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

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## Summary

• 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* (Caesalpiniaceae), 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 Nino-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* (Caesalpiniaceae), 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 caesalpiniaceous 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 preceeded 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. (Caesalpiniaceae, 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 ≈ 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-$m^2$ subplots randomly positioned to assess seed fall in each of P1–P4; in P5, seedlings were counted under each of thirty-one 3.5-$m^2$ 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-$m^2$ 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 $m^2$ 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 $m^2$ per trap and 108.5 $m^2$ 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 $m^2$

of each respective fruit part. To obtain an estimate of mast flower dry mass, 1-$m^2$ 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 $m^2$; 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-$m^2$ 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 Nino 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 Nino 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.) |
|---|---|---|---|---|---|---|---|---|
| *Dicymbe corymbosa* | 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 | | | |

[a]Values represent the mean ± standard error of the mean for $n = 5$ plots.
[b]Trees were individuals of 10 cm diameter at breast height.
[c]Dominance crown area: cumulative crown areas of D. corymbosa as percentage of total area of plot.
[d]Seedlings/saplings: total number of *D. corymbosa* seedlings/saplings in 20 $3 \times 3$ $m^2$ subsampling units in P1–P4; 31 $1 \times 3.5$ $m^2$ subsampling units in P5 (seedlings only); the total area sampled/plot was 180 $m^2$ in P1–P4; 108 $m^2$ 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) |

[a]Values represent the mean (standard error of the mean) for the upper 10 cm of mineral soil ($n = 4$ bulked subsamples per plot).
[b]Values 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. (Caesalpiniaceae) (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 $m^2$ 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; 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.

**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 |

[a]Potaro-Ireng transect plots. Distance from Upper Potaro site: plot 6, 15 km; plot 7, 22 km; and plot 8, 36 km.
[b]Values represent the mean ± standard error of the mean; $n = 20$ for plots 1–4 and 6–8, $n = 31$ for plot 5.

