Recruitment dynamics and ectomycorrhizal colonization of *Dicymbe corymbosa*, a monodominant tree in the Guiana Shield

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Abstract: The dynamics of early life-history stages are important for understanding regional diversity patterns in tropical trees. In this study, patterns of seed removal, seedling survival and ectomycorrhizal (ECM) colonization in monodominant and mixed tropical rain forests in Guyana were investigated during a masting event of an ECM monodominant tree, *Dicymbe corymbosa*. Two seed densities ($1\,m^{-2}$ and $6\,m^{-2}$) were tested in two forest types (monodominant versus mixed) with 10 plots per treatment (40 plots total). Germination success, seed and seedling survival after 1 y were measured for the monodominant tree, and four non-dominant canopy tree species found in both forest types (*Eschweilera sagotiana*, *Licania laxiflora*, *Chrysophyllum sanguinolentum* and *Carapa guianensis*). A significant effect of forest type was detected for seed removal and seedling survival. In the mixed forest, seed removal was higher for all species, with 27% average removal compared with 7% average seed removal in the monodominant forest. Germination success was significantly lower for all but one species in the mixed forest, with average germination of 41% compared with 78% germination in the monodominant forest. Seed and seedling survival of the monodominant tree was greatest within the monodominant forest with 93% of seeds germinating and 85% of seedlings surviving after 1 y compared with 65% germination and 15% seedling survival in the mixed forest. Per cent ectomycorrhizal colonization of *Dicymbe corymbosa* was near 100% in the monodominant forest, but significantly lower (14%) in the mixed forest. These results suggest that seedling survival patterns, rather than seed survival, are more important for recruitment success in this system and that ectomycorrhizal inoculum may limit establishment of *Dicymbe corymbosa* in the mixed forest.

Key Words: *Dicymbe corymbosa*, diversity, ectomycorrhizas, Guyana, masting, monodominance, seed survival, seedling dynamics, tropical rain forest

INTRODUCTION

Monodominant rain forests, where one tree species comprises 50–100% of the rain-forest canopy, are found throughout all tropical regions, but it is not understood how these systems are maintained within areas of otherwise highly diverse rain forest (Connell & Lowman 1989, Hart 1990, Leigh *et al.* 2004). The mechanisms by which these particular trees maintain dominance may pertain to traits common to several monodominant species: masting, generalized resistance to natural enemies, and/or a near-parent advantage due to the formation of ectomycorrhizal (ECM) associations (Torti *et al.* 2001). Masting may increase seed and seedling survival via predator satiation, such that more seeds are produced than can be consumed by seed predators (Janzen 1974).

Predator satiation favours seedling establishment (that is, persistence in the understorey for over 1 y) where conspecific, adult density is high, but only if the existing forest patch is large enough to produce a sufficiently large seed crop. Thus, predator satiation through masting may explain the maintenance of monodominance in existing clumps of forest (Boucher 1981). Generalized resistance to negative density-dependent forces coupled with poor primary and secondary seed dispersal would also favour seedling establishment close to conspecific adults. These resistance mechanisms may include chemical defences against fungal rot and seed predators, and chemical and/or structural deterrence of herbivores. These types of defences have been found in Dipterocarpaceae seeds (Numata *et al.* 1999), but other monodominant species have not been explicitly tested for seed defences.

The predominance of ECM associations in monodominant trees may also explain the superior survivorship of conspecific seedlings in the monodominant understorey

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(Connell & Lowman 1989, Torti & Coley 1999). Most tropical trees form arbuscular mycorrhizal (AM) associations (Janos 1983, 1985), and the structural and physiological differences between the groups of fungi that form each of these mycorrhizal associations would provide ECM fungi with an advantage in nutrient-poor soils such as those in many tropical regions (Buscot *et al.* 2000). Other advantages of ECM compared with AM associations in these systems may include assimilate transfer from ECM adults to seedlings through the common ECM network, access to organically bound nutrients, increased pathogen resistance and increased water capture. The phenomenon of masting may also be related to ectomycorrhizal status, as most masting species worldwide have been found to be ectomycorrhizal (Newbery *et al.* 1998a). It has been proposed that ECM species are better able than non-ECM species to build up sufficient quantities of resources during intermast periods to reproduce with such high output (Curran 1994, Newbery *et al.* 2006a).

Based on the implications of these common monodominant traits and associated hypotheses, several predictions can be generated regarding seed and seedling survival as a function of seed density (high vs. low) and forest type (mixed vs. monodominant, Table 1). If predator satiation through masting contributes to higher recruitment, then survival should be positively correlated with seed density, because a threshold number of seeds is required to escape predation. Thus, seeds that fall outside of the monodominant forest should not survive as well as seeds falling within the monodominant patch. Conversely, within the monodominant patch, high-density concentrations of seeds should survive better than low densities of seeds according to this hypothesis. Alternatively, if defences to counter predators, pathogens and herbivores contribute to higher recruitment, then survival should be higher than other species everywhere, irrespective of seed density and forest type. If ECM advantages are promoting successful recruitment in the monodominant forest, then the prediction is that survival should be high in the ECM forest and low in the mixed forest, regardless of seed density. This is due to the presumed limitation of ECM inoculum in the mixed forest, where most of the trees are AM. Thus, successful establishment will be dependent on conspecific adult density, rather than initial seed density.

