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Gorillas and seed dispersal in the Lopé Reserve, Gabon. II: Survival and growth of seedlings

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ABSTRACT. Evidence is presented for the importance of western lowland gorillas as seed dispersers in the Lopé Reserve, Gabon. The survival and growth of seedlings of three tree species, growing from dung deposited at gorilla nest sites, were monitored for up to 2 y after deposition. A comparison was made between this and seeds (i) deposited in dung on gorilla feeding trails, (ii) dropped (spat out) under conspecific canopies, and (iii) scatter-dispersed (spat out) by other consumers away from conspecific trees but under intact forest canopy. The highest survival and the best performance of seedlings was always at a gorilla nest site, although not every site was favourable for survival or growth. Seedling performance was related to the surrounding vegetation conditions: better performance was observed in seedling clumps with less vegetation cover. Gorillas at Lopé apparently provide high quality seed dispersal for these species, not just because they consume large quantities of seeds, but because the pattern of seed deposition, especially in nest sites, can result in the enhanced survival and growth of seedlings.

KEY WORDS: gorilla, regeneration, seed dispersal, seedlings, tropical forest

INTRODUCTION

Seed dispersal is a well established subject within the field of tropical ecology (e.g. Bawa & Hadley 1990, Estrada & Fleming 1986, Fenner 1992, Fleming & Estrada 1993, Wheelwright 1991). The importance of the dispersal of seeds away from conspecifics has been recognized for some time, and has been formalised into particular hypotheses: that of colonisation (establishment in new areas); escape (avoidance of density- or distant-dependent mortality); and

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directed dispersal (the deposition of seeds in favourable 'safe' sites) (Connell 1971, Howe & Smallwood 1982, Janzen 1970). Studies of seed and seedling survival, many of them in the neotropics, have largely confirmed the importance of the environmental conditions of the site where seeds are deposited (see review by Clark & Clark 1984, and Clark 1990, Schupp 1988a). In spite of the range of regeneration strategies exhibited by tropical trees, it has frequently been found that seedling survival and/or growth is better in gap sites than in understorey conditions (e.g. Augspurger 1984, De Steven 1994, De Steven & Putz 1984, Forget 1997, Howe *et al*. 1985, Osunkoya *et al*. 1993, Schupp 1988b).

Few studies have followed the fate of seeds and seedlings for any length of time, and even fewer have forged a link between the seed removal by a particular consumer and the fate of deposited seeds (Chapman *et al*. 1993, Dinerstein & Wemmer 1988, Fragoso 1997, Howe *et al*. 1985). This post-dispersal component of quality has to be addressed in order to establish the importance of a particular disperser. The transition from seed to established seedling is the most vulnerable part of a plant's life-cycle and as such represents a very narrow survival window. It is therefore a crucial element of plant population dynamics.

Western lowland gorillas (*Gorilla gorilla gorilla* Savage & Wyman) at the Lopé are highly frugivorous (Tutin & Fernandez 1993, Voysey *et al*. 1999) and large numbers of seeds of many of the fruit species they consume are swallowed and passed out intact in dung. In addition, their nest-building behaviour is a critical factor in terms of seed dispersal. Much of their faecal output occurs at nest sites (the term used for the group of nests built by a group of gorillas). Fresh nests are built in a new locality each night, so aggregate effects of seed accumulation are minimised, with nest sites acting as potential seed and seedling banks. Nests are most often made on the ground (64 % of 2435 nests, Tutin *et al*. 1995), but nest position is also influenced by habitat type. Nest sites are often found in areas of more open tree canopy, and 25 % of 373 nest sites at Lopé were in light gaps (Tutin *et al*. 1995).

The role of large frugivores as seed dispersers in African forests is little known from the perspective of seed and seedling survival (Chapman *et al*. 1993, Tutin *et al*. 1991, Wrangham *et al*. 1994). This paper describes the survival and growth of seedlings of three tropical rain forest tree species following seed dispersal by gorillas. A preliminary study had indicated that deposition at nest sites can make a significant difference to seed and seedling survival (Tutin *et al*. 1991). Questions guiding our study were: Does dispersal by gorillas make a difference to the plant's chances of initial establishment? Are some deposition sites better than others for establishment and growth? By comparison with seeds that were spat out by other consumers under or away from the conspecific tree, we hoped to establish if some of the seeds removed by gorillas are reliably deposited in favourable sites. This is the first study to detail the importance of gorillas as seed dispersers by following the survival and growth of seedlings from dung, especially of those growing in nest sites, beyond the first few months.

STUDY SITE AND SPECIES

A description of the study site and characteristics of gorillas as frugivores can be found in the accompanying paper (Voysey *et al*. 1999). The three tree species selected for study over a period of 2 y were *Ganophyllum giganteum* (Chev.) Haum. (Sapindaceae), *Cola lizae* Hallé (Sterculiaceae) and *Uapaca guineensis* Müll. Arg. (Euphorbiaceae). Detailed descriptions of these species are also given in Table 1 of Voysey *et al*. 1999. Seeds of *Cola* measure typically 31 mm × 17 mm and germinate within a few days of deposition; the majority of *Ganophyllum* seeds (typically 19 mm × 10 mm) germinate promptly (within 1–3 wk) although some germinate up to 8 wk after deposition; this is also the case for *Uapaca* seeds, which measure typically 17 mm × 10 mm. *Cola* and *Ganophyllum* seedlings are epigeal with fleshy cotyledons, but those of *Uapaca* have leafy cotyledons. Data come from two fruiting seasons (1992 and 1993) for *Ganophyllum*, and one fruiting season (1992) for *Cola* and *Uapaca*. *Cola* failed to produce fruit in 1993, and *Uapaca* seeds in 1993 were deposited only 1–3 wk before the end of the study, precluding data gathering on growth and survival.