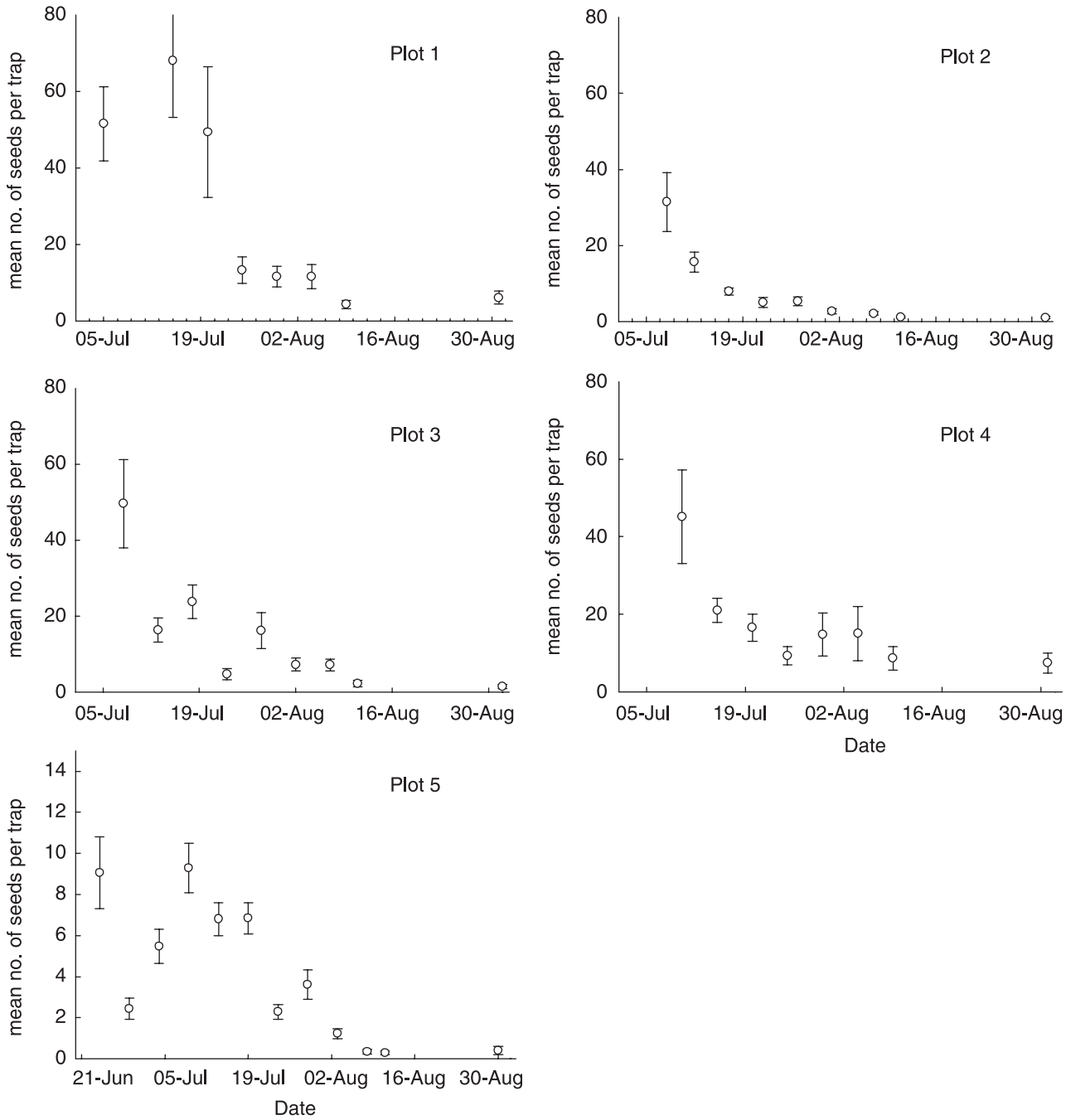


**Fig. 1** Phenology of *Dicymbe corymbosa* mast seed fall from late June to late August, 2003, in five 0.25-ha study plots at the Upper Potaro study site, Pakaraima Mountains, Guyana. Values represent the mean (and error bars the standard error of the mean) of samples taken at 5-d intervals; the first 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 $m^2$ ($n$ = 10); for plot 5, the suspended trap area is 3.5 $m^2$ ($n$ = 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 $m^2$ 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 (± standard error) dry weight of *D. corymbosa* seeds was 5.1 ± 0.1 g, with seeds constituting 15–29% of the reproductive mass, while fruit valves (mean dry weight: 12.6 ± 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 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).

**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 ± SE | 2963 ± 330 | 29.6 ± 3.3 | 1.5 ± 0.2 | 4.7 ± 0.5 | 2.5 ± 0.3 |

[a]For calculation of the dry mass, the seeds, fruit valves, and flower parts found per $m^2$ were each multiplied by their mean dry weight, summed, and reported on a per hectare basis for each plot.
[b]For determination of mineral nutrients, the seeds, fruit valves, and flower parts found per $m^2$ 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).

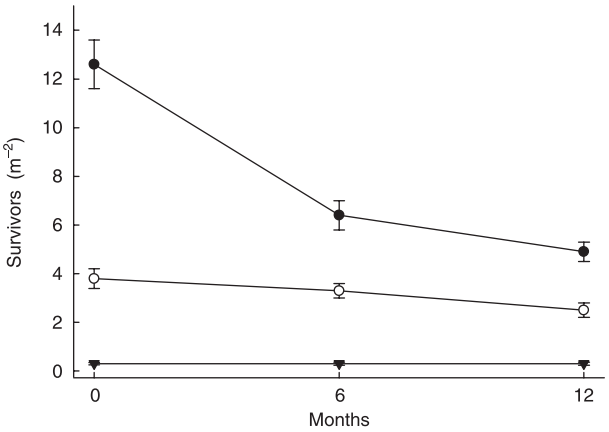


**Fig. 2** Twelve-month survivorship curves for pre-2003 *Dicymbe corymbosa* seedlings and saplings, and 2003 mast cohort seedlings, at the Upper Potaro site, Pakaraima Mountains, Guyana. Values shown represent the mean (and error bars the standard error of the mean) number of living seedlings or saplings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

## 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, ≈ 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 $m^{-2}$ was maintained among the plots. Saplings exhibited no mortality at a mean density of 0.3 $m^{-2}$. The 2003 seedlings exhibited higher mortality (≈ 60%) relative to the pre-2003 seedlings (≈ 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 Nino 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).