To test these hypotheses, the effects of forest type (low diversity, monodominant vs. high diversity, mixed) and seed density on post-dispersal seed fate and seedling survival were investigated during a masting event (2002–2003) of the monodominant species *Dicymbe corymbosa* Spruce ex Benth. (Caesalpiniaceae) in Guyana. The objective of this study was to determine the role of seed and seedling dynamics in controlling for observed mosaics of high- and low-diversity forest patches. To determine which of the three previously mentioned hypotheses (Table 1) were contributing to successful recruitment of *D. corymbosa*, seed output and seedling densities of *D. corymbosa* were estimated for both years, and a seed predation experiment was conducted using seeds from *D. corymbosa* and four other tree species encountered in both forest types.

METHODS

Study site

This study was carried out near the upper Potaro River (5°18′N, 59°54′W; 720 m asl) within the Pakaraima Mountain Range of Guyana. This region is characterized as aseasonal tropical rain forest with an annual precipitation of 3000–4000 mm. The local vegetation is dense, primary rain forest with extensive stands of monodominant *D. corymbosa*. *Dicymbe corymbosa* is an emergent tree species reaching 30–40 m. It forms ectomycorrhizal associations and reaches dominance levels of 70–90% where it occurs (Henkel 2003, McGuire, unpubl. data). *Dicymbe corymbosa* also forms occasional co-dominant stands with *D. altsonii*, but only pure stands of *D. corymbosa* were investigated in this study. The *D. corymbosa* forest shares many traits with other monodominant forests including a deep, uniform canopy, deep leaf litter layer, poor dispersal, mast fruiting, ectomycorrhizas, shade tolerance and large seeds (Torti *et al.* 2001). Adjacent to these monodominant forests are patches of high diversity, mixed rain forest where *Dicymbe* species are absent, with no apparent geographic or edaphic separation between forest types (Fanshawe 1952, ter Steege *et al.* 2000b, Whitton 1962). Both *D. corymbosa* and *D. altsonii* are known to mast, and synchronous fruiting events were observed in 1989, 1991, 1993, 1998 and 2003 (Henkel 2003, Zagt 1997, Zagt & Werger 1997). The mammal community in this area is intact (Burton Lim, unpubl. data).

Seed fate

To determine the fate of seeds as a function of species, forest type and seed density, seeds below fruiting individuals were collected from *D. corymbosa* (seeds 3–4 cm long) *Eschweilera sagotiana* Miers (Lecythidaceae, seeds 3–4 cm), *Licania laxiflora* Fritsch (Chrysobalanaceae, seeds 2.5–4 cm), *Chrysophyllum sanguinolentum* (Pierre) Baehni (Sapotaceae, seeds 1.4–2.5 cm) and *Carapa guianensis* Aubl. (Meliaceae, seeds 4–5 cm) in May 2002. Other than *D. corymbosa*, all of these species occur in both high- and low-diversity forests and are common throughout the Guiana Shield (ter Steege *et al.* 2000a, van Andel 2001). Seeds were placed in high-density (six seeds per species) and low-density (one seed per species) plots (1 ×

1 m) in both mixed and monodominant forest types, with ten replicates per treatment, for a total of 40 plots. Seeds were randomly placed in the plots using a randomized grid. All pre-existing seeds were removed from the plot areas so that only the five species investigated would influence seed fate outcomes. Seeds were observed every 2–3 d for two consecutive months. After 2 mo, the fate of all seeds was known and placed in the following categorical observations: successful germination, ant predation, fungal rot and removed. Ant predation was identified by observations of ants consuming seed coat and cotyledon fragments, which resulted in seed germination failure. Seedling survival was quantified after 1 y for the remaining seeds in the plots.

Ectomycorrhizal colonization

To assess ECM colonization, the roots of all surviving seedlings in 2003 were collected, stored in formalin acetic-alcohol (FAA) and transported to the University of Michigan for processing. Per cent ECM colonization was quantified by counting the total number of visibly colonized roots and dividing that number by the total number of roots. Positive ECM colonization was noted if an ECM tip was visible under a dissecting scope or a mantle and Hartig net were detected in root cross-sections stained with Trypan Blue under a compound microscope.

Seed production

To quantify seed output, eight rectangular transects of 1×100 m were randomly placed in each of three sites (24 plots total) dominated by *D. corymbosa*. All *D. corymbosa* fruits occurring in these transects were collected after a moderate fruiting event in 2002 and again after a large, mast-fruiting event in 2003. Seed production was estimated by quantifying seed scars in woody fruits collected after the fruiting event. This method has been used in other seed-production studies for tropical legumes (Blake & Fay 1997, Green & Newbery 2002) and thus, results are reliably comparable to other systems. *Dicymbe corymbosa* fruits are explosively dehiscent and there are no known primary dispersers of the seeds. The last fruits were observed to fall in mid-September, so fruit counts were made in mid-October. The woody, bi-valved fruits persist for several months, allowing for accurate estimates of seed production. Within the fruits, viable and aborted seed scars were easily distinguishable, so seed output was estimated by dividing all viable seed scars in half.