METHODS

Seeds dispersed by gorillas

Gorilla dung at nest sites located during the fruiting season of each tree species was marked and checked at intervals thereafter to monitor the survival and growth of seeds and seedlings. The gorillas were not habituated so could not be followed, hence nest sites were difficult to find. Upon finding a nest site, the total number of seeds of the study species in each dung pile was counted, and every dung pile was marked with a numbered aluminium tent peg. Data were also collected from dung piles that were deposited on gorilla feeding trails. For the most part, these dung piles were on or close to animal paths used by the gorillas when travelling.

A measure of the canopy cover at three heights (≤ 4, 5–20, > 20 m) above each dung pile was obtained using a clinometer. Looking vertically upwards, vegetation was recorded at each height if it covered the hairline in the clinometer's sight. A canopy cover score was given to each clump at nest sites. The scoring was weighted to reflect the importance of herbaceous vegetation immediately above any seed or seedling. If cover over a dung pile was recorded at ≤ 4 m, it scored six points, at 5–20 m, three points, and at > 20 m, one point, giving a maximum of 10 points if vegetation was recorded at all three levels. The stem density of the principal herbaceous species in the 1-m^2 area around each dung pile was also recorded. Other salient features were noted, such as the position of the dung pile relative to the nest construction (inside, on the rim, outside), the abundance of leaf litter, slope, proximity to a log or tree, distance to a savanna/forest boundary or whether the dung pile was under a vine tower.

Dung piles were then monitored to follow germination and seedling survival and growth. Dung was checked every week for 6 wk, then every 2 wk for 6 wk, then monthly for 3 mo and thereafter every 3 mo. Only the number of surviving seedlings was counted, because the disturbance of the pile of seeds required to count ungerminated seeds and those at the early stages of germination would have damaged emerging radicles or otherwise influenced survival. Once the seedlings started to emerge, the following data were recorded: number surviving in the clump; range of their heights (ground level to apical bud); length of the longest leaf in the clump; greatest number of leaves on any one seedling in the clump; and any indication of the cause of mortality (e.g. browsing by herbivores, trampling, or attack by pathogens). Measurements were taken for the clump as a whole, because it was initially unfeasible to tag, measure and monitor individual seedlings without causing damage. Height, longest leaf and number of leaves were taken as an indication of seedling performance.

Scattered and dropped seeds

Monkeys (*Cercopithecus* spp, *Cercocebus albigena*) either drop seeds of the three species under the conspecific tree or transport them in their cheekpouches up to 80 m away, spitting them out under the trees in which they stop to process the fruit (see Voysey *et al.* 1999). They may occasionally swallow seeds of *Ganophyllum* and *Uapaca*.

(i) *Seed quadrats*. Seeds that had been spat out by monkeys were placed in quadrats under conspecific trees and away from them, under intact forest canopy up to 80 m distant from the nearest conspecific. Each quadrat measured 50 cm × 50 cm, with seeds placed regularly at 10 cm spacing, giving a total of 36 seeds per quadrat (for the large *Cola* seeds only 25 were placed per quadrat). Aluminium tent pegs were used to mark the corners of the quadrats. For *Ganophyllum*, 14 quadrats of seeds (a total of 504 seeds) were set out, all in the second season of 1993: eight were located under different conspecific trees and six were located under intact forest canopy away from conspecifics. Ten quadrats of *Cola* seeds were set out underneath three conspecific trees in 1992, a total of 250 seeds. In the case of *Uapaca*, 14 quadrats of seeds were placed under five conspecific trees, and 10 quadrats away from conspecifics, a total of 864 seeds.

(ii) *Labelled seedlings*. As another means of following the growth and survival of seedlings originating from dropped and scatter-dispersed seeds, searches were made for seedlings under a sample of trees of each species 1–4 mo after fruiting. Seedlings (of that season) were individually labelled with white plastic tags, and their heights recorded. These seedlings were checked and remeasured every 3 mo. Labels found without a seedling, and the disappearance of labels, were used in the estimation of seedling mortality. The use of labelled seedlings compensated for the high losses of seeds and early seedlings from quadrats which severely reduced sample sizes.

In 1992, under 11 *Ganophyllum* trees, 168 seedlings were found and labelled.

In 1993, it was noticed that a proportion of *Ganophyllum* seeds exhibited delayed germination, emerging in April rather than January. One cohort of newly-germinated seedlings was labelled in February (74 seedlings under eight conspecifics and 98 seedlings found away from conspecifics, a result of scatter-dispersal) and another cohort in May (140 seedlings under eight trees and 80 seedlings away from conspecifics). For *Cola*, only those seedlings growing under conspecific canopies were labelled in 1992 (200 seedlings under seven trees). A total of 300 seedlings under three *Uapaca* trees in the forest interior were labelled in two cohorts. The first cohort of 150 seedlings was labelled in January, and the second cohort, from fruit that fell later in the season, in May.