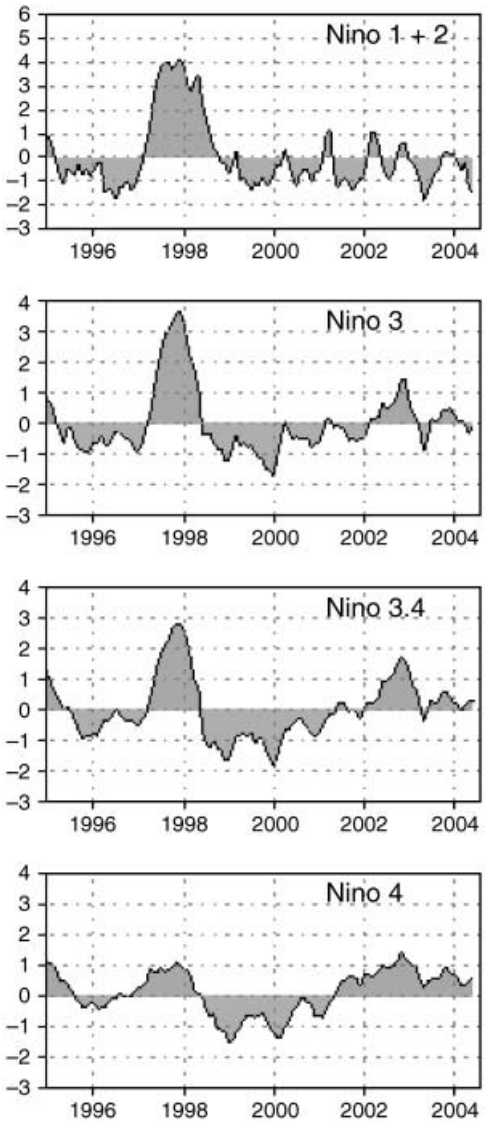


**Fig. 3** Sea surface temperature anomalies in the four El Nino regions of the central Pacific Ocean, from 1995 to 2004. Monthly fluctuations in the sea surface temperature (°C), around the 28°C baseline temperature, are shown. Nino 1+2: 0–10S, 80–90W. Nino 3: 5S–5N, 150W–90W. Nino 3.4: 5S–5N, 170W–120W.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

## 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 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 rodieae* 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.