Wild cohort survey and plot census

A census of the wild seedling cohort was undertaken in 2002 and 2003 to determine if the natural distributions

and abundances of the species used in the manipulative study were reflective of experimental results. In both 2002 and 2003 seedlings were censused in October. At these times, seedlings were 1 y old and 1–3 mo, respectively. Seedlings were defined as individuals < 1 m height. In 2002 the census was taken before any fruiting occurred, so seedling densities correspond to individuals that persisted in the understorey at least since the previous mast in 1998. For the 2002 census, nine belt transects (three within each site) of 2×100 m were randomly placed within each forest type for a total census area of $1800 \, \text{m}^2$. In 2003, the seedling census was conducted for *D. corymbosa* seedlings only after the masting event by randomly quantifying 80 4-m^2 plots within the monodominant forest for a total of $320 \, \text{m}^2$. It is recognized that methodology differences between the two years may influence the precision of seedling density estimates. However, the first year of the mast was not anticipated and pre-established transects were used for the seed and seedling counts. Seedlings pre-existing in 2002 were easily distinguishable from the new 2003 seedling cohort using cotyledon scars, so these were separated during the census. An estimation of seed mortality was calculated by dividing seedling density by seed output estimates.

Statistical analyses

To test for main and interactive effects of density on germination and survival, likelihood ratio χ^2 tests were used in a logistic regression model. Because the outcome of germinated or survived for a given species within a plot at low density was binary (i.e. either the single seed planted for a species within a plot at low density germinated/survived or not), and the outcome for a given species within a plot at high density was a proportion ranging from 0 to 1.0 (i.e. from 0 to 10 of the total of 10 seeds planted for a species could have germinated/survived), a different analysis for the low- and high-density plots was used. Low-seed-density plots were analysed using a cross-tabulation with a Fisher's exact test. For the high-density plots, a two-way analysis of variance was used on the arcsine-transformed proportion of germinated/survived, with species and forest type and their interaction as predictors. Programmed contrasts within the ANOVA model were used to test for the effect of forest type on individual species. Total survival is defined as survival from the seed to the seedling stage inside the plots after one year. Per cent ECM colonization as a function of forest type and seed density was analysed using a two-way ANOVA. All statistical analyses were run using SPSS (Chicago, Illinois, USA).

RESULTS

Seed density

Seed density in the experimental plots did not affect germination or survival of seedlings after 1 y. Seed density did not have a significant main effect on germination across forest types ($\chi^2 = 2.33$, df $= 1,184$, P $= 0.127$) and did not have a significant interactive effect with forest type ($\chi^2 = 0.03$, df $= 1,184$, P $= 0.872$) or species ($\chi^2 = 1.57$, df $= 4,184$, P $= 0.815$). Thus, density was removed from further analyses and survival comparisons were applied to the high- and low-density plots separately.

Germination

In the low-density plots, there was no effect of forest type on germination for any of the species, but in the high-density plots results were species-specific (Figure 1). In the high-density plots there was significantly greater germination success in the monodominant forest for *Dicymbe corymbosa*, *Carapa guianensis* and *Licania laxiflora* (Table 1). There was no effect of forest type on germination for *Eschweilera sagotiana* or *Chrysophyllum sanguinolentum*. In the monodominant forest 95% of *D. corymbosa* seeds germinated, whereas only 65% of the non-dominant seeds germinated (Figure 2, Table 2). Germination success for *D. corymbosa* seeds was equivalent to non-dominant seed species in the mixed forest with average germination success of 41% for all species. Overall, there was more seed removal in the mixed forest compared to the monodominant forest (F $= 5.35$, df $= 6,99$, P < 0.001, Table 3). Across all seed plots, 27% more seeds were removed in the mixed forest compared to 7% seed removal in the monodominant forest. Seed removal for *D. corymbosa* in the mixed forest was equivalent to that of the non-dominant species ($\chi^2 = 24.1$, df $= 1,24$, P $= 0.46$). For *E. sagotiana*, seed removal was not significantly different across forest types (F $= 0.94$, df $= 5,39$, P $= 0.47$). Ants of two

Table 1. Predictions for seed/seedling survival based on forest type (mono = monodominant and mixed = mixed forest) and seed density for each proposed mechanism of survival. These predictions are not uniform survival predictions, but rather relative predictions for survival compared with the survival of other non-dominant species.

Forest type	Seed density	Predator satiation through masting	Seed/seedling defences	ECM advantages
		Survival	Survival	Survival
Mono	High	High	High	High
	Low	Low	High	High
Mixed	High	High	High	Low
	Low	Low	High	Low

Table 2. The effect of forest type on seed fate and seedling survival after 1 y. Analysis of variance results for high-density seed plots and Fisher's exact test results for low-density seed plots are reported. Chi-square approximations are given for the Fisher's exact tests. Data for high-density seed plots were arcsine-transformed prior to analysis. F-test statistics are given for the high-density plots and χ^2 approximations are given for low-density plots.