Analysis of results

Non-parametric statistical tests were used in almost all cases (Fowler & Cohen 1992, Siegel & Castellan 1988). Tests were two-tailed unless otherwise stated, with 5 % as the level of significance. Some aspects of the terminology used in the data analysis require further explanation. The cover score is derived from the assessment of vegetation cover over each dung pile as described above. The height, longest leaf and number of leaves of a seedling were used as an index of performance. The performance of a seedling or clump of seedlings was also expressed in terms of duration (the length of time that a clump still had seedlings up to the end of the study) and growth, expressed as relative growth rate (height increment over time). The term 'site' refers to a gorilla nest site (a group of night nests), unless otherwise stated. Each has a code number reflecting the year and a numbered identity: e.g. G2/5 is the fifth nest site found in 1992; G3/9 is the ninth nest site found in 1993. Only a sample of nest sites found during a year as part of long term research at SEGC were used in this study.

RESULTS

Seed deposition sites

The details of the gorilla dung piles that were monitored, their immediate environments, and the performance of seedlings growing from them, are shown in Table 1. The sites used were *Ganophyllum* – G2/5, G2/6 (1992), G3/5, G3/6, G3/8 and G3/9 (1993); *Cola* – G2/19, G2/22, G2/23, G2/26 (1992); *Uapaca* – G2/81, G2/83, G2/84, G2/89 and G2/90 (1992), G3/91, G3/93, G3/95, G3/97, G3/103 and G3/104 (1993).

A total of 82 dung piles with 7225 *Ganophyllum* seeds, 66 with 2342 *Cola* seeds and 43 with 6524 *Uapaca* seeds were marked and monitored. The nest sites contained from 495 to over 2000 *Ganophyllum* seeds (six sites), from 97 to 844 *Cola* seeds four sites) and from 110 to over 3000 *Uapaca* seeds (11 sites). The number of seeds in dung piles marked ranged from 5-391 *Ganophyllum* seeds, 3-113 *Cola* seeds and 1-1196 *Uapaca* seeds.

Table 1. The vegetation around gorilla dung piles in nest sites and on feeding trails which contain the seeds of three tree species studied in the Lopé Reserve, Gabon, in two fruiting seasons (*Ganophyllum giganteum*, *Cola lizae* and *Uapaca guineensis*), and the performance of seedlings in the growing clumps. Methods for calculation and explanation of the terms are given in the text. The maximum cover score is 10. The herbaceous stem density is the number of stems per square metre. Seedling performance measures are the highest value in each clump still with seedlings in each nest site. ND = no data; a + indicates that seedlings persisted to the end of the study period and were likely to survive for longer.

	Ganophyllum giganteum								*Cola lizae*				
Year of fruiting	1992			1993					1992				
Location (code of nest site, or trail)	G2/5	G2/6	trail	G3/5	G3/6	G3/8	G3/9	trail	G2/19	G2/22	G2/23	G2/26	trail
Number of seeds per clump													
Median	23.2	139	29	45	41	59	114	76	17	7	47	54	19.5
Range	5–143	65–391	14–76	13–115	9–238	9–274	52–296	24–163	3–113	1–17	28–95	10–84	7–106
Total number of seeds	495	2073	285	634	690	580	1110	1358	284	97	377	844	740
Number of clumps	14	13	8	11	8	7	8	13	9	11	7	17	22
Vegetation cover													
Median cover score	7	4	4	6	9.5	7	4	4	3	3	7	7	4
Percentage of clumps with cover at heights of ≤ 4 m	79	15	12.5	50	80	57	38	7.7	22	46	86	71	0
5–20 m	50	85	87.5	0	100	43	100	77	78	55	29	65	71
>20 m	79	62	87.5	0	70	86	100	85	56	0	86	53	77
Herbaceous stems:													
Median stem density (m^{-2})	4	6	ND	9	8.5	11.5	12	ND	7	ND	3.5	2	ND
Seedling performance													
Duration (wk)													
Median	83	4	1	3	3	0	8	3	84+	6	84+	84+	47.5
Range	1–92+	3–92+	0–6	2–8	2–16	0–2	0–44+	0–16	3–84+	3–6	21–84+	10–84+	1–84+
Maximum height of clump (cm)													
Median	17.5	8	ND	ND	10	ND	11.5	ND	24.5	ND	23	23.5	12.5
Range	12–34	8–15			9–12.5		9–14		12–27		9–24	9.5–27	7–28
Relative growth rate (cm mo^{-1})													
Median	0.8	0.3	ND	ND	0.92	ND	0.33	ND	0.6	ND	0.75	1.65	0.51
Range	0.1–1.2	0–0.7			0.33–1.5		0–2		0.27–1.15		0.39–2.1	0–7	0–5
Length of longest leaf (mm)													
Median	66	42	ND	ND	45	ND	52	ND	110	ND	100	108	95.5
Range	31–120	22–50			35–55		51–57		80–134		58–111	23–134	51–150
Maximum number of leaves													
Median	7	4	ND	ND	2	ND	3	ND	5	ND	2.5	3	2.5
Range	3–13	2–6	3–5	3–6	2–4	1.7	1–4						