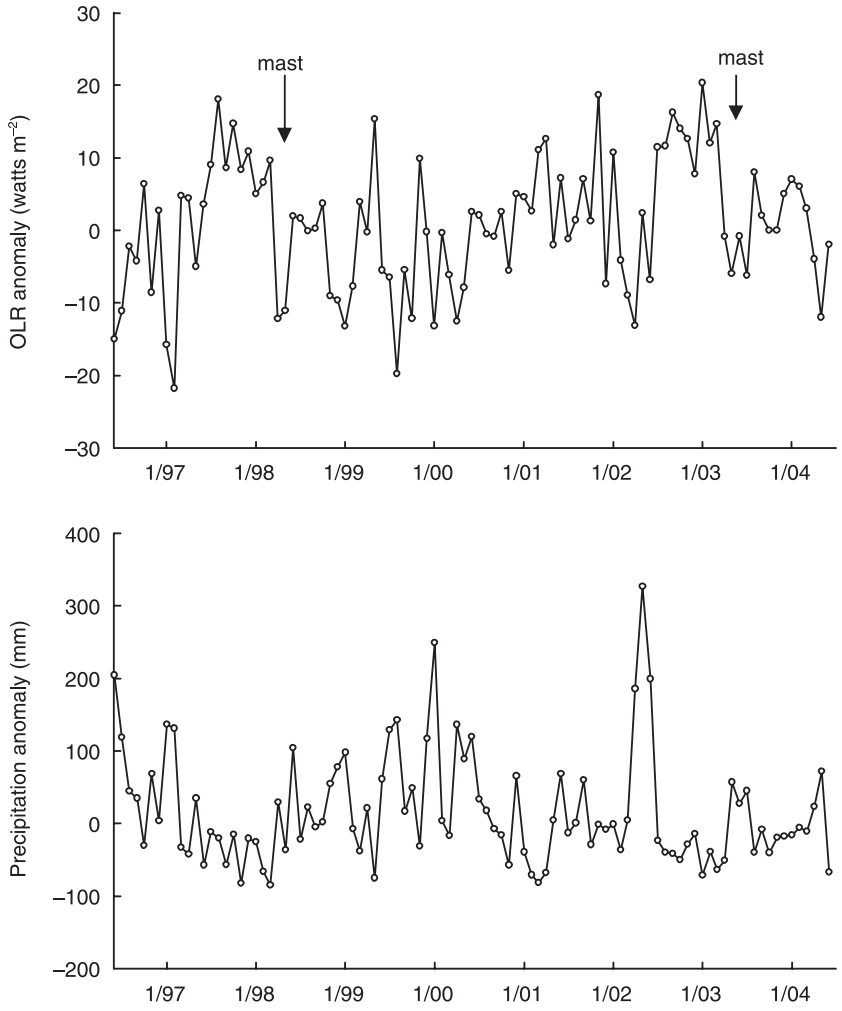


**Fig. 4** Monthly outgoing long-wave radiation (OLR) and precipitation anomalies from May 1996 to June 2004 and time of the previous two mast fruitings of *Dicymbe corymbosa* in the central Pakaraima Mountains, Guyana. The OLR anomaly is departure of the monthly OLR from the long-term monthly mean; 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 0.2–1.3 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 (1.3–1.56 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 (Kozlowski *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 understorey 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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## References

**Aceituno P. 1988.** On the functioning of the Southern Oscillation in the South American sector. Part I. Surface climate. *Monthly Weather Review* **116**: 505–524.

**Alexander IJ. 1989.** Systematics and ecology of ectomycorrhizal legumes. *Monographs in Systematic Botany of the Missouri Botanical Garden* **29**: 607–624.

**AOAC. 2003.** *Official Methods of Anaylsis of AOAC International*, 17th edn. Gaithersburg, MD, USA: AOAC International.

**Appanah S. 1985.** General flowering in the climax forests of South-east Asia. *Journal of Tropical Ecology* **1**: 225–240.

**Ashton PS. 1982.** *Dipterocarpaceae.* In: van Steenis, CGGJ, ed. *Flora Malesiana*, Series I, 9. The Hague, the Netherlands: M. Nijhoff, 237–252.

**Ashton PS. 1987.** Dipterocarp reproductive biology. In: Leith H, Werger MJA, eds. *Biogeographical and Ecological Studies.* Amsterdam, the Netherlands: Elsevier, 219–240.

**Ashton PS, Givnish TJ, Appanah S. 1988.** Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* **132**: 44–66.

**ASTM. 1998.** *Standard Test Method for Particle Size Analysis of Soils.* Lincoln, NE, USA: American Society for Testing and Materials, 04.08.

**Aubreville A. 1938.** *La Foret Coloniale; les Forets de l'Afrique Occidentale.* Paris, France: Annales de l'Academie des Sciences Coloniales.

**Bereau M, Gazel M, Garbaye J. 1997.** Les symbioses mycorrhizennes des arbres de la foret tropical humid de Guyane francaise. *Canadian Journal of Botany* **75**: 711–716.

**Berry PE, Holst BK, Yatskievych K. 1995.** *Flora of the Venezuelan Guayana*, Vol. I. *Introduction.* Portland, OR, USA: Timber Press.