Species	Density	Test statistic	P
Germination			
Dicymbe corymbosa	high	12.1	0.001
	low	2.2	0.24
Carapa guianensis	high	21.5	< 0.001
	low	2.2	0.240
Chrysophyllum sanguinolentum	high	2.7	0.100
	low	1.3	0.290
Eschweilera sagotiana	high	0.03	0.880
	low	1.0	0.310
Licania laxiflora	high	11.0	0.001
	low	1.0	0.310
Survival			
Dicymbe corymbosa	high	68.8	0.000
	low	13.3	0.001
Carapa guianensis	high	7.8	0.007
	low	2.0	0.16
Carapa sanguinolentum	high	15.3	0.000
	low	3.2	0.179
Eschweilera sagotiana	high	4.1	0.045
	low	–	–
Licania laxiflora	high	0.21	0.650
	low	1.1	0.305

species, *Atta cephalotes* (Linneaus) (Hymenoptera: Attini) and *Acromyrmex octospinosus* (Reich) (Hymenoptera: Formicidae), were the only observed seed predators on *D. corymbosa* seeds, and overall, *D. corymbosa* suffered the highest levels of observed ant predation.

Survival

Dicymbe corymbosa consistently survived better within its own forest type, with average survival after 1 y being 85% within the monodominant forest and 15% in the mixed forest. Results for the non-dominant species were mixed, however, and varied by species. Survival for *D. corymbosa* was also significantly higher than survival for all non-dominant species within the monodominant forest, but was not significantly different from non-dominant species within the mixed forest (Figure 2). Within the monodominant forest non-dominant species had 20% seedling survival, which was significantly lower than the 85% seedling survival observed for *D. corymbosa* in this forest type. Survival of the individual non-dominant species after 1 y were variable across forest type and density treatment. *Eschweilera sagotiana* had significantly higher survival in the mixed forest compared with the monodominant forest in high-density plots, but since no seeds germinated in the low-density plots in either forest type, a survival comparison could not be
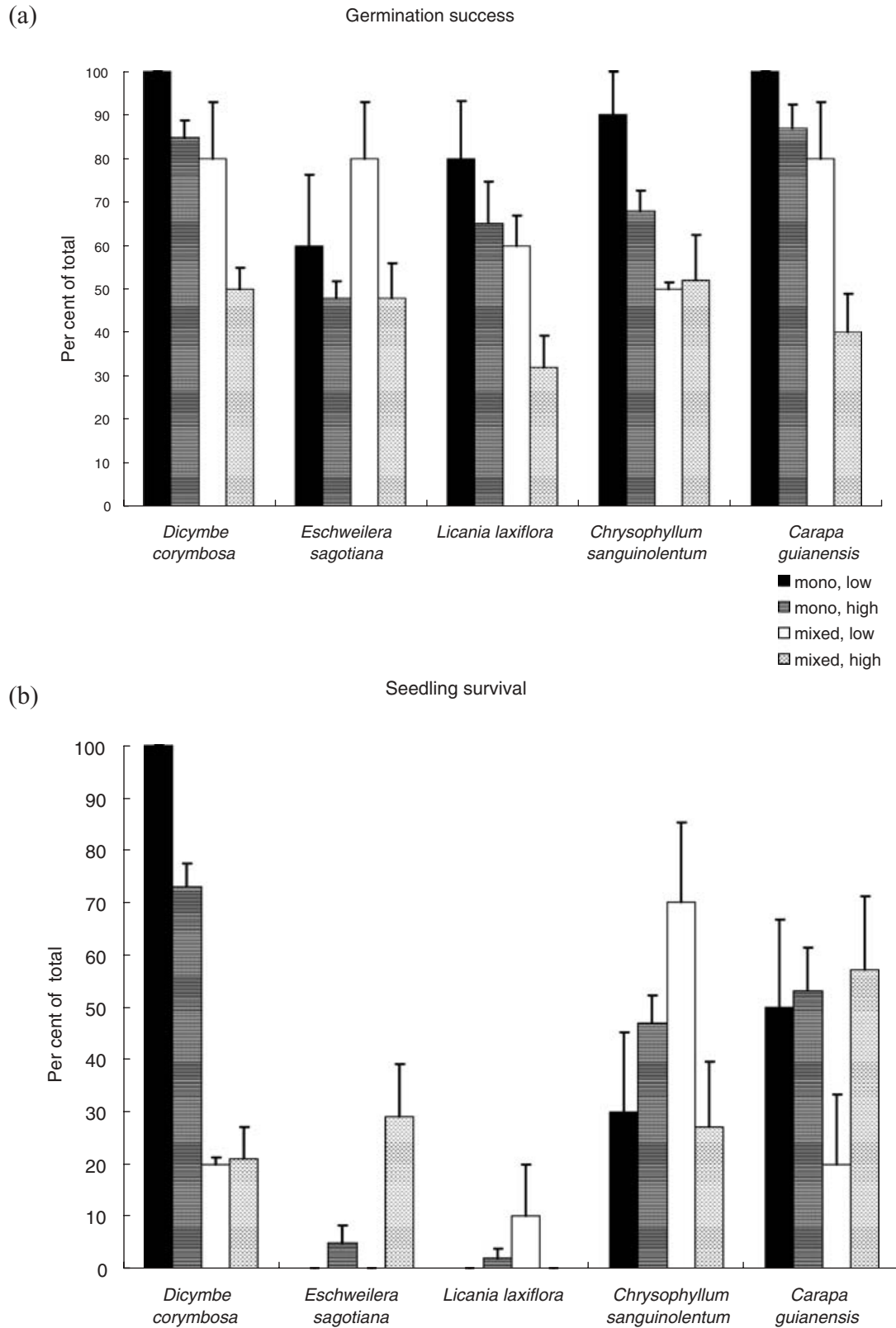
(a)

