998; Miyazaki *et al.*, 2002).

Tropical examples of mast fruiting are found in the Dipterocarpaceae of south-east Asia (e.g. Janzen, 1974; Appanah, 1985; Curran & Leighton, 2000) and selected caesalpinia-ceous leguminous species ('caesalps') from African rainforests (Gerard, 1960; Hart, 1995; Newbery *et al.*, 1998; Green & Newbery, 2002). These mast fruiting trees are ectomycorrhizal, tend towards family level or single-species dominance, and establish large seedling cohorts following supra-annual masting events preceded by above-average dry season solar irradiance (Goldammer & Seibert, 1990; Curran, 1994; Hart, 1995; Newbery *et al.*, 1997; 1998; Yasuda *et al.*, 1999). Seedling cohorts resulting from mast years may contribute to long-term site persistence by providing a substantial number of conspecifics ultimately reaching reproductive age (Fox, 1967; Hart, 1995, but see Green & Newbery, 2002). An emerging resource-based hypothesis is that the timing and size of mast fruiting in persistently dominant, ectomycorrhizal tropical tree species is set primarily by energy limitation for fruit production and secondarily by mineral nutrient limitations, in particular phosphorus, ameliorated periodically by ectomycorrhiza-mediated uptake, with predator satiation being the selective factor (Newbery *et al.*, 1998; Green & Newbery, 2002).

Dicymbe corymbosa Spruce ex Benth. (Caesalpiniaaceae, tribe *Amherstieae*) is a leguminous, ectomycorrhizal canopy tree species exhibiting one of the most striking examples of monospecific dominance in Neotropical forests (Richards, 1996; Henkel, 2003), and interannual variability in seed production may play a role in this dominance. In the Pakaraima Mountains of western Guyana, *D. corymbosa* occurs in a mosaic of stands, ranging from one to many hectares in extent, immersed in a matrix of tree species-rich, arbuscular mycorrhizal (AM) mixed rainforest. In these stands, which occur on a wide variety of soil types, *D. corymbosa* has been found to comprise 70–95% of the basal area and to maintain high densities of seedlings and saplings, indicative of self-replacement ('persistent monodominance' *sensu* Connell & Lowman, 1989; Henkel *et al.*, 2002; Henkel, 2003). Both above- and below-ground life history traits of *D. corymbosa* may contribute to its persistent site dominance through competitive exclusion of AM tree species, including epicormic shoot reiteration and resulting vegetative regeneration into canopy gaps, and closed nutrient recycling from litter via ectomycorrhizas (Henkel *et al.*, 2002; Henkel, 2003; Mayor & Henkel, 2004). Additionally, the high densities and uniform distributions of *D. corymbosa* seedlings and saplings in numerous stands, with conspecific overstorey dominance, within a 60-km radius in the Pakaraima Mountains, was suggestive of large, synchronized reproductive events.

Annual field observations in the region over the past 11 years have suggested a high interannual variability in seed production in *D. corymbosa*: in 1993 and 1998 large fruitings were observed, with little or no seed production seen in the intervening years (1994–97 and 1999–2000). The perceived relationship between large, supra-annual seeding events and establishment of dense seedling cohorts that were apparently free from significant density-dependent mortality, led to the hypothesis that mast fruiting contributes, at the recruitment level, to *D. corymbosa*-persistent dominance, allowing the eventual replacement of large, vegetatively regenerating individuals that dominate the stands (Henkel, 2003). At the onset of fieldwork along the Upper Potaro River in May 2003, it was clear that *D. corymbosa* was masting, the tree crowns forest-wide being densely laden with developing fruits. Consequently, study plots were established to more fully quantify seed production, seed fate and reproductive resource investment by *D. corymbosa* associated with the 2003 mast fruiting event.

The specific objectives of the study were to: (1) determine the absolute levels of 2003 seed production; (2) assess local and regional synchrony in seed production; (3) determine seed predation rates and sources, germination rates and early establishment of seedlings; (4) determine carbon and mineral nutrient investment in seed production; and (5) assess the relationship of regional climatic trends and seed production.

Materials and Methods

Study area

Seed output, in 2003, of *D. corymbosa* Spruce ex Benth. was assessed in monodominant *D. corymbosa* forest along the Upper Potaro River in Guyana's Pakaraima Mountains. Study plots were located within a 5-km radius of a permanent base camp at 5°18'04.8" N; 59°54'40.4" W, elevation 710 m. The site was situated in an undulating valley \approx 20 km east of Mt Ayanganna, and was densely forested with a mosaic of primary *Dicymbe*-dominated and mixed forests of the *Eschweilera-Licania* association (Fanshawe, 1952). Regional synchrony of *Dicymbe* seed production was assessed along a 37-km transect from the Upper Potaro to the Upper Ireng River. Details of climate, geology, soils and forest structure have been published previously (Henkel *et al.*, 2002; Henkel, 2003).

Study plots

Five 0.25-ha plots were randomly positioned at the Potaro site within larger areas of monodominant *D. corymbosa* forest. Plot 1 (P1) was located 3 km west-south-west from the base camp on level terrain of well-drained sandy loam soil. Plot 2 (P2) was situated 0.3 km southeast of the base camp on a level ridgeline on ironstone clay soil. Plot 3 (P3) was located 1.2 km south-east of P2, on the same ridge, on soils rich in

finely eroded ironstone. Plot 4 (P4) was situated 0.7 km east of P1 on poorly drained sandy loam soil. Plot 5 (P5) was located 0.5 km south of the base camp on a gentle, west-facing slope, on ironstone clay soil.

Forest structure

Within each Potaro plot, all trees ≥ 10 cm diameter at breast height (d.b.h.) (1.3 m above the ground) were measured for d.b.h. Trees with buttresses at 1.3 m were measured immediately above the buttresses. Methods for determining basal areas of multistemmed *Dicymbe* trees can be found in Henkel (2003). Trees were assigned to plant families and identified to genus and species when possible, or otherwise assigned to morpho-species (Richards, 1996). Basal area and number of stems were calculated for each tree species in the plots. Seedlings and saplings of *D. corymbosa*, established before 2003, were subsampled in twenty 9-m² subplots randomly positioned to assess seed fall in each of P1–P4; in P5, seedlings were counted under each of thirty-one 3.5-m² suspended litter-fall traps. Saplings were defined as woody individuals when ≥ 1 m in height but < 10 cm d.b.h.; seedlings were < 1 m in height.

The crown area was estimated for all *D. corymbosa* individuals that were ≥ 10 cm d.b.h. in each plot. For each tree, the distance from the base to the outer crown edge was measured in each of four cardinal directions. The mean crown radius was calculated and used to estimate the total crown area of *D. corymbosa* in each plot.

Soils

Edaphic characteristics of the *D. corymbosa* stands were determined for P1–P4. Logistical difficulties prevented the sampling of soils in P5. A-horizon subsamples were collected at a 10-cm depth in the mineral soil beneath the leaf litter at four points surrounding four random locations within each plot. These subsamples were bulked, air-dried and passed through a 2-mm sieve to produce a final 100 g of sample ($n = 4$ per plot). Upon returning from the field, soils were stored at 5°C until analyzed.