**Brugiere D, Gautier JP, Moungazi A, Gautier-Hion A. 2002.** Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *International Journal of Primatology* **23**: 999–1024.

**Chan HT. 1980.** Reproductive biology of some Malaysian dipterocarps. In: Furtado JI, ed. *Tropical Ecology and Development.* Kuala Lumpur, Malaysia: International Society of Tropical Ecology, 169–175.

**Chanderbali A. 2001.** *Contributions to the systematics of Lauraceae. I. Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes and II. A Monograph of Endlicheria*

*(Lauraceae)*. PhD dissertation. St Louis, MO, USA: University of Missouri.

**Chapin FS, Moilainen L. 1991.** Nutritional controls over nitrogen and phosphorus resorption in Alaskan birch leaves. *Ecology* **72**: 709–715.

**Chuyong GB, Newbery DM, Songwe NC. 2000.** Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees. *New Phytologist* **148**: 493–510.

**Connell JH, Lowman MD. 1989.** Low-diversity tropical rainforests: some possible mechanisms for their existence. *American Naturalist* **134**: 88–119.

**Cowan RS, Polhill RM. 1981.** Tribe 5. *Amherstieae*. In: Polhill RM, Raven PH, eds. *Advances in Legume Systematics*. Kew, UK: Royal Botanic Gardens, 135–142.

**Curran LM. 1994.** *The ecology and evolution of mast-fruiting in Bornean Dipterocarpaceae: a general ectomycorrhizal theory*. PhD dissertation. Princeton, NJ, USA: Princeton University.

**Curran LM, Leighton M. 2000.** Vertebrate responses to spatio-temporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* **70**: 101–128.

**Curran LM, Caniago I, Paoli GD, Astianti D, Kusneti M, Leighton M, Nirarita CE, Haeruman H. 1999.** Impact of El Nino and logging on canopy tree recruitment in Borneo. *Science* **286**: 2184–2188.

**Davis TAW. 1941.** On the origin of the endemic trees of the British Guiana peneplain. *Journal of Ecology* **29**: 525–530.

**Diaz F, Markgraf V. 2000.** *El Niño and the Southern Oscillation: Multiscale Variability and Global and Regional Impacts*. Cambridge, UK: Cambridge University Press.

**Eis S, Garman EH, Ebell LF. 1965.** Relation between cone production and diameter increment of Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco.), grand fir (*Abies grandis* [Dougl.] Lindl.), and western white pine (*Pinus monticola* Dougl.). *Canadian Journal of Botany* **43**: 1553–1559.

**Emmons LH. 1984.** Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* **16**: 210–222.

**Fanshawe DB. 1952.** *The Vegetation of British Guiana: a Preliminary Review*. Institute Paper no. 39. Oxford, UK: Imperial Forestry Institute.

**Finlay RD, Read DJ. 1986.** The structure and function of the vegetative mycelium of ectomycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. *New Phytologist* **103**: 157–166.

**Fogel R, Hunt G. 1979.** Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. *Canadian Journal of Forest Research* **9**: 245–256.

**Forget PM. 1992.** Regeneration ecology of *Eperua grandiflora* (Caesalpiniaceae), a large-seeded tree in French Guiana. *Biotropica* **24**: 146–156.

**Fox JED. 1967.** An enumeration of lowland dipterocarp forest in Sabah. *Malaysian Forester* **30**: 263–279.

**Gavlak R, Horneck D, Miller RO, Kotuby-Amacher J. 2003.** *Soil, Plant and Water Reference Methods for the Western Region. WREP–125*, 2nd edn. Fairbanks, AK, USA: University of Alaska, 160–166.

**Gentry AH, Emmons LH. 1987.** Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* **19**: 216–227.

**Gerard P. 1960.** *Etude Ecologique de la Foret Dense a Gilbertiodendron Dewevrei Danse la Region de l'Uele*. Brussels, Belgium: INEAC (Institut National pour l'Etude Agronomique du Congo) Serie scientifique no. 87.