	Uapaca guineensis												
Year of fruiting	1992						1993						
Location (code of nest site, or trail)	G2/81	G2/83	G2/84	G2/89	G2/90	trail	G3/91	G3/93	G3/95	G3/97	G3/103	G3/104	trail
Number of seeds per clump													
Median	72	8	15	41	469	13	18	9	56	12	30	37	48
Range	50–198	1–67	5–77	20–50	129–1196	5–190	5–68	3–17	11–127	5–71	7–56	8–88	6–110
Total number of seeds	728	112	225	152	3002	327	237	95	725	127	158	274	362
Number of clumps	7	7	11	4	6	8	9	9	13	5	5	7	7
Vegetation cover													
Median cover score	0	10	4	6	1	3.5	7	6	6	9	4	10	3
Percentage of clumps with cover at heights of ≤ 4 m	0.14	57	45.5	75	16.7	37.5	55.6	55.6	75	63.5	0	100	14.3
5–20 m	0	100	63.6	0	33.3	87.5	44.4	44.4	50	87.5	100	62.5	85.7
<20 m	0	100	54.6	0	83.3	37.5	88.9	0	8	25	100	87.5	42.9
Herbaceous stems:													
Median stem density (m^{-2})	0	5.5	0	20	9.5	ND							
Seedling performance													
Duration (wk)													
Median	54+	11	53+	38	47+	30	(these data not collected, due to short monitoring period)						
Range		1–21	11–53+	24–52+		5–47+							
Maximum height of clump (cm)													
Median	20.8	8.5	12	15	28.5	11							
Range	12–24.5	7–9	10–15	12–24	16–34	4.5–12.5							
Relative growth rate (cm mo^{-1})													
Median	1.19	0	0.39	2	1.41	0.22							
Range	0.57–1.5	0–1	0.15–4.0	1.21–2.69	0.29–1.95	0-0.55							
Length of longest leaf (mm)													
Median	116	40	66	57.5	170	82							
Range	62–144	40	48–108	20–105	58–222	63–106							
Maximum number of leaves													
Median	9.5	1	4	1.5	7.5	6							
Range	5–11	1	2–7	1–6	3–9	2–6							

The difference in vegetation cover score for the two nest sites with *Ganophyllum* seeds monitored in 1992 was not significant, and of those monitored in 1993, only two sites differed, site G3/9 having less cover than site G3/6 (Kruskal-Wallis one-way ANOVA by ranks $K = 8.1$, $df = 3$, $P < 0.05$). Of the nest sites with *Cola* seeds, site G2/19 was the most open although differences were not significant. The *Uapaca* nest site G2/90 was the most open of the forest interior sites ($K = 8.68$, $df = 3$, $P < 0.05$). Site G2/81 was in grass savanna and understandably had less cover than sites G2/83 and G2/84 ($K = 16.36$, $df = 4$, $P < 0.01$), but not site G2/90. Dung piles located on gorilla feeding trails generally had little or no cover at ≤ 4 m.

Seedling survival

(i) *Seed predation.*

Levels of predation on seeds in dung piles prior to germination differed: seeds of *Uapaca* seemed to suffer no predation, those of *Cola* were rarely affected, whereas those of *Ganophyllum* suffered predation of varying severity.

Ganophyllum. In 1992, from 43–77 % of marked dung piles with *Ganophyllum* seeds suffered some predation. In dung left on trails, a median of 50 % of the original number of seeds deposited were predated, but only 6 and 7 % of seeds in dung at nest sites were predated ($P > 0.1$). Predation was probably by small rodents, judging from the broken endocarps found. Severe predation of *Ganophyllum* seeds occurred in 1993. Every dung pile that was located and marked for monitoring was affected, whether it was on feeding trails or in a nest site. Seeds in quadrats (dropped and scatter-dispersed seeds) were also severely affected. Median predation levels at the four nest sites and in dung on feeding trails ranged from 96 to 100 % of seeds.

Cola and *Uapaca*. Only six dung piles were noted to have suffered the loss of some *Cola* seeds to predation. No evidence of predation of *Uapaca* seeds was recorded at any of the 98 dung piles monitored.

(ii) Seeds dispersed by gorillas: survival in nest sites.

Survival of seedlings of the three study species at nest sites and on feeding trails is shown in Figures 1 and 2. For reasons of clarity not all nest sites are shown, but those included indicate the highest, lowest and intermediate results. Generally, most mortality occurred in the first few weeks of growth. No association was detected between the number of seeds in a dung pile and the proportion of seedlings surviving at any stage thereafter, for any of the three species, suggesting no density dependence.

Ganophyllum. Figure 1a shows the survival of *Ganophyllum* seedlings growing from dung piles deposited in 1992. Overall, 2 % of the total number of seeds deposited in monitored dung in 1992 survived as seedlings after 92 wk. The difference in survival between sites and trails was already significant 3 wk after deposition (K = 12.54, df = 2, P < 0.01). Seeds and seedlings on feeding trails did not last long: none remained after 8 wk. After 28 wk the difference between the two nest sites was still significant (Mann-Whitney U-test, U = 0, P < 0.001); there were too few seedlings in site G2/6 after this time for statistical tests.

Clumps of *Ganophyllum* seedlings lasted longer at site G2/5 than at site G2/6 and on feeding trails (K = 13.82, df = 2, P < 0.01). At the end of the study, there was a larger contribution to the seedling bank at site G2/5, where 59 seedlings in seven clumps survived from an initial 14 clumps, but only one seedling remained as a potential adult in site G2/6.

Due to seed predation very few *Ganophyllum* seeds in 1993 survived: typically 1–3 % of deposited seeds were surviving as seedlings after the first 4 wk (Figure 1b). Overall, mortality in 1993 was 99.98 % of the 4372 seeds deposited in monitored gorilla dung, with only one seedling at site G3/9 surviving until the end of the study (49 wk after deposition).