Soil texture was determined by using standard particle size analysis (ASTM, 1998); the levels of extractable P, Ca, Mg and Al were determined by using Mehlich III extraction (Mehlich, 1984); pH was determined by using the methods of McClean, 1982; the organic matter content was estimated by using ashing procedures (Storer, 1984); and the cation exchange capacity (CEC) was assessed by using a modified summation of the Mehlich III-extracted cations and hydrogen (Sumner & Miller, 1996).

Fruit fall, seed predation, germination and tree fertility

In total, twenty 9-m² ground traps were randomly positioned in each of P1–P4 for seed and fruit valve counts resulting from

the 2003 mast fruiting event (the sample area was 180 m² per plot). Initially, 10 of these subplots were established in early July, 2003, to assess the phenology of seed fall. The second group of 10 subplots was established in early August to obtain one-time seed counts near the end of the dispersal period; these subplots were then utilized to follow the establishment of 2003 cohort seedlings. In P5, 31 suspended seed traps were randomly positioned in early July. These traps were constructed of fibreglass screening and attached to four wooden stakes ≈ 1 m above the ground (the areas were 3.5 m² per trap and 108.5 m² per plot), with positions adjusted by 1–2 m to the closest location free from obstructions (e.g. saplings).

On P1–P4, seed and fruit valves were counted at 5-d intervals, in the first traps established, from July 5 to August 11. A final late season count was obtained on August 30. Seeds and fruit valves were removed, counted and visually assessed for seed-predator damage at each 5-d interval. Predation categories, based on direct observation of predators and characteristic damage symptoms, included: (1) harvester ant damage, postdispersal; (2) arthropod (putatively collembolan) larval damage, predispersal; and (3) fungal damage, evidenced by hyphal growth and putrescence of seed flesh. Vertebrate damage was qualitatively assessed by noting tooth marks, ground disturbance and other signs of vertebrate presence. Germination of seeds was assessed within the 5-d intervals. In the second set of 10 ground traps established in P1–P4, seeds and fruit valves were counted in place (not removed), once, between August 5 and 8. This provided a total mast seed output sample of $n = 20$ per plot, with $n = 10$ for subsequent seedling establishment studies. In P5, suspended trap seeds and valves were counted at 5-d intervals and removed, with only predispersal predation assessed. Seeds were randomly placed beneath the traps for the subsequent tracking of seedling establishment. Screens were removed on September 1.

To assess seed fall 1 year postmast, seed traps in the Potaro plots were revisited on July 10 and August 5, 2004, and any freshly fallen seeds were counted.

To estimate local synchrony of seed production, the fertility of individual trees was assessed. The dense crowns of the *D. corymbosa* trees prevented accurate visual determination of fruit-bearing trees. As an alternative method, in mid-August the fertility of each *D. corymbosa* tree of 10 cm d.b.h. was estimated by scoring whether or not a tree had accumulated seeds and fruit valves at its immediate base.

Dry mass and mineral nutrient investment of masting

Freshly fallen seeds ($n = 150$) and fruit valves ($n = 120$) were randomly collected from various plots in mid-July and weighed after drying. The dry mass of seeds and fruit valves was estimated for each plot by multiplying the mean dry weights of seeds and fruit valves by the mean number per m²

of each respective fruit part. To obtain an estimate of mast flower dry mass, 1-m² subplots were randomly positioned within each plot ($n = 10$ for each of plots P1–P4; $n = 31$ for plot P5) and previously fallen buds, bracteoles and perianth parts were collected from the ground. Before weighing, all fruit and flower parts were air-dried followed by drying, for a minimum of 72 h, over low heat until a constant weight was obtained. Dry mass values were reported on a kg ha⁻¹ basis.

To determine the mineral nutrient concentrations of reproductive components, mature seeds, valves and flower parts were collected and dried with silica gel beads for a minimum of 36 h until a constant weight was obtained ($n = 4$ for each). Samples were stored in humidity-free containers at ambient temperature until returning from the field. Samples were analyzed for percentage N by flash combustion and gas chromatography (AOAC, 2003), and the percentage of P, Ca and Mg was determined by an acid digest and emission spectrometry (Gavlak *et al.*, 2003). Mast mineral investment for each plot was estimated by multiplying the mean nutrient concentration of each reproductive component by the mean quantity of that component per m²; summed component mineral quantities were reported on a kg ha⁻¹ basis.

Mechanical dispersal of *D. corymbosa* seeds

In mid-July, four *D. corymbosa* trees, > 100 cm d.b.h. and free from crown overlap with conspecifics, were chosen. For each tree, a line transect was laid out from the base in each of four cardinal directions and the distance to the outer crown edge was recorded. Seeds were counted from the tree base outwards on each transect, in successive 1 × 2 m intervals, until the counts reached zero. The mean crown radius was determined for each tree, and the percentage of seeds that had fallen within the mean crown radius was calculated.

Seedling establishment, survival and mortality

Pre-2003 seedlings and saplings and 2003 cohort seedlings were tagged on subplots in late August 2003 and the initial densities were determined ($n = 10$ for P1–P4; $n = 31$ for P5). Sapling densities were not obtained in P5. Subplots were revisited at 6- and 12-month intervals, and surviving pre-2003 seedlings and saplings, and 2003 seedlings, were counted.

Mortality agents of 2003 seedlings were assessed on 50 dead seedlings ($n = 10$ per plot) randomly collected from outside the sampling subplots. Seedlings were scrutinized for signs of animal and fungal damage.

Regional synchrony in seed production

To assess regional synchrony in seed production, three spatially disjunct, 0.25-ha *D. corymbosa* plots were established in mid-August, 2003, along a 37-km transect from the Potaro

site south to the Upper Ireng River. All plots were randomly positioned in upland monodominant *D. corymbosa* forest. Distances of the plots from the Potaro base camp were as follows: plot 6 (P6), 15 km; plot 7 (P7), 22 km; and plot 8 (P8), 36 km. For each plot, ten 9-m² ground traps were randomly positioned and *D. corymbosa* seeds were counted on a single date and assessed for predation, as described previously in the section 'Fruit fall, seed predation, germination and tree fertility'.

Climatic data

To examine the possible concurrence of *D. corymbosa* masting and El Niño Southern Oscillation (ENSO) events, satellite data for outgoing long wave radiation (OLR) anomalies and ground-based data for precipitation anomalies on a 2.5 × 2.5 deg. lat/lon grid resolution scale centered on the Potaro site (5° N, 60° W), were downloaded for the period 1996–2004, encompassing the previous two *D. corymbosa* masting events (International Research Institute for Climate Prediction: <http://iridl.ldeo.columbia.edu/maproom/.Global/>). Monthly OLR anomalies (deviation from the long-term monthly mean) are inversely correlated with cloud cover and precipitation, climatic factors which are greatly reduced in north-eastern South America in the months following a strong ENSO event in the central Pacific (Kogan, 2000). If ENSO teleconnections affect the Pakaraima Mountains, OLR anomalies should have risen and precipitation anomalies fallen in the months following significant rises in equatorial Pacific sea surface temperature. Additionally, anecdotal information concerning dry season conditions following recent El Niño events was obtained from Patamona Amerindians inhabiting the central Pakaraima Mountains.