**Germain R, Evrard C. 1956.** *Etude Ecologique et Phytosociologique de la Foret a* Brachystegia laurentii. Brussels, Belgium: INEAC (Institut National pour l'Etude Agronomique du Congo) Serie scientifique no. 67.

**Goldammer JG, Seibert B. 1990.** The impact of droughts and forest fires on tropical rain forest of East Kalimantan. In: Goldammer JG, ed. *Fire in the Tropical Biota*. Berlin, Germany: Springer-Verlag, 11–31.

**Green JJ, Newbery DM. 2001.** Light and seed size affect establishment of grove-forming ectomycorrhizal rain forest tree species. *New Phytologist* **151**: 271–289.

**Green JJ, Newbery DM. 2002.** Reproductive investment and seedling survival of the mast-fruiting rain forest tree, *Microberlinia bisulcata* A. chev. *Plant Ecology* **162**: 169–183.

**Hamann A. 2004.** Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes. *Journal of Ecology* **92**: 24–31.

**Hammond DS, Brown VK. 1995.** Seed size of woody plants in relation to disturbance, dispersal, and soil type in wet neotropical forests. *Ecology* **76**: 2544–2561.

**Hammond DS, Brown VK. 1998.** Disturbance, phenology, and life history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newbery DM, Prins HHT, Brown ND. *Dynamics of Tropical Communities*. Oxford, England: Blackwell Science, 51–78.

**Hammond DS, ter Steege H. 1998.** Propensity for fire in Guianan rainforest. *Conservation Biology* **12**: 944–947.

**Harper JL. 1977.** *Population Biology of Plants*. London, UK: Academic Press.

**Hart TB. 1995.** Seed, seedling and subcanopy survival in monodominant and mixed forest of the Ituri Forest, Africa. *Journal of Tropical Ecology* **11**: 443–459.

**Henkel TW. 2003.** Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae) from Guyana. *Journal of Tropical Ecology* **19**: 417–437.

**Henkel TW, Terborgh J, Vilgalys RJ. 2002.** Ectomycorrhizal fungi and their leguminous hosts in the Pakaraima Mountains of Guyana. *Mycological Research* **106**: 515–531.

**Herendeen PS, Bruneau A, Lewis GP. 2003.** Phylogenetic relationships in caesalpinoid legumes: preliminary analyses based on morphological and molecular data. In: Klitgaard BB, Bruneau A, eds. *Advances in Legume Systematics, Part 10, Higher Level Systematics*. Kew, UK: Royal Botanic Gardens, 37–62.

**Herrera CM, Jordano P, Guitlan J, Traveset A. 1998.** Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist* **152**: 576–594.

**Isagi Y, Sugimura K, Sumida A, Ito H. 1997.** How does masting happen and synchronize? *Journal of Theoretical Biology* **187**: 231–239.

**Janzen DH. 1971.** Seed predation by animals. *Annual Review of Ecology and Systematics* **2**: 465–492.

**Janzen DH. 1974.** Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**: 69–103.

**Janzen DH. 1978.** Seeding patterns in tropical trees. In: Tomlinson PB, Zimmermann MH, eds. *Tropical Trees as Living Systems*. Cambridge, UK: Cambridge University Press, 83–128.

**Kelly D. 1994.** Evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* **9**: 465–470.

**Kelly D, Sork VL. 2002.** Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**: 427–447.

**Koenig WD, Knops JMH. 2000.** Patterns of annual seed production by Northern Hemisphere trees: a global perspective. *American Naturalist* **155**: 59–69.

**Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD. 2003.** Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* **102**: 581–591.

**Kogan F. 2000.** Satellite-observed sensitivity of world land ecosystems to El Nino/La Nina. *Remote Sensing of Environment* **74**: 445–462.

**Kozlowski TT, Kramer PJ, Pallardy SG. 1991.** *The Physiological Ecology of Woody Plants*. New York, NY, USA: Academic Press.

**Lalonde RG, Roitberg BD. 1992.** On the evolution of masting behavior in trees: predation or weather? *American Naturalist* **139**: 1293–1304.