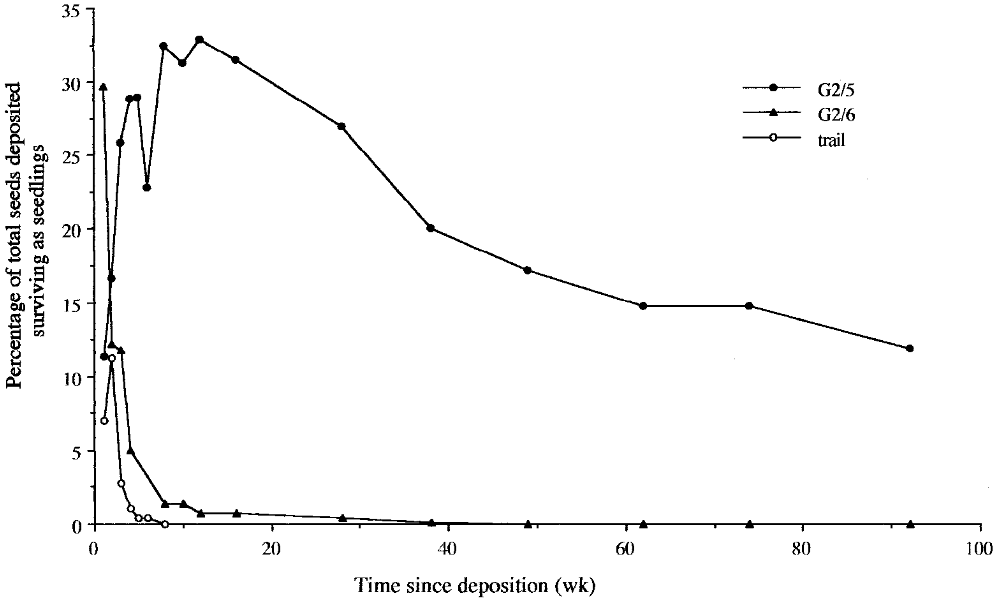
Cola. The survival of *Cola* seedlings growing from gorilla dung in nest sites and on feeding trails is shown in Figure 2a. After 5 wk, 20–60 % of seeds were surviving as seedlings. Apart from the dramatic loss of all seedlings in site G2/22 (thought to be due to desiccation) there were no large differences in survival among different nest sites or dung on feeding trails after the first few months, although the highest percentage survival (median of n clumps still with seedlings) was in site G2/19.

After 84 wk, site G2/19 made the biggest contribution to the seedling bank, with 30 seedlings in seven clumps (78 % of the original number of clumps), and there were 13 seedlings in six clumps (27 % of original number) on feeding trails. Nest site G2/23 had 14 seedlings in four clumps (57 % of original number) and site G2/26 had 22 seedlings in nine clumps (53 % of original number).

Uapaca. Figure 2b shows the survival of *Uapaca* seedlings growing from dung deposited in the nest sites and on feeding trails until the end of the study. Survival rates after 12 wk were typically 10–30 % of the seeds deposited. Site G2/83 was evidently not favourable for the few *Uapaca* seedlings growing there, as none remained after 38 wk. After 4 wk, seedling survival at site G2/90 (most open forest interior) was significantly higher than at site G2/81 (savanna site) (K = 17.13, df = 5, P < 0.01) and seedlings in site G2/90 still had the highest survival at the end of the study (47–54 wk after deposition; sites G2/83 and G2/89 excluded due to small sample sizes).

Although a low proportion of seedlings survived at site G2/81 (in savanna), all the clumps originally deposited still had seedlings in them at the end of the study (six clumps, 45 seedlings), as did site G2/90, which had the largest seedling bank (six clumps, 363 seedlings). Only six seedlings remained in four clumps located on feeding trails.