Results

Forest structure and soils

Basal area and stem density for *D. corymbosa* and combined mixed forest woody species, and the crown area only of *D. corymbosa*, were calculated for P1–P5. *D. corymbosa* was dominant on P1–P5, ranging from 82 to 94% of the stand basal area, 32–72% of individual trees, with crown areas 83–193% of the plot area (Table 1). Crown areas of > 100% in P2–P4 were caused by overlapping crowns and dense mid-story reiteration. The relative density and frequency of *D. corymbosa* seedlings and saplings established before the 2003 mast were calculated for their subsampled areas. Pre-2003 recruitment by *D. corymbosa* was high in the plots, with seedlings ranging from 2 to 7 m⁻² in P1–P5 at a high frequency among the subplots (100% of subplots in P1–P4; 97% of subplots in P5). Saplings on P1–P4 ranged from 0.05 to 0.3 saplings m⁻² (60–80% frequency). Other tree species contributed few trees of large diameter. Commonly occurring

Table 1 Stand structure of *Dicymbe corymbosa* relative to all mixed forest tree species for five 0.25-ha masting study plots in the Upper Potaro site, Pakaraima Mountains, Guyana^a

Species	No. of trees ^b	Basal area (m ²)	Crown area (m ²)	Density (%)	Dominance basal area (%)	Dominance crown area ^c (%)	No. of seedlings ^d (freq.)	No. of saplings (freq.)
<i>Dicymbe corymbosa</i>	38 ± 6.6	15.4 ± 1.5	3078 ± 466	50.8 ± 7.7	88.9 ± 1.9	119.3 ± 19.4	642 ± 160.2 (99.4)	57.3 ± 9.9 (72.5)
range	23–57	13–21.2	2084–4834	32.4–72.2	82.4–94	83.4–193.4	400–1255	33–81
Mixed spp.	39 ± 8.6	1.94 ± 0.4	–	49.2 ± 7.7	11.1 ± 1.9	–	–	–
range	15–57	1–2.8	–	27.8–67.6	6–17.6	–	–	–

^aValues represent the mean ± standard error of the mean for $n = 5$ plots.

^bTrees were individuals of 10 cm diameter at breast height.

^cDominance crown area: cumulative crown areas of *D. corymbosa* as percentage of total area of plot.

^dSeedlings/saplings: total number of *D. corymbosa* seedlings/saplings in 20 3 × 3 m² subsampling units in P1–P4; 31 1 × 3.5 m² subsampling units in P5 (seedlings only); the total area sampled/plot was 180 m² in P1–P4; 108 m² in P5 (freq.: percentage of subsamples containing seedlings/saplings); *D. corymbosa* seedlings were < 1 m tall; saplings were 1 m, but < 10 cm diameter at breast height.

Table 2 Soil physical and chemical characteristics in four 0.25-ha *Dicymbe corymbosa* masting study plots at the Upper Potaro site, Pakaraima Mountains, Guyana^{a,b}

Plot	Clay (%)	Silt (%)	Sand (%)	Organic matter (%)	pH	CEC (meq 100 g ⁻¹)	P (mg kg ⁻¹)	Ca (mg kg ⁻¹)	Mg (mg kg ⁻¹)	Al (mg kg ⁻¹)
P1	15.7 (1.3)	17.8 (0.9)	66.5 (0.7)	6.8 (0.6)	5.3 (0.2)	2.6 (0.4)	7.5 (0.9)	250.5 (75.6)	20.8 (2.1)	1056 (40)
P2	40.7 (2.8)	20.6 (1.0)	38.7 (2.4)	13.8 (0.4)	4.9 (0.2)	1.4 (0.2)	6.3 (0.6)	78.3 (8.4)	17.8 (1.8)	617 (13)
P3	7.8 (5.0)	16.3 (3.8)	76.0 (8.6)	11.5 (1.0)	4.6 (0.1)	3.4 (0.5)	9.5 (1.9)	164.3 (35.4)	35.0 (3.9)	454 (55)
P4	11.7 (2.9)	14.4 (1.3)	73.9 (4.0)	3.0 (0.8)	4.9 (0.1)	2.8 (0.9)	11.5 (2.5)	188.3 (85.6)	26.5 (0.3)	1337 (36)

^aValues represent the mean (standard error of the mean) for the upper 10 cm of mineral soil ($n = 4$ bulked subsamples per plot).

^bValues for P, Ca, Mg, and Al are Mehlich III extractable fractions.

CEC, cation exchange capacity.

species included *Eschweilera sagotiana* Miers (Lecythidaceae), *Licania laxiflora* Fritsch and *L. heteromorpha* var. *perplexans* Sandwith (Chrysobalanaceae), and *Macrolobium* sp. (Caesalpinaceae) (Henkel, 2003). The mean and variance for soil parameters were calculated for P1–P4. Soils were variable in texture but uniformly acidic and low in extractable P (6.3–11.5 mg kg⁻¹; Table 2).

Seed output, phenology, dispersal and synchrony of seed production

The mean and variance values for *D. corymbosa* seed output during the 2003 mast were calculated for P1–P8 and ranged from 6.6 ± 0.81 to 16.1 ± 2.3 seeds per m² on P1–P5, yielding estimates of 66 056 to 161 056 seeds per hectare (Table 3). To examine interplot variation in seed output, the mean values for P1–P8 were log-transformed and analyzed with analysis of variance (ANOVA) followed by Student–Newman–Keul's multiple comparison. Plot 2 had significantly lower seed output ($P = 0.05$) but still yielded tens of thousands of seeds per hectare.

In P1–P5, seed fall was generally higher through July as periodic afternoon sunshine, concurrent with the waning rainy season, drove the explosive dehiscence of mature fruits;

Table 3 Total outputs and percentage predation of *Dicymbe corymbosa* seeds over an 8-wk sampling period during the 2003 masting event in five 0.25-ha study plots at the Upper Potaro site and in three 0.25-ha plots on a 37-km Potaro-Ireng transect, Pakaraima Mountains, Guyana

Plot	Seeds (m ⁻²)	Seeds ha ⁻¹	Predispersal predation (%)	Postdispersal predation (%)
1	16.1 ± 2.3 ^b	161 056	4.0	3.2
2	6.6 ± 0.8	66 056	17.1	3.9
3	13.4 ± 1.4	132 723	7.6	5.6
4	12.8 ± 1.4	126 779	6.8	3.3
5	13.5 ± 1.3	138 005	–	–
6 ^a	2.5 ± 0.7	25 612	12.0	6.0
7 ^a	7.0 ± 1.8	70 559	3.3	5.8
8 ^a	10.7 ± 3.5	107 861	6.0	1.7

^aPotaro-Ireng transect plots. Distance from Upper Potaro site: plot 6, 15 km; plot 7, 22 km; and plot 8, 36 km.

^bValues represent the mean ± standard error of the mean; $n = 20$ for plots 1–4 and 6–8, $n = 31$ for plot 5.

seed fall had decreased to low levels by mid-August (Fig. 1). The minimal number of seeds caught at the late August date indicated that sampling had encompassed the majority of the seed fall period.