Germination success

(b)

Seedling survival

Figure 1. Germination success (a) and seedling survival after 1 y (b) of *Dicymbe corymbosa*, *Eschweilera sagotiana*, *Licania laxiflora*, *Chrysophyllum sanguinolentum* and *Carapa guianensis* in monodominant forest and mixed forest in low-density and high-density seed plots. Error bars indicate 1 SE of mean.
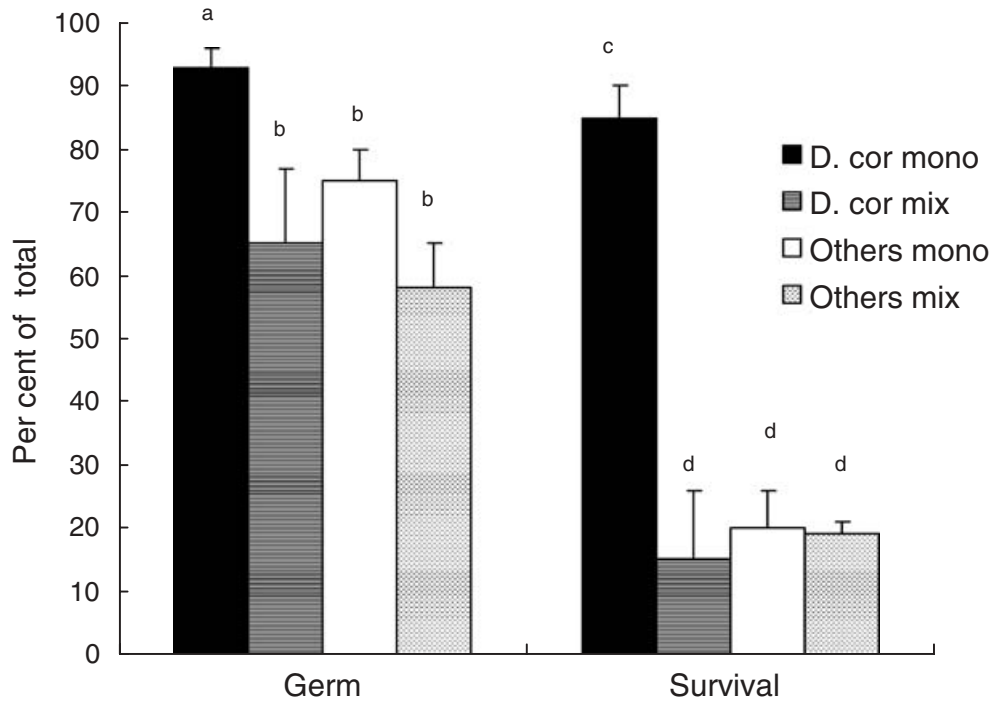
Figure 2. Per cent of successfully germinated seeds (germ), and total individuals that survived (survival) of all transplanted seeds after 1 y. Effects of seed density are removed to view only the effects of forest type on *Dicymbe corymbosa* and the combined non-dominant species in this study. Error bars indicate 1 SE of the mean. Letters above the bars show significant differences between treatments for germination (a,b) and survival (c,d).

accomplished. *Licania laxiflora* had low survival overall and there were no significant differences in survival in either low- or high-density plots. *Chrysophyllum sanguinolentum* had significantly higher survival in the

monodominant forest within the high-density plots, but there were no significant differences in survival within low-density plots across forest types. *Carapa guianensis* also had higher survival in the monodominant forest

Table 3. Seed fate (per cent of total seeds planted) is listed for *Dicymbe corymbosa*, *Licania laxiflora*, *Eschweilera sagotiana*, *Carapa guianensis* and *Chrysophyllum sanguinolentum* in both monodominant and mixed forests. Seed fate categories include survived to germination, predated by ants, fungal rot, predated from unknown causes and removed.