(a) *Ganophyllum giganteum* 1992



(b) *Ganophyllum giganteum* 1993

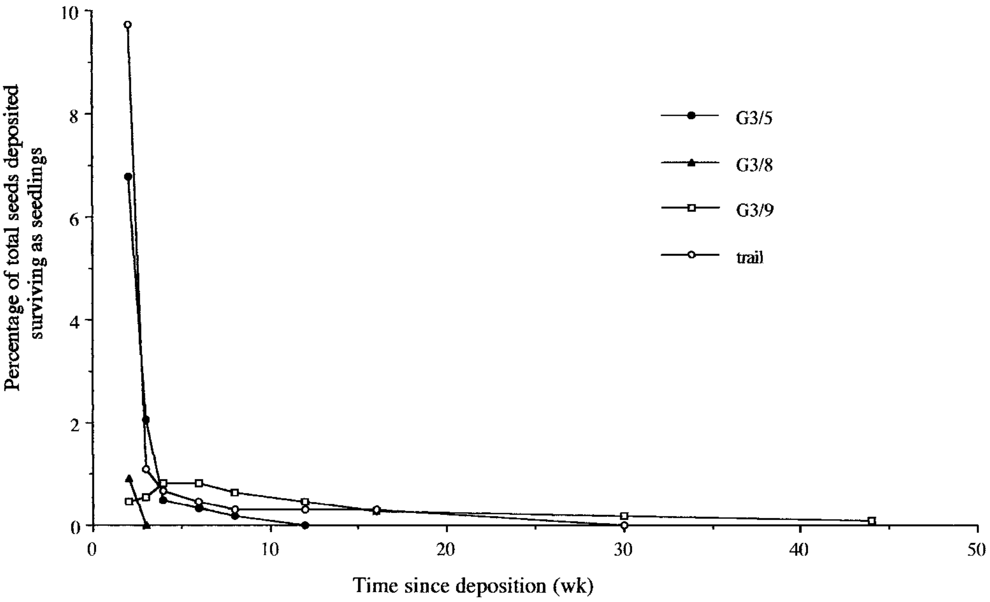
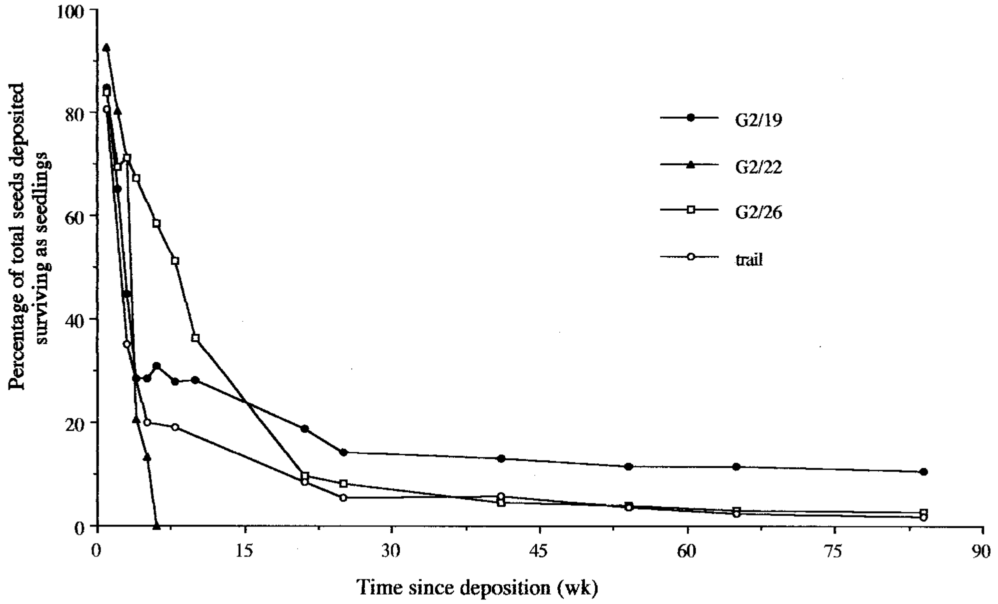


Figure 1. Survival of *Ganophyllum giganteum* seedlings growing from gorilla dung in nest sites and on feeding trails marked in (a) 1992 and (b) 1993 in the Lopé Reserve, Gabon. Values are the percentage of the total seeds deposited at each nest site, or on trails, surviving as seedlings (in *n* clumps still with seedlings). At the time of deposition, seeds were counted; thereafter, only seedlings were counted. In some instances, therefore, the first few weeks show an increase in seedlings recruited to the clump as seeds germinated over a period of time.

(a) *Cola lizae* 1992



(b) *Uapaca guineensis* 1992

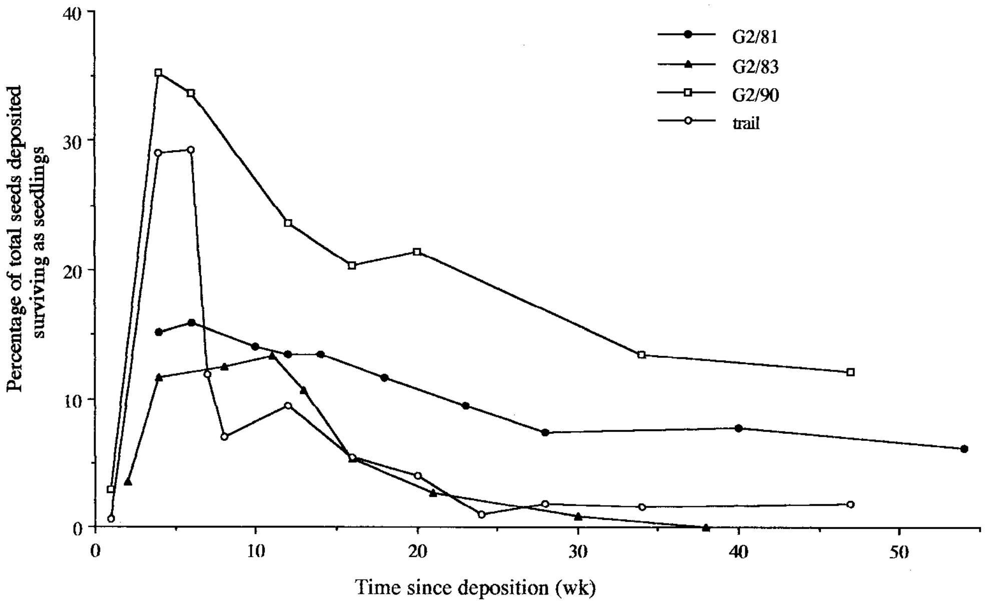


Figure 2. Survival of (a) *Cola lizae* and (b) *Uapaca guineensis* seedlings growing from gorilla dung in nest sites and on feeding trails marked in 1992 in the Lopé Reserve, Gabon. Explanation for variables is as for Figure 1.

(iii) Survival of seedlings from scattered and dropped seeds

Generally, it was found that the survival of seeds and seedlings either dropped (under conspecifics) or scattered (under intact forest canopy away from conspecifics) was lower than in most nest sites. This result was clear for *Ganophyllum* and *Uapaca*, but was not so clear for the more shade-tolerant *Cola*.

Ganophyllum. In 1992, the survival of an initial 168 labelled *Ganophyllum* seedlings growing under 11 conspecific canopies was significantly lower than that of seedlings in nest site G2/5 ($U = 12$, $P < 0.01$). Labelled seedlings in 1993 that germinated promptly survived better than those exhibiting delayed germination (after 12 wk: $U = 7$, $P = 0.053$; after 24 wk: $U = 5$, $P < 0.05$), but there was no significant difference in survival between labelled seedlings under parents and those away from conspecifics.