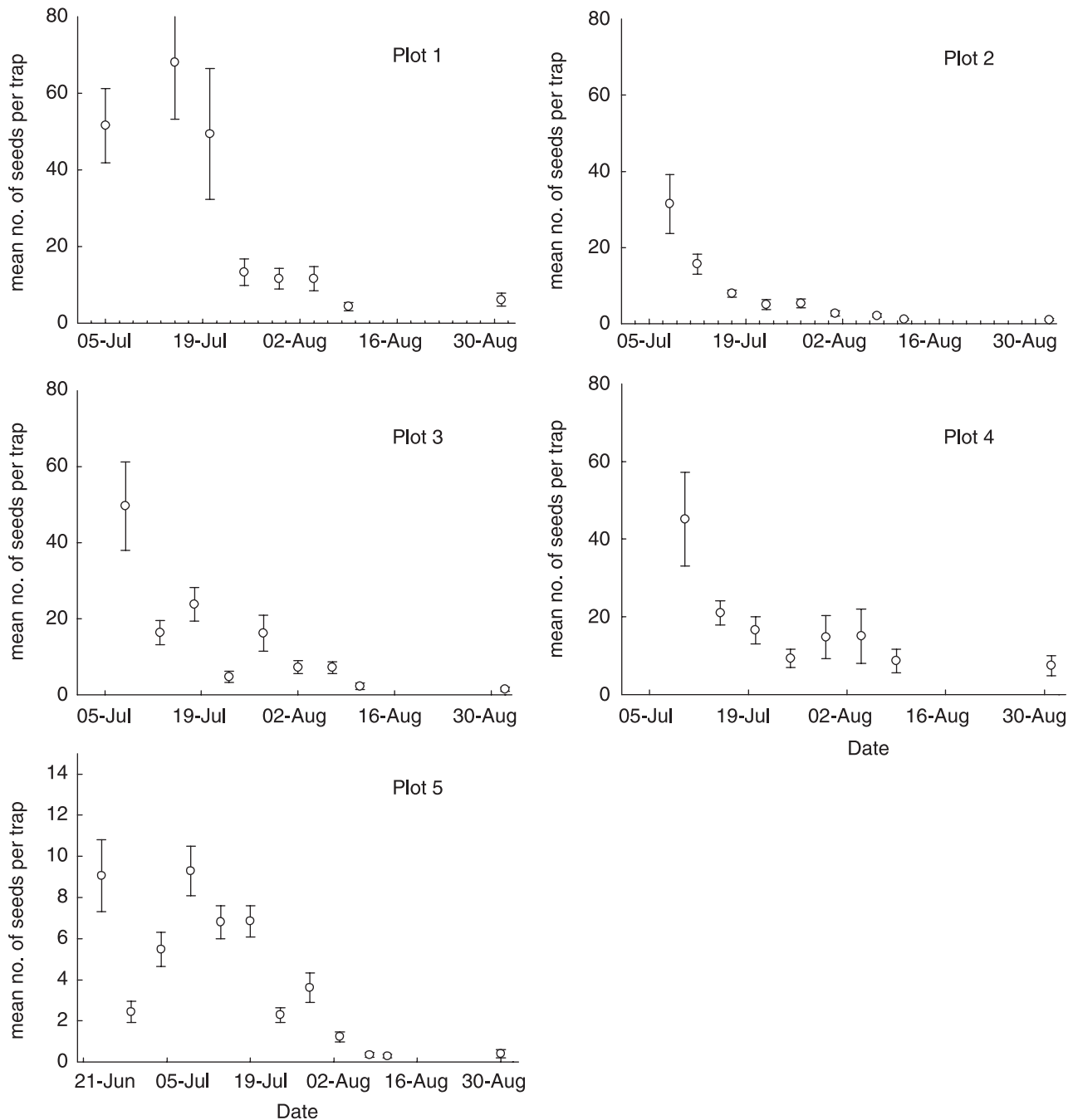


Fig. 1 Phenology of *Dicymbe corymbosa* mast seed fall from late June to late August, 2003, in five 0.25-ha study plots at the Upper Potaro study site, Pakaraima Mountains, Guyana. Values represent the mean (and error bars the standard error of the mean) of samples taken at 5-d intervals; the first value in each plot indicates the mean number of seeds present in the ground area of traps at the onset of sampling; the last value is a late-season count performed 2–3 wk after the last 5-d count. For plots 1–4, the ground trap area is 9 m² ($n = 10$); for plot 5, the suspended trap area is 3.5 m² ($n = 31$).

Local fruiting synchrony was evidenced by similar seed fall phenologies in P1–P5. Synchrony across plots was also inferred from the high frequency of randomly positioned seed traps receiving seeds (100%) in each plot and the percentage of putatively fertile *D. corymbosa* trees (73–84% among plots

by August 10). *D. corymbosa* flower parts occurred at high densities on the forest floor and were uniformly distributed throughout P1–P5 (mean dry weight: 41.1–71.1 g m⁻², 100% of subsamples), suggesting uniformity among the stands in the preceding mass flowering event. Mechanical dispersal of

the large (3–4 cm diameter), explosively dehisced *D. corymbosa* seeds was poor; the sample of four isolated *D. corymbosa* trees indicated that 88.9–96.6% of seeds fell within the mean crown radius of each respective tree.

D. corymbosa-dominated forest occurred over 70% of the 37-km Potaro-Ireng transect. Within this extensive forest, the regional masting synchrony of *D. corymbosa* was confirmed on P6, P7 and P8 at distances of 15, 22 and 36 km from the Potaro site. On P6–P8, seeds from the 2003 mast occurred at densities of 2.5–10.7 m⁻² (Table 3).

Seed production: 2004

No *D. corymbosa* seeds were found in grounds traps in any of the Potaro plots (P1–P5) on July 10 and August 5, 2004. Additionally, forest traverses revealed no seeds or fruit valves on the forest floor, although some riverside *D. corymbosa* trees bore a few immature fruits.

Seed predation

Predation of 2003 *D. corymbosa* seeds was low and limited to arthropods and fungi, with no evidence of vertebrate damage (Table 3). Within the 5-d sampling intervals on P1–P4, postdispersal seed predation was limited to harvester ants and ranged from 3.2 to 5.6%. Predispersal predation occurred primarily by larvae observed infesting seeds within fruits before dispersal and secondarily by fungi apparently introduced within the fruits by larval activity. Larval predation ranged from 3.4 to 5.5% on P1, P3 and P4, but (at 15.6%) was higher on P2; fungal predation ranged from 0.6 to 2.6% on P1–P4. Combined predation ranged from 7.1 to 21.1% on P1–P4. A low percentage of seed predation was corroborated on P6–P8 (Table 3).

Seed germination

Epigeal seed germination was rapid in *D. corymbosa*; within the 5-d sampling intervals, germination ranged from 10.7 to 25.7% on P1–P4.

Dry mass and mineral nutrient investment in masting

Dry mass and mineral nutrient investment in masting by *D. corymbosa* was determined for P1–P5 on a per m² basis and reported on a per hectare basis. Stand-level dry mass production of *D. corymbosa* fruiting and flower parts was high, ranging from 2225 to 4082 kg ha⁻¹ on P1–P5 (Table 4). The mean (\pm standard error) dry weight of *D. corymbosa* seeds was 5.1 \pm 0.1 g, with seeds constituting 15–29% of the reproductive mass, while fruit valves (mean dry weight: 12.6 \pm 0.5 g) comprised 54–65% of the reproductive mass, with the remainder composed of flower parts. Stand-level investment in N for the combined reproductive parts ranged from 21.2

Table 4 Dry mass and mineral nutrient investment^{a,b} of *Dicymbe corymbosa* associated with the 2003 masting event in five 0.25-ha study plots at the Upper Potaro site, Pakaraima Mountains, Guyana

Plot	Dry mass (kg ha ⁻¹)	N (kg ha ⁻¹)	P (kg ha ⁻¹)	Ca (kg ha ⁻¹)	Mg (kg ha ⁻¹)
1	4082	39.3	2.0	6.2	3.3
2	2225	21.2	0.9	3.5	1.8
3	3200	33.0	1.6	5.4	2.7
4	2909	30.6	1.6	5.0	2.6
5	2400	23.8	1.5	3.5	2.0
Mean \pm SE	2963 \pm 330	29.6 \pm 3.3	1.5 \pm 0.2	4.7 \pm 0.5	2.5 \pm 0.3

^aFor calculation of the dry mass, the seeds, fruit valves, and flower parts found per m² were each multiplied by their mean dry weight, summed, and reported on a per hectare basis for each plot.