**Maguire B. 1970.** On the flora of the Guayana Highland. *Biotropica* **2**: 85–100.

**Mayor JR, Henkel TW. 2004.** Ectomycorrhizal influence on leaf litter decomposition within a monodominant *Dicymbe corymbosa* (Caesalpiniaceae) forest in Guyana. *Inoculum* **55**: 27.

**McClean EO. 1982.** Soil pH and lime requirement. In: Page AL, Miller RH, Keeney DR, eds. *Methods of Soil Analysis. Part 2 – Chemical and Microbiological Properties*, 2nd edn. Madison, WI, USA: American Society of Agronomy, 33–49.

**McDowell SCL, McDowell NG, Marshall JD, Hultine K. 2000.** Carbon and nitrogen allocation to male and female reproduction in Rocky Mountain Douglas fir (*Pseudotsuga menziesii* var. *glauca*, Pinaceae). *American Journal of Botany* **87**: 539–546.

**Mehlich A. 1984.** Mehlich 3 soil test extractant: a modification of the Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis* **15**: 1409–1416.

**Miyazaki Y, Huira T, Kato E, Funada R. 2002.** Allocation of resources to reproduction in *Styrax obassia* in a masting year. *Annals of Botany* **89**: 767–772.

**Moyersoen B, Alexander IJ, Fitter AH. 1998.** Phosphorus nutrition of ectomycorrhizal and arbuscular mycorrhizal tree seedlings from a lowland tropical rain forest in Korup National Park, Cameroon. *Journal of Tropical Ecology* **14**: 47–61.

**Newbery DM, Gartlan JS. 1996.** Structural analysis of the rain forest at Korup and Douala Edea, Cameroon. *Proceedings of the Royal Society of Edinburgh, B.* **104**: 177–224.

**Newbery DM, Alexander IJ, Rother JA. 1997.** Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. *Ecological Monographs* **67**: 367–409.

**Newbery DM, Songwe NC, Chuyong GB. 1998.** Phenology and dynamics of an African rain forest at Korup, Cameroon. In: Newbery, DM, Prins, HHT, Brown, ND, eds. *Dynamics of Tropical Communities*. Oxford, UK: Blackwell Science, 267–308.

**Newbery DM, Chuyong GB, Green JJ, Songwe NC, Tschuenteu F, Zimmermann L. 2002.** Does low phosphorus supply limit seedling establishment and tree growth in groves of ectomycorrhizal trees in a central African rainforest? *New Phytologist* **156**: 296–311.

**Newbery DM, van der Burgt XM, Moravie MA. 2004.** Structure and inferred dynamics of a large grove of *Microberlinia bisculata* trees in central African rainforest: the possible role of periods of multiple disturbance events. *Journal of Tropical Ecology* **20**: 131–143.

**Ng FSP. 1977.** Gregarious flowering of dipterocarps in Kepong, 1976. *Malaysian Forester* **40**: 126–137.

**Norton DA, Kelly D. 1988.** Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* **2**: 399–408.

**Perez-Moreno J, Read DJ. 2000.** Mobilization and transfer of nutrients from litter to tree seedlings via the vegetative mycelium of ectomycorrhizal plants. *New Phytologist* **145**: 301–309.

**Piovesan G, Adams JM. 2001.** Masting behavior in beech: linking reproduction and climatic variation. *Canadian Journal of Botany* **79**: 1039–1047.

**Pires JM, Prance GT. 1977.** The Amazon forest: a natural heritage to be preserved. In: Prance GT, Elias TS, eds. *Extinction Is Forever*. New York, UK: New York Botanical Garden, 158–194.

**Poorter L, Bongers F, van Rompaey RSAR, de Klerck M. 1996.** Regeneration of canopy tree species at 5 sites in West-African moist forest. *Forest Ecology and Management* **84**: 61–69.

**Proctor J. 1984.** Tropical forest litterfall II. the data set. In: Chadwick, AC, Sutton, SL, eds. *Tropical Rain Forest: the Leeds Symposium*. Leeds, UK: Leeds Philosophical and Literary Society. 83–113.