The severe predation of seeds in 1993 affected scattered and dropped seeds as much as seeds in dung: only one seedling in each of two quadrats survived at the end of the study, a mortality of 99.6 % of seedlings after 49 wk. In 1993, there was no significant difference in the survival of *Ganophyllum* seeds placed in quadrats under conspecific canopies and those placed away from conspecifics.

Cola. No seedlings growing from dropped seeds under conspecific canopies survived beyond 65 wk. No significant differences were found between the survival of *Cola* seedlings from scatter dispersed seeds and those growing from gorilla dung. No significant differences were found in the survival of seedlings that were labelled under conspecific canopies and those of a similar age that had survived from gorilla dung. These data suggest that in terms of survival alone, seeds dropped under the conspecific, if they survived to become seedlings, fared no worse than those dispersed in gorilla dung, although the highest proportion of surviving seedlings was nonetheless at a nest site.

Uapaca. Initially (up to 10 wk) there was no significant difference in the survival of seedlings form dropped or scattered seeds. After 21 wk however, seedling survival was significantly higher away from conspecific canopies ($U = 2$, $P < 0.05$). No seedlings remained from the sample under conspecifics after 28 wk.

Seedling performance

The various aspects of seedling performance are summarised in Table 1.The maximum height of a *Ganophyllum* seedling in a clump was found to correlate significantly with the length of the longest leaf and with the maximum number of leaves (Kendall's coefficient of concordance $W = 0.892$, $\tau = 37.5$, $df = 14$, $P < 0.001$; average $r_s = 0.838$). These same measures did not correlate in the case of *Cola* seedlings, but in the case of *Uapaca* seedlings, these parameters were all closely associated ($W = 0.876$, $\tau = 65.7$, $df = 25$, $P < 0.001$; average $r_s = 0.814$).

Ganophyllum. The median heights of seedlings growing in the two nest sites and under conspecific canopies are shown in Figure 3a (Seedlings growing from dung on trails did not last long enough to grow to a measurable height.) *Ganophyllum* seedlings in site G2/5 were taller and had more and longer leaves than seedlings in site G2/6. Heights of the tallest seedlings in clumps at the two sites did not differ significantly 12 wk after deposition, but those in site G2/5 were significantly taller than those at G2/6 after 28 wk ($U = 2.5$, $P < 0.05$). Seedlings in clumps at site G2/5 were taller than the tallest ones under each of the conspecific canopies sampled, although no significant difference was found between median heights (range of maximum heights: 12.5 – 34 cm at site G2/5; 10–20.5 cm under conspecifics).

Seedlings growing under conspecifics were no taller than those growing away from conspecifics after 24 wk, whether they were prompt-germinating ($P > 0.1$) or delayed-germinating ($P > 0.05$). Prompt-germinating seedlings were taller than delayed seedlings when about 20 wk old, whether under or away from conspecifics (z-test; under, $z = 2.2$; away, $z = 2.44$; both $P < 0.05$).

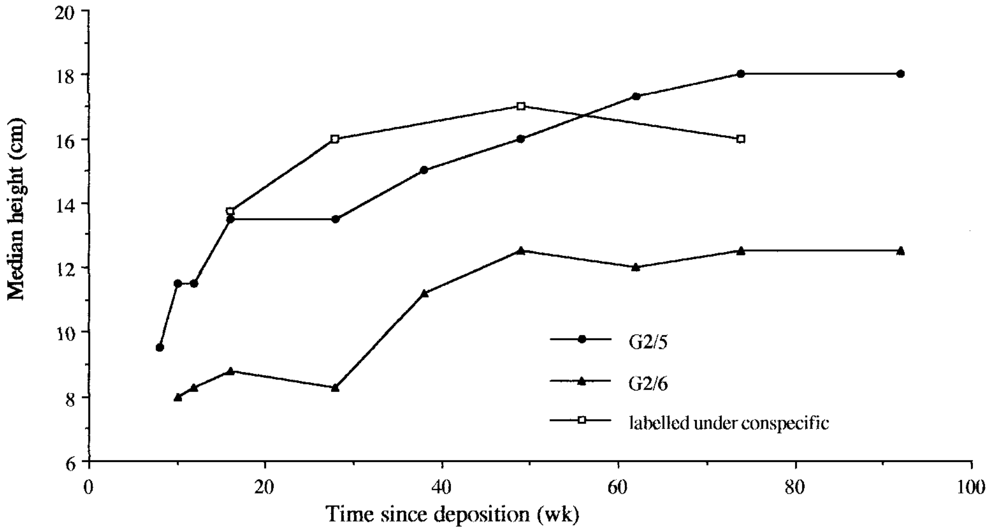
Seedlings that grew more vigorously had higher survival rates: a significant positive correlation emerged between the growth of seedlings and their survival until the end of the study ($r_s = 0.59$, $P < 0.05$, $n = 16$). There was no statistically significant difference in relative growth rates between the two nest sites, suggesting that surviving *Ganophyllum* seedlings at site G2/6 grew as fast as those at site G2/5, for the length of time they survived.

There were too few survivors from any dung pile or quadrat in 1993 to use in comparisons of heights.