^bFor determination of mineral nutrients, the seeds, fruit valves, and flower parts found per m² were each multiplied by their mean concentration, summed, and reported on a per hectare basis for each plot. The mean nutrient concentrations in various reproductive parts were as follows. Seeds: N, 1.2%; P, 0.2%; Ca, 0.1%; Mg, 0.1%. Valves: N, 0.8%; P, 0.02%; Ca, 0.13%; Mg, 0.06%. Flower parts: N, 2.0%; P, 0.05%; Ca, 0.4%; Mg, 0.2% ($n = 4$ for all parts).

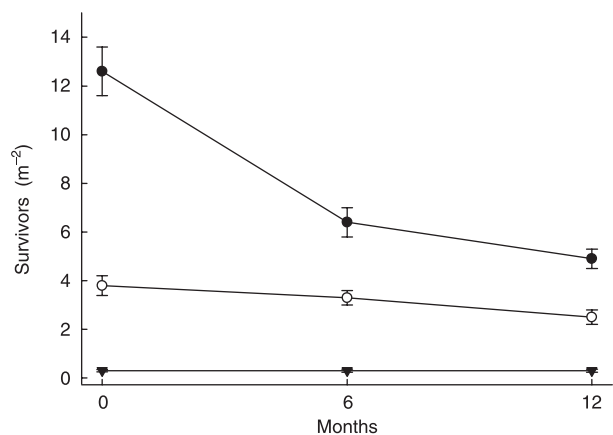


Fig. 2 Twelve-month survivorship curves for pre-2003 *Dicymbe corymbosa* seedlings and saplings, and 2003 mast cohort seedlings, at the Upper Potaro site, Pakaraima Mountains, Guyana. Values shown represent the mean (and error bars the standard error of the mean) number of living seedlings or saplings per m² for each cohort, all plots combined; for pre-2003 and 2003 seedlings, the values are derived from $n = 71$ subplots on plots 1–5 first standardized to a m² basis (a total area of 468.5 m²); sapling values are derived from $n = 40$ subplots on plots 1–4 (a total area of 360 m²). Closed circle, 2003 seedlings; open circle, pre-2003 seedlings; inverted closed triangle, saplings.

to 39.3 kg ha⁻¹; for P, 0.9–2 kg ha⁻¹; Ca, 3.5–6.2 kg ha⁻¹; and Mg, 1.8–3.3 kg ha⁻¹ (Table 4).

Seedling survivorship

Survivorship curves were plotted from the global means of surviving 2003 seedling cohort and pre-2003 seedlings and

saplings at 0-, 6- and 12-month intervals following the 2003 masting event. Figure 2 shows initial seedling and sapling densities and 6- and 12-month survivorship for the pooled Potaro plots. One year following the mast, $\approx 40\%$ of the 2003 seedlings had survived, yielding a mean density of five seedlings per m^2 ; with inclusion of the pre-2003 seedlings, a total seedling density of $> 8 \text{ m}^{-2}$ was maintained among the plots. Saplings exhibited no mortality at a mean density of 0.3 m^{-2} . The 2003 seedlings exhibited higher mortality ($\approx 60\%$) relative to the pre-2003 seedlings ($\approx 20\%$) and saplings (0%) over the 12-month postmast sampling period. Overall, the recruitment bank maintained by *D. corymbosa* 1 year postmast was 41 000–92 000 seedlings per hectare and 1800–4500 saplings per hectare, densities similar to those determined previously (Henkel, 2003).

ENSO-related climate effects and *D. corymbosa* masting

Figure 3 shows sea surface temperature anomalies from 1995 to 2004 in the four El Niño regions of the equatorial Pacific, indicating the elevated anomalies associated with the 1997 and 2002 ENSO events. The 1997 ENSO event was one of the strongest of the 20th century, and resulted in extreme drought conditions in north-eastern South America (Hammond & ter Steege, 1998; Kogan, 2000). The 2002 event, although of lesser intensity, also resulted in drought in Guyana (T. W. Henkel, pers. obs.). Amerindians occupying the central Pakaraimas reported dramatic increases in daily sunshine in the 1997–98 and 2002–03 dry seasons, greatly reduced river and stream levels, and numerous accidental forest fires associated with slash-and-burn farming. ENSO effects in the Pakaraima Mountains were evidenced by extended periods of above-average OLR and below-average precipitation from July 1997 to March 1998 and from August 2002 to April 2003; the last two mast fruitings of *D. corymbosa* occurred at the end of these time-periods (Fig. 4).

Discussion

Mast seed output and phenology

In 2003, high seed outputs of *D. corymbosa* constituted a large, synchronized reproductive effort. Seed outputs of 66 056–161 056 ha^{-1} were on par with or greater than those reported for other masting caesalps, such as *Microberlinia bisulcata* (83 000 ha^{-1} ; Green & Newbery, 2002) and *Gilbertiodendron dewevrei* (10 721 ha^{-1} ; Gerard, 1960) in Guinea-Congolian Africa, and *Dicymbe altsonii* (52 000 ha^{-1} ; Zagt, 1997) in Guyana. The peak seed output of *D. corymbosa*, observed to occur in July, facilitated rapid postdispersal seedling establishment, with sufficient sun to drive fruit dehiscence yet ample soil moisture for seedlings to root. This pattern of rainy season seed dispersal, also observed in 1998

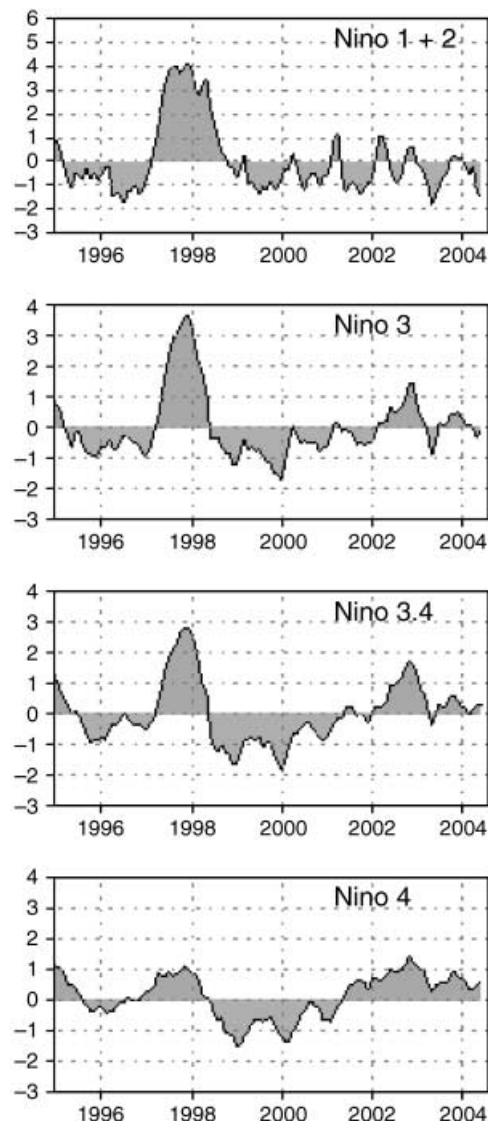


Fig. 3 Sea surface temperature anomalies in the four El Niño regions of the central Pacific Ocean, from 1995 to 2004. Monthly fluctuations in the sea surface temperature ($^{\circ}\text{C}$), around the 28°C baseline temperature, are shown. Nino 1+2: 0° – 10°S , 80° – 90°W . Nino 3: 5°S – 5°N , 150°W – 90°W . Nino 3.4: 5°S – 5°N , 170°W – 120°W . Nino 4: 5°S – 5°N , 160°E – 150°W (source: <http://iridl.ldeo.columbia.edu/maproom/.Global/>).