Species	Forest type	Ant predation	Fungal rot	Other	Removed
Low density					
Dicymbe corymbosa	monodominant	0	0	0	0
	mixed	0	0	10	10
Licania laxiflora	monodominant	0	10	0	10
	mixed	0	0	0	40
Eschweilera sagotiana	monodominant	10	10	10	10
	mixed	0	0	10	10
Carapa guianensis	monodominant	0	0	0	0
	mixed	0	0	0	20
Chrysophyllum sanguinolentum	monodominant	0	0	0	10
	mixed	0	10	0	20
High density					
Dicymbe corymbosa	monodominant	12	0	2	2
	mixed	8	0	13	28
Licania laxiflora	monodominant	0	0	7	18
	mixed	0	0	5	63
Eschweilera sagotiana	monodominant	0	17	30	5
	mixed	0	0	23	28
Carapa guianensis	monodominant	5	0	7	2
	mixed	2	0	38	20
Chrysophyllum sanguinolentum	monodominant	0	0	18	13
	mixed	0	3	12	33

within high-density plots, but no significant differences in survival in the low-density plots.

Ectomycorrhizal colonization

Ectomycorrhizal colonization of surviving *Dicymbe corymbosa* seedlings after 1 y was highly dependent on forest type. Per cent ECM colonization was significantly higher in seedlings surviving in the monodominant forest compared with the mixed forest (F = 783, df = 1,59, P < 0.001). Per cent colonization was near 100% for all *D. corymbosa* seedlings within the monodominant forest, but averaged only 14% in the mixed forest. There were no significant differences between seed density treatments within each forest type on per cent colonization (P = 0.59).

Seed production and wild seedling density

Seed output estimates for 2002 were low, confirming a moderate fruiting event for that year. In 2003, by contrast, seed output was extremely high throughout the monodominant forest and average seed output was about 19 times higher than seed output for 2002. Estimated seed output was 8150 ± 3900 (mean $\pm$ 1 SE) seeds ha^{-1} in 2002 and $154\,000 \pm 9800$ seeds ha^{-1} in 2003. In 2002, few individuals fruited, and those that did were larger in size (threshold dbh = 84.0 cm), but > 90% of canopy adults with dbh > 10 cm produced fruit in 2003.

Wild seedling densities for the species used in this study were consistent with the results found in the seed predation experiment (Table 4). No individuals of *D. corymbosa* were found in the mixed forest, but very high densities of seedlings were found in the monodominant forest. There were 200 to over 6000 times as many *D. corymbosa* seedlings as seedlings of the non-dominant species. In the seed predation experiment, *D. corymbosa* seedlings had 65% greater survival after 1 y, reflecting

this large difference in survival magnitude found in the wild seedling cohorts. Seedling densities of the non-dominant species were variable across forest types, with the exception of *Licania laxiflora*, which seems to exhibit a preference for the monodominant forest. This result was also reflected in the seed predation experiment.

Wild seedling density counts for *D. corymbosa* reflected seed output patterns for both fruiting years. Wild seedling density following the 2002 fruiting event was $79\,708 \pm 3325$ seedlings ha^{-1} and $111\,000 \pm 4970$ seedlings ha^{-1} after the 2003 mast. At the transition zone, the *D. corymbosa* seed that was found extending the furthest into the mixed forest after the 2003 mast was 17.4 m. From the seed output estimates and wild cohort survey, natural seed mortality was estimated as 28% per mast event.

DISCUSSION

Seed fate

Forest type had a significant effect on the fate of seed survival, such that all species except *Eschweilera sagotiana* had significantly higher survival in the monodominant forest compared to the mixed forest. This pattern suggests that conditions for germination of most species are superior in the monodominant forest, perhaps due to lower densities of mammal and insect seed predators. The greater number of seeds removed in the mixed forest further indicates that mammal and/or insect densities might be lower within the monodominant forest. This may be true for several reasons. First, since *D. corymbosa* seeds are not preferentially removed in the mixed forest relative to the other seed species, seed predators may not be particularly attracted to the monodominant forest since fruiting is discontinuous with little or no reproductive output in intermediate years. Generalist seed predator populations may be deterred from extensively foraging in the monodominant forest where seed availability is

Table 4. Density (individuals ha^{-1}) of all species utilized in this study are separated by forest type (monodominant and mixed) and the following size-class categories: seedlings (< 3.18 cm dbh; < 0.5 m height), small saplings (< 3.18 cm dbh; 0.5 – < 1.0 m) and juveniles + adults ($\geq$ 3.18 cm dbh; $\geq$ 1.0 m). Seedling numbers correspond to the 2003 census. These census data reflect the patterns observed in the manipulative study, validating the importance of seedling dynamics in the monodominant forest, and indicating that dispersal limitation does not prevent the non-dominant species from colonizing the monodominant forest.