**Rathcke B, Lacey EP. 1985.** Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179–214.

**Richards PW. 1996.** *The Tropical Rainforest. An Ecological Study*, 2nd edn. Cambridge, UK: Cambridge University Press.

**Ropalewski CF, Halpert MS. 1987.** Global and regional scale precipitation patterns associated with the El Nino-Southern Oscillation. *Monthly Weather Review* **115**: 1606–1626.

**Sabatier D. 1985.** Saisonnalite et determinisme du pic de fructification en foret Guyanaise. *Revue d'Ecologie (Terra et la Vie)* **40**: 289–320.

**Silvertown JW. 1980.** The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnaean Society* **14**: 235–250.

**Singh SP, Rawat YS, Rana BS, Negi GCS. 1990.** Effects of unusually large seed crop on litterfall and nitrogen retranslocation in Himalayan oaks. *Forest Ecology and Management* **32**: 79–86.

**Sork VL. 1993.** Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio* **108**: 133–147.

**Sork VL, Bramble J, Sexton O. 1993.** Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* **74**: 528–541.

**ter Steege H, Persaud CA. 1991.** The phenology of Guyanese timber species: a compilation of a century of observations. *Vegetatio* **95**: 177–198.

**ter Steege H, Sabatier D, Castellanos H, Van Andel T, Duivenvorden J, De Oliveira AA, Ek R, Lilwah R, Maas P, Mori S. 2000.** A regional perspective. *Analysis of Amazonian Floristic Composition and Diversity That Includes the Guiana Shield*. In: ter Steege H, ed. *Plant diversity in Guyana. Tropenbos series number 18*. Wageningen, the Netherlands: The Tropenbos Foundation, 19–34.

**Storer DA. 1984.** A simple high volume ashing procedure for determining soil organic matter. *Communications in Soil Science and Plant Analysis* **15**: 79–82.

**Sumner ME, Miller WP. 1996.** *Modified Summation of Cations. Soil Science Society of America Book Series 5: Methods of Soil Analysis. Part 3 – Chemical Methods.* Madison, WI, USA: Soil Science Society of America.

**Thomas RS. 2001.** *Forest Productivity and Resource Availability in Lowland Tropical Forests of Guyana. Tropenbos-Guyana, Series 7*. Georgetown, Guyana: Tropenbos-Guyana Programme.

**Van Schaik CP. 1986.** Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* **2**: 327–347.

**Van Schaik CP, Terborgh JW, Wright SJ. 1993.** The phenology of tropical forests – adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* **24**: 353–377.

**Vitousek PM, Sanford RL. 1986.** Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**: 137–167.

**Vogt KA, Grier CC, Meier CE, Edmonds RL. 1982.** Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology* **63**: 370–380.

**Waller DM. 1993.** How does mast fruiting get started? *Trends in Ecology and Evolution* **8**: 122–123.

**Wheelwright NT. 1986.** A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. In: Estrada A, Fleming TH, eds. *Frugivores and Seed Dispersal*. Dordrecht, Germany: W.A. Junk, 19–35.

**Wich SA, Van Schaik CP. 2000.** The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* **16**: 563–577.

**Wright SJ, Van Schaik CP. 1994.** Light and the phenology of tropical trees. *American Naturalist* **143**: 192–199.

**Wright SJ, Carrasco C, Calderon O, Paton S. 1999.** The El Nino Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* **80**: 1632–1647.

**Wyatt-Smith J. 1958.** Seedling/sapling survival of *Shorea leprosula*, *Shorea parviflora*, and *Koompassia malaccensis*. *Malaysian Forester* **21**: 185–193.

**Wycherley PR. 1973.** The phenology of plants in the humid tropics. *Micronesia* **9**: 75–96.

**Yasuda M, Matsumoto J, Osada N. 1999.** The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* **15**: 437–449.

**Zagt RJ. 1997.** Pre-dispersal and early post-dispersal demography, and reproductive litter production, in the tropical tree *Dicymbe altsonii* in Guyana. *Journal of Tropical Ecology* **13**: 511–526.