for *D. corymbosa* (Henkel, 2003), was consistent with that of other large-seeded, barochorous tree species, such as *Mora excelsa*, *M. gongrijpii*, *Eperua falcata*, *D. altsonii* and *Chlorocardium rodiaei* in Guyana (ter Steege & Persaud, 1991; Hammond & Brown, 1995; Zagt, 1997), *G. dewevrei* and *Tetraberlinia* spp. in Africa (Hart, 1995; Green & Newbery, 2002), and many Malesian dipterocarps (Chan, 1980; Ashton, 1987), exhibiting dominance with shade tolerant seedlings under low disturbance regimes.

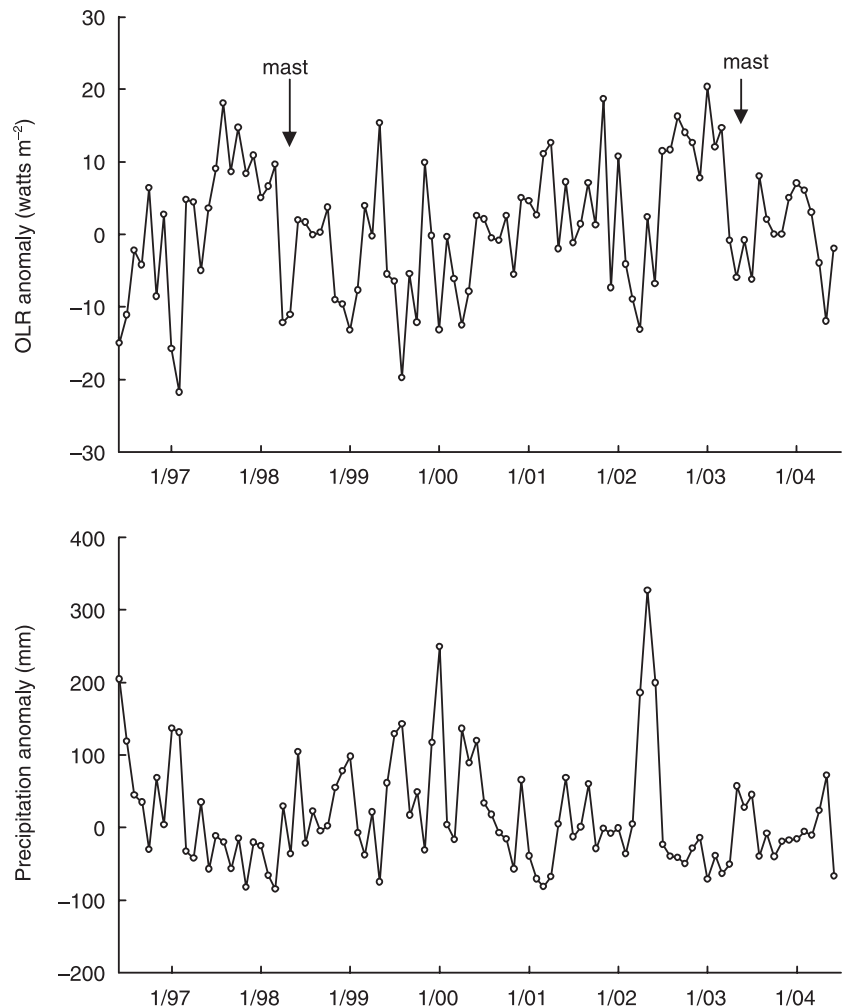


Fig. 4 Monthly outgoing long-wave radiation (OLR) and precipitation anomalies from May 1996 to June 2004 and time of the previous two mast fruitings of *Dicymbe corymbosa* in the central Pakaraima Mountains, Guyana. The OLR anomaly is departure of the monthly OLR from the long-term monthly mean; negative anomalies imply increased cloudiness and enhanced probability of precipitation; positive anomalies imply decreased cloudiness/precipitation (satellite data); precipitation anomaly is departure of the monthly precipitation from the long-term monthly mean (ground data). Data are derived from a 2.5×2.5 deg. lat/long grid centered on 5° N and 60° W (source: <http://iridl.ldeo.columbia.edu/maproom/.Global/>).

Mast variability, synchrony and periodicity in *Dicymbe corymbosa*

Mast fruiting in a tree species has three key elements: interannual variability in fruit production, synchrony and periodicity (Kelly & Sork, 2002). Population-level variation of a masting species results from the interaction of individual variability in seed output over time and synchrony among these individuals (Koenig *et al.*, 2003). For the 2003 masting event, *D. corymbosa* exhibited high seed output on all plots, and local and regional synchrony, followed by no detectable seed output in 2004. Masting periodicity of *D. corymbosa* was inferred from observations of mastings in 1993, 1998 and 2003, with little or no seed production in the intervening years or 2004 (T. W. Henkel, pers. obs.; this study). This putative 5-year masting cycle is consistent with that of a 'normal, bimodal' masting species (*sensu* Kelly, 1994) exhibiting multiyear intermast periods with minimal seed production, punctuated by large fruiting episodes. Annual monitoring of seed production through the next masting cycle will shed light

on the intermast variability in *D. corymbosa* and allow a more accurate calculation of the coefficient of variation for the species (Kelly, 1994).

Resource investment and the role of ectomycorrhizas in masting

The nearly 3 t ha^{-1} mean dry mass of *D. corymbosa* mast litterfall far exceeded the range of $0.2\text{--}1.3 \text{ t ha}^{-1}$ annual reproductive litterfall over 18 pantropical sites reported by Proctor (1984) and was greater than that reported for individual masting events for the caesalps *D. altsonii* (2 t ha^{-1} ; Zagt, 1997) and *M. bisulcata* (1.3 t ha^{-1} ; Green & Newbery, 2002), Bornean dipterocarps ($1.3\text{--}1.56 \text{ t ha}^{-1}$; Curran & Leighton, 2000, as reported in Green & Newbery, 2002), and North American oaks (1.12 t ha^{-1} ; Sork *et al.*, 1993, as reported in Green & Newbery, 2002). Mast litterfall values comparable to those for *D. corymbosa* were reported by Singh *et al.* (1990) for the Himalayan oaks, *Quercus leucotrichophora* and *Q. floribunda*, as 3.5 t ha^{-1} in exceptional mast years,

with a normal mast year of 2.5 t ha^{-1} . In terms of mineral nutrients, the *D. corymbosa* mean nitrogen investment of 29.6 kg ha^{-1} was 2–10-fold higher, and the mean phosphorus investment of 1.5 kg ha^{-1} was 2–5-fold higher, than values reported by Proctor (1984) and Green & Newbery (2002); the phosphorus investment was similar to the value of 1.3 kg ha^{-1} for *D. altsonii* reported by Zagt (1997). While carbon and mineral investment in mast reproduction thus appears to be high in *D. corymbosa*, data are currently lacking on leaf litter production in the species, which would allow a more complete assessment of relative resource investment with masting.