Species	Forest type	Juveniles + adults (indiv. ha^{-1})	Small saplings (indiv. ha^{-1})	Seedlings (indiv. ha^{-1})
Dicymbe corymbosa	monodominant	5816	7988	80088
	mixed	0	0	0
Licania laxiflora	monodominant	2	0	138
	mixed	91	19	175
Eschweilera sagotiana	monodominant	229	225	365
	mixed	107	99	364
Carapa guianensis	monodominant	1	0	13
	mixed	2	2	14
Chrysophyllum sanguinolentum	monodominant	4	13	125
	mixed	14	4	33

neither predictable nor guaranteed. It is possible that generalist predator densities in the monodominant forest may be higher in years when trees other than *Dicymbe corymbosa* are fruiting, but even during those events it would presumably be more cost efficient to forage in the mixed forest where there are more fruiting individuals per area and a more diverse array of seeds (McGuire, unpubl. data). In addition, if masting events are spaced at sufficiently large intervals, specialist predators may not be able to maintain viable populations in the years between masts.

It is possible that predator satiation enabled the survival of *D. corymbosa* seeds during the fruiting events of 2002 and 2003. However, if as few as 8000 seeds ha^{-1} is sufficient for a successful seedling cohort, as was observed in 2002, then seed predators may not be the selective agents for the synchronous fruiting in this system. If trees are investing enough reserves to produce over 150 000 seeds ha^{-1}, as in 2003, then either the selective agents for masting are not present now or large numbers of seedlings are needed for successful recruitment, rather than large numbers of seeds. Alternatively, it may be that seed predators were originally selective agents for masting and that the inter-mast years provide enough food scarcity that their densities become low enough to prevent extensive crop damage.

The lack of a seed density effect in this study may be due to the spatial scale that mammals and other seed predators forage over. If seed predators have a relatively large foraging area, then the 1-m^2 plots would not be an ecologically relevant spatial unit. In this circumstance, seed density would be uniformly high in the monodominant forest and uniformly low in the mixed forest for *D. corymbosa*. This would rearrange the predictions for Table 1 and the predator satiation category would become 'high, high, low, low', making it indistinguishable from the ECM hypothesis. Since ants were the only observed seed predators of *D. corymbosa* and very few seeds were removed from the plots in the monodominant forest, it is unclear how density was perceived. Foraging patterns in *Atta* species are highly variable and can range from tens to hundreds of metres from a nest entrance (Kost *et al.* 2005). However, little is known about the role of these ant species as seed predators (but see Nascimiento & Proctor 1996 for another example). Ideally one could add seeds during a non-mast year in future experiments. However, due to the lack of seed dormancy in *D. corymbosa* this is currently not possible. This study attempted the next best scenario by manipulating seed densities during a low-density fruiting event.

In this study, it was not possible to discern the fate of removed seeds as suggested by Vander Wall *et al.* (2005). However, if certain extreme scenarios are considered, interpretation of the results may not be significantly altered. The two extreme possibilities for the removed seeds are: (1) all seeds failed to germinate or (2) all seeds germinated and survived to seedlings. If all seeds died, the results for total survival would look exactly as the graphs do for total survival. If all removed seeds germinated and survived to seedlings, the overall patterns would still be apparent. A scenario that would alter results significantly is if seeds were secondarily dispersed into more advantageous locations for seedling establishment (Fragoso & Huffman 2000, Fragoso *et al.* 2003, Silvius & Fragoso 2003). If this were the case, then reduced seed movement in the monodominant forest may mean less secondary seed dispersal events that would favour the establishment of non-dominant species.

Seedling survival

Dicymbe corymbosa seedling survival was significantly higher in the monodominant forest than in the mixed forest, indicating that recruitment success is much greater within its own forest type. Compared with the non-dominant species within the monodominant forest *D. corymbosa* seedling survival was significantly higher. This is the reverse of the pattern observed for seed germination success, which was high in the mono-dominant forest. Since the actual canopy abundance of these species in the monodominant forest is low (Table 2), seedling success seems to more accurately reflect natural diversity patterns in the community. This indicates that recruitment success may be driven more by dynamics at the early seedling stages than dynamics at the seed stage. These results are consistent with patterns of seed and seedling survival for *Dicymbe altsonii*, where seedling establishment is high within its own forest type (Zagt & Werger 1997). Although comparative seed and seedling survival was not tested in mixed forest in the above study, the authors suggest that regeneration pressure from the high density of seedlings in the understorey may drive the dominance of this species. The importance of seedling dynamics in the maintenance of monodominance is also supported by results found in African monodominant systems (Green & Newbery 2002, Hart 1995).

In another study by Henkel *et al.* (2005), comparative seed and seedling densities were estimated for the 2003 mast of *D. corymbosa*. They found seed output to be an average of 103 581 seeds ha^{-1} and seedling density to be an average of 2568 seedlings ha^{-1}. This estimate for seed output is lower than in the present study, but comparable, whereas the mean seedling density is dramatically lower in their census. This may be due to a smaller sampling area in their study or the cessation of their sampling in August when fruiting continued through September. The use of seed traps also differed from the methodology in this study, which may further account for different output estimates. Additionally, they use single

date seed and seedling counts in three sites along a 36-km transect, which may add variability to the estimates. Site differences may also account for the variability, but this is unlikely since these sites overlap and at the most distant points are no more than 40 km apart. Agents of seed predation in the Henkel *et al.* (2005) study were also found to be limited to harvester ants with estimated post-dispersal seed predation at 3–6%. In the current study, post-dispersal seed predation of *D. corymbosa* in the monodominant forest was 13–15%, which is a slightly higher estimate and may be due again to methodological differences.

Compared with other monodominant species, seed and seedling survival for *D. corymbosa* is extremely high. In Africa, the ectomycorrhizal monodominant *Gilbertiodendron dewevrei* has only been found to have a 9.1% seed survival during a masting event. *Julbernardia seretii*, another African dominant from the same study, exhibited 48.4–60.0% seed survival and 14–32% seedling survival over the same time span. Poor recruitment has also been documented for the dominant African legume, *Microberlinia bisulcata*, where only 12% of dispersed seeds survived after 6 wk and only 21% of seedlings survived to 31 mo (Green & Newbery 2002).

Ectomycorrhizas

Ectomycorrhizal colonization of seedlings after 1 y was significantly higher in the monodominant forest compared with the mixed forest. This suggests that ECM inoculum is limiting in the mixed, AM forest, which may prevent successful establishment of *D. corymbosa* seedlings. AM colonization of seedlings that established in the mixed forest was not measured in this study. *Dicymbe corymbosa* has been observed to form dual AM and ECM associations (McGuire, unpubl. data), but the consequences of dual infection for seedling survival is not known.

One reason why *D. corymbosa* seedlings survive better in the monodominant forest may be due to common ectomycorrhizal networks that link seedlings to conspecific adults (McGuire in press). In this study, seedlings that were restricted from access to the common ECM network had significantly lower survival and growth than seedlings with ECM network access. The precise mechanism by which the common ECM network confers survival advantages to these seedlings has not yet been determined, but assimilate transport such as carbon through the common ECM network is likely (Simard *et al.* 1997). Carbon augmentation through the ECM network may enable seedlings to persist for long periods of time in the understorey of the rain forest where light is limiting. It is possible that other factors simultaneously contribute to higher *D. corymbosa* seedling survival in the

monodominant forest, but to date, no other mechanisms have been detected.

Despite the significant recruitment success of *D. corymbosa*, results of this study suggest that dispersal limitation coupled with inoculum limitation in the mixed forest may explain containment of the monodominant patch. Furthermore, if seed predators are more abundant within the mixed forest, then they are probably not satiated by poorly dispersed *D. corymbosa* seeds, as only a few seeds would be expected to make it into (or be produced within) the mixed forest. The furthest point into the transition zone that new *D. corymbosa* seedlings were found was 17.4 m, and this distance was similar for both fruiting events in 2002 and 2003, despite the significantly lower seed output in 2002. The furthest seedlings from conspecific adults in 2001 extended 15 m toward the mixed forest, indicating either stability at the ecotone or extremely slow rates of spread of *D. corymbosa* into the mixed forest. Recent census data from Africa indicate that the monodominant forest comprised of *Gilbertiodendron dewevrei* is expanding at a rate of 0.34 m y^{-1} (Sean Thomas, unpubl. data). In this system it is speculated that large, catastrophic disturbances prevent the indefinite spread of this forest type, but during periods when disturbance is absent, the forest is expanding. The opposite scenario, however, has been proposed for the co-dominant species *Microberlinia busulcata* in Africa (Newbery *et al.* 2006b). Further studies of *D. corymbosa* survival in all size classes and long-term forest monitoring are important for accurately quantifying the dynamics in the transition zone. Specifically, the following questions need to be addressed in future studies: (1) Why is there such an abrupt transition between the monodominant and mixed forests? (2) How does a monodominant forest begin within the boundaries of a mixed forest? (3) What is the fate of seedlings that survive past the early stages of establishment? and (4) What constrains the monodominant forest from ultimately taking over all the mixed forest?

Conclusions

Monodominance of *Dicymbe corymbosa* appears to be related to low levels of seed predation and high seedling survival within areas of high conspecific adult density. The results presented here support predictions that ECM associations confer an advantage within the monodominant forest for *D. corymbosa*, but not in the mixed forest where ECM inoculum is possibly limiting. While it is likely that other life-history traits contribute to the monodominance of *Dicymbe corymbosa*, this study suggests that ECM associations play a major role in early establishment within the monodominant forest. Seed output of *D. corymbosa* during the masting

event was high and seeds successfully survived to the seedling stage without significant predation. In the seed predation experiment, seed density did not affect seed survival, but the experimental seed density was not as high as the observed natural seed density. Thus, seed predators may not have detected a difference in density for this experiment. Seeds of all species but one survived better in the monodominant forest suggesting that the seed predator community may be different in the monodominant forest. Seedling survival was only greater for *D. corymbosa* seedlings in the monodominant forest compared with the mixed forest, which indicates that *D. corymbosa* seedlings have an establishment advantage within the monodominant forest, possibly related to ECM inoculum availability.

ACKNOWLEDGEMENTS

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