The apparently large amount of carbon and minerals devoted to masting by *D. corymbosa* is consistent with resource depletion incurred and implies that a long intermast period may be necessary to recover from such an event (Janzen, 1974; Kelly, 1994; Newbery *et al.*, 1998). During masts, *D. corymbosa* may divert resources away from vegetative growth and allocate them to reproduction. The cost of reproduction, in terms of depressed vegetative capacity, is well demonstrated for masting plants (Eis *et al.*, 1965; Harper, 1977; Norton & Kelly, 1988). According to the model of Lalonde & Roitberg (1992), fluctuating and synchronized seed production in weather-entrained masting species can occur over a wide range of reproductive and vegetative costs; as these costs increase, the greater the degree of oscillation in seed output and thus the likelihood of years of no seed production. *D. corymbosa* seemed to conform to this model; the apparent masting periodicity is coupled with high vegetative maintenance costs, as evidenced by stand basal areas in the upper range for tropical forests worldwide, and continual reiterative shoot production to compensate for canopy shoot turnover of large reproductive individuals (Henkel, 2003). Large trees generally sustain the greatest respiratory loads (Kozłowski *et al.*, 1991). Extensive below-ground vegetative allocation has been suggested for *D. corymbosa* (Henkel, 2003); fine roots supported a robust community of ectomycorrhizal mycobionts, critical for mineral recycling but requiring large carbon subsidies from the host (Fogel & Hunt, 1979; Vogt *et al.*, 1982; Henkel *et al.*, 2002). These vegetative demands, along with high fruit production costs, may require an extended intermast period for proper functioning, and dictate low seed years (Harper, 1977; Rathcke & Lacey, 1985).

Soils of *D. corymbosa* forests were universally low in available P and other mineral nutrients, yet mineral investment in masting was substantial. As P most often limits plant growth in tropical forests (Vitousek & Sanford, 1986, but see Newbery *et al.*, 2002), an efficient ectomycorrhiza-mediated nutrient recycling mechanism may be necessary to replenish P and other minerals lost to mast flowering and fruiting. *D. corymbosa* was strongly ectomycorrhizal in all age classes, with ectomycorrhizal rootlets and extramatrical hyphae of adults abundant in litter and upper soil strata (Henkel, 2003; Mayor & Henkel, 2004). Ectomycorrhizal hyphae appear to

be highly effective at scavenging minerals from the soil solution (Finlay & Read, 1986; Newbery *et al.*, 1997; Moyersoen *et al.*, 1998) and may be able to obtain organic N and P compounds indirectly or directly from litter (Perez-Moreno & Read, 2000; Chuyong *et al.*, 2000). For *D. corymbosa*, both processes could result in a closed, ectomycorrhiza-mediated nutrient cycle, fundamental to resource recovery following masts, but necessarily energy-expensive for the host trees to maintain. Similar resource-allocation patterns have been suggested for ectomycorrhizal *D. altsonii* in Guyana (Zagt, 1997) and for *M. bisulcata* and *Tetraberlinia* spp. in Cameroon (Newbery *et al.*, 1998).

Seed predation

While full confirmation of predator satiation must demonstrate higher percentage seed predation during small seed crop years, the low rate of invertebrate and fungal predation (7–21% among plots), the absence of detectable vertebrate predation, and the high rate of seedling establishment associated with the 2003 mast, rendered seed predation irrelevant in determining the fate of *D. corymbosa* seeds. The rapid germination and seedling establishment of *D. corymbosa*, coupled with the lack of mechanical seed defence structures, suggests that *D. corymbosa* may have engaged in predator escape (Hammond & Brown, 1998). The likelihood of this strategy was reinforced by the extremely low phenolic content of *D. corymbosa* seeds (0.04 mg kg^{-1} , $n = 5$; T. W. Henkel, unpublished), suggesting that chemical defence was not at play. Additionally, animal densities, including seed predators such as peccaries and various scatterhoarders (e.g. agoutis), were lower in nutrient-poor regions of the Neotropics, including the Guianas (Emmons, 1984; Gentry & Emmons, 1987), and were greatly reduced in climax, caesalp-dominated rainforests of central Africa (Brugiere *et al.*, 2002). Such relative paucity of vertebrates in highly oligotrophic regions, such as the Guiana Shield, may limit the current impact of seed and seedling predation, suggesting prior evolutionary selective forces for masting (Janzen, 1971, 1974; Waller, 1993).

Seedling establishment and survivorship

The 2003 mast established a dense, uniform seedling cohort of *D. corymbosa*. The higher mortality of the 2003 cohort seedlings postmast, relative to the pre-2003 seedlings and saplings, was consistent with patterns of heavy mortality of the early seedling stage demonstrated for tropical trees, including numerous dipterocarps (Wyatt-Smith, 1958; Ashton, 1987) and masting caesalps (Hart, 1995; Zagt, 1997; Green & Newbery, 2002). In *D. corymbosa* stands, the ratio of seedlings/saplings/trees implied considerable mortality over time. Additionally, large crown areas of monodominant *D. corymbosa* forests yielded a densely shaded understory likely to inhibit seedling and sapling photosynthesis. Yet, the homogenous

recruitment bank of *D. corymbosa* in all stands measured to date implies resistance in survivors to such suppression, probably at slow growth rates (this study; Henkel, 2003). The relatively flat 12-month mortality curves of the pre-2003 seedlings and saplings supported this idea. The ability to endure a long suppression period under heavy shade is a specialized characteristic of many late successional rainforest trees, often coupled with large, nutrient-rich seeds that allow seedlings to grow to a size where they may survive suppression (Pires & Prance, 1977; Hammond & Brown, 1995; Richards, 1996; Green & Newbery, 2001). In addition to apparent shade tolerance, *D. corymbosa* may achieve such ends through rapid ectomycorrhization of seedlings (> 90% by 12 months; T. W. Henkel, unpublished) and resulting enhanced soil water and mineral access, and, possibly, carbon, mineral, and water networking with neighbouring adult conspecifics via ectomycorrhizal connections (Henkel, 2003). Such mechanisms would tend to buffer seedlings from external mortality agents, leaving intraspecific competition as the main source of mortality ('self-thinning'; Janzen, 1974).

ENSO events and *D. corymbosa* masting

The concurrence of *D. corymbosa* masting with ENSO-intensified dry seasons was consistent with patterns observed in other tropical masting species. Reduced cloudiness, decreased precipitation, increased solar irradiance and above-average temperatures occur in most of the wet tropics following ENSO events (Ropalewski & Halpert, 1987; Aceituno, 1988; Diaz & Markgraf, 2000) and these effects are especially pronounced in northern South America (Kogan, 2000). ENSO droughts preceded masting in east Malesian dipterocarps (Ng, 1977; Van Schaik, 1986; Ashton *et al.*, 1988; Curran *et al.*, 1999) but not in west Malesia and the Philippines (Wich & Van Schaik, 2000; Hamann, 2004). Increased forest-wide fruit production followed above-average dry season irradiance in Central American rainforest trees (Wright *et al.*, 1999), and was implied by the long-term fruiting records for lowland trees of Guyana (ter Steege & Persaud, 1991; Thomas, 2001) and elsewhere in the tropics (Wright & Van Schaik, 1994). High dry season irradiance and low minimum night-time temperatures were strongly correlated with masting in *M. bisulcata* and *Tetraberlinia* spp. in Cameroon (Newbery *et al.*, 1998), and drought preceding mast was a strong predictor for masting in extra-tropical *Fagus* and *Quercus* spp. (Sork, 1993; Piovesan & Adams, 2001).

From a physiological standpoint, elevated irradiance during ENSO dry seasons may have allowed *D. corymbosa* to accrue photosynthates to threshold levels necessary for mast flower and fruit production, as well as providing the required entrainment cue (Janzen, 1978; Newbery *et al.*, 1998). Evidence suggests that tropical forests are radiation-limited, especially under cloudy conditions, and in most seasonal habitats 1.4–3-fold more new leaves and flowers are produced in the

dry season (Wright & Van Schaik, 1994). Recent accumulation of sunshine hours has been proposed as the underlying basis for mass flowering and fruiting in dipterocarps (Wycherley, 1973; Ng, 1977). Given the preponderance of large reproductive trees in the *D. corymbosa* stands and their high maintenance costs, photosynthesis during periods of ENSO-enhanced irradiance may contribute carbohydrates necessary for masting (Newbery *et al.*, 1998). Direct allocation of reproductive shoot photosynthates to fruit production has been shown for temperate trees (Chapin & Moilainen, 1991; McDowell *et al.*, 2000) and suggested for dipterocarps, which do not flower unless part of the crown is exposed to direct sunlight (Ashton, 1982). Ongoing studies are examining *D. corymbosa* ecophysiology and vegetative/reproductive resource allocation through the next masting cycle.

Implications for monodominance

The mast fruiting of *D. corymbosa* contributes to a suite of evolved life history traits that facilitate persistent monodominance. The enormous numbers of large, barochorous seeds produced during masting events, low seed and seedling predation, and resulting seedling establishment, allows *D. corymbosa* to maintain a robust recruitment bank through time, while stand resources are dominated by large, vegetatively regenerating individuals (Henkel, 2003). While the naturally coppicing individuals are long-lived and appear to be less subject to wind-throw than single-boled trees, they must eventually be replaced by sexual recruits, probably over centuries-long timescales. Self-replacement has been noted for other monodominant caesalps in Congolian Africa that successfully recruit via mast fruiting (e.g. *G. dewevrei*; Hart, 1995) and is consistent with numerous dominant tree species with large, poorly dispersed seeds recruiting under low light regimes elsewhere in Guyana (Davis, 1941; Hammond & Brown, 1995). Conversely, self-replacement of dominant West African tree species has long been questioned (e.g. Aubreville, 1938; Poorter *et al.*, 1996), and poor recruitment following mast fruiting has recently been documented for the codominant *M. bisulcata* in Cameroon (Newbery & Gartlan, 1996; Newbery *et al.*, 1998; Green & Newbery, 2002). The declining recruitment of *M. bisulcata* was attributed to climatic shifts over the past two centuries from excessively dry towards wetter, more densely shaded current conditions that are unfavorable to seedling establishment, leaving the *M. bisulcata* stands composed mostly of large, senescing canopy individuals (Newbery & Gartlan, 1996; Newbery *et al.*, 1998; Green & Newbery, 2001; Newbery *et al.*, 2004). With *D. corymbosa*, any recruitment failures caused by previous climatic fluctuations may have been buffered by the persistence of large, vegetatively regenerating reproductive individuals, preventing significant shifts in stand composition. The homogenous dominance of *D. corymbosa* in all size classes, from seedling to canopy, provides no evidence for such shifts, in concordance with the

low disturbance regimes and stable climate posited for the Guianas (Davis, 1941; Hammond & Brown, 1995; Henkel, 2003).

Evolutionary considerations

Mast fruiting occurs primarily in select, monophyletic woody plant groups with iteroparous reproduction (e.g. *Quercus* and *Fagus* in the Fagaceae and Pinaceae, Silvertown, 1980; Dipterocarpaceae, Ashton *et al.*, 1988). Masting probably evolved independently in ancestors of these phylogenetically distant groups and was retained during subsequent speciation and radiation (Janzen, 1974; Ashton *et al.*, 1988). In the Neotropics, interannual variation in seed production has been documented in canopy tree species of the Caesalpiniaceae, Lecythidaceae and Lauraceae (Sabatier, 1985; Wheelwright, 1986; ter Steege & Persaud, 1991; Forget, 1992) but in tropical South America bimodal masting appears to be restricted to *Dicymbe* (Zagt, 1997, this study). The paucity of masting species in Neotropical Caesalpiniaceae, the most abundant canopy tree family in the Guianas (ter Steege *et al.*, 2000), prompts us to question whether masting in *Dicymbe* evolved *in situ* or is a phylogenetically constrained trait of Gondwanan origin. *Dicymbe* is currently restricted to the Guayana Highlands, a distinct phytogeographic region with high plant endemism and Gondwanan relictual species (Maguire, 1970; Berry *et al.*, 1995; Chanderbali, 2001). In Guyana, *D. corymbosa* is restricted to protected, high-rainfall valleys in the Pakaraima Mountains, a region considered to be a refugium during prior climatic fluctuations (Davis, 1941; Fanshawe, 1952). *Dicymbe* and *Macrolobium* were traditionally considered to be the lone Neotropical representatives of the otherwise African tribe, *Amherstieae* (Cowan & Polhill, 1981). The recent phylogenetic analysis of Herendeen *et al.* (2003) implied a Gondwanan origin for *Dicymbe*. In that study, *Dicymbe* was sister to the West African *Polystemonanthus* and nested within a larger clade composed of African taxa including *Gilbertiodendron*, *Microberlinia*, *Tetraberlinia* and *Brachystegia*, species of which share the ectomycorrhizal habit, tendency toward forest dominance, and, in many cases, mast fruiting (Germain & Evrard, 1956; Gerard, 1960; Alexander, 1989; Hart, 1995; Newbery *et al.*, 1998). Interestingly, *Macrolobium*, traditionally placed in the *Amherstieae* based on floral morphology (Cowan & Polhill, 1981), was resolved in another clade containing strictly Neotropical taxa (Herendeen *et al.*, 2003). *Macrolobium* has been repeatedly shown to lack ectomycorrhizas, reinforcing that it is not, unlike *Dicymbe*, closely allied with African taxa (Bereau *et al.*, 1997; Henkel *et al.*, 2002). It appears unlikely that mast fruiting, the ectomycorrhizal habit, and a tendency to dominate forests, traits shared by many of these phylogenetically allied caesalps, evolved independently in *D. corymbosa*. Janzen (1974) theorized that the highly oligotrophic regions surrounding the Guayana Highlands were an ideal milieu for the evolution of mast

fruiting, and lamented the dearth of masting species then known. We have here recorded such a species, *D. corymbosa*, whose apparent vicariant distribution may have its origin in an ancestral leguminous radiation on the Gondwanan supercontinent.

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