Cola. Seedlings from dropped seeds under conspecifics lasted for less time than clumps in sites G2/19 and G2/23 ($K = 11.51$, $df = 3$, $P < 0.01$). Initial differences in height between the tallest seedlings at the different nest sites diminished over time (Figure 3b). At the first measuring, seedlings at site G2/26 were significantly taller than at the other sites ($K = 6.82$, $df = 3$, $P < 0.05$). Seedlings growing from dung left on feeding trails were significantly shorter than those at site G2/26 after 8 wk ($K_{df3} = 14.65$, $df = 3$, $P < 0.01$). After 84 wk, however, differences in height were not significant ($P > 0.2$), although seedlings in site G2/19 were clearly taller than those at other locations (Figure 3b).

The heights of seedlings growing from seed quadrats are also shown in Figure 3b. They were significantly shorter than those at site G2/26 initially (10 wk; $K = 16.25$, $df = 3$, $P < 0.01$) and significantly shorter than those at sites G2/19 and G2/23 after *c.* 38 wk ($K = 10.62$, $df = 3$, $P < 0.02$). No significant difference was found between the median heights of the tallest seedlings in clumps at nest sites and the tallest labelled seedlings under individual conspecific trees.

(a) ***Ganophyllum giganteum*** 1992



(b) *Cola lizae* 1992

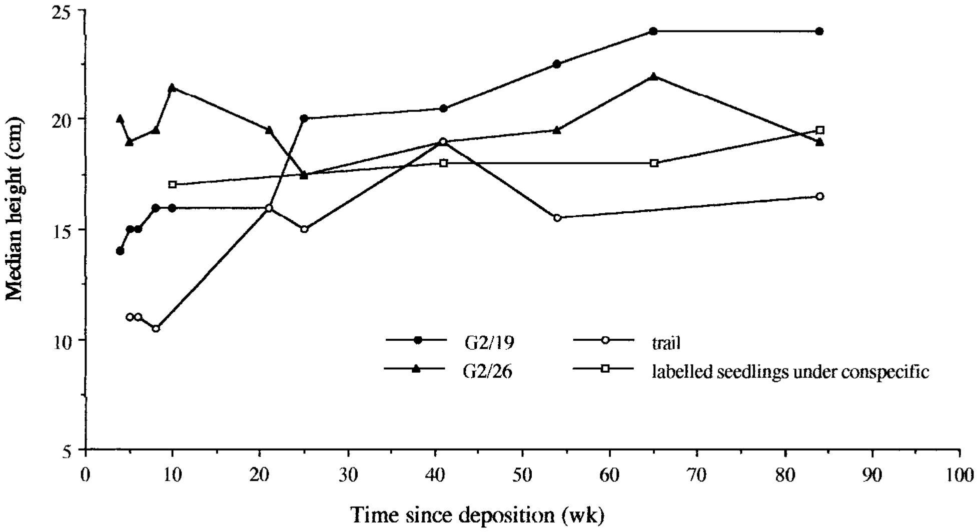
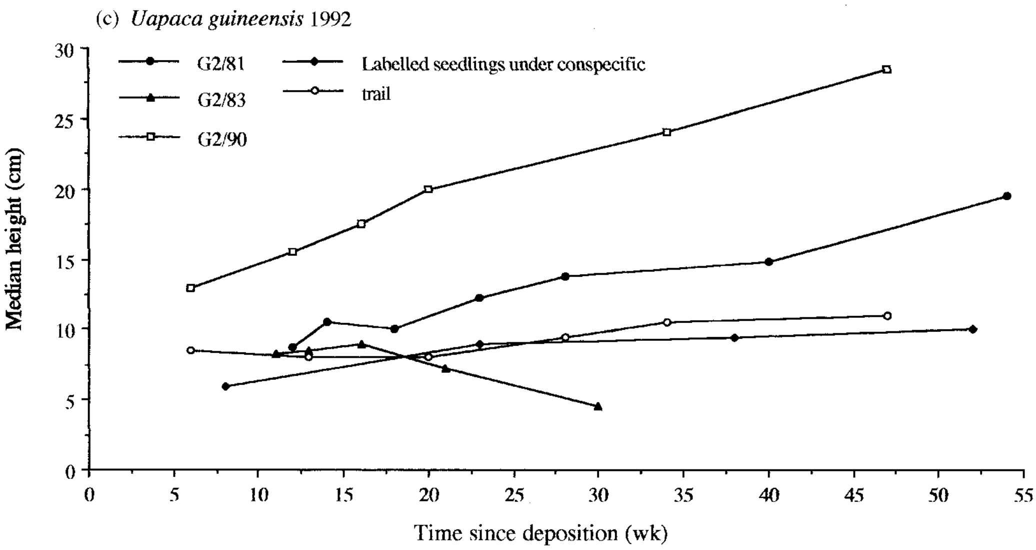


Figure 3. Change in height of seedlings over time for (a) *Ganophyllum giganteum*, (b) *Cola lizae* and (c) *Uapaca guineensis* in nest sites in the Lopé Reserve, Gabon. Explanation: G2/.. – nest sites (median height of the tallest seedlings in all clumps); labelled – under conspecific crowns (median height of the tallest seedlings under a sample of tree); trail – in dung on feeding trails.



(c) *Uapaca guineensis* 1992

Figure 3 (continued).

Nearly all clumps of *Cola* seedlings were browsed during the study period, probably by forest ungulates. Browsing usually affected more than one seedling in the clump and the tallest ones were often those that were browsed, but there were always some which were not damaged. Seedlings were able to recover, either by growing new leaves or a new apical bud if the previous one was removed, but this was less likely for seedlings growing in less favourable locations. The rate of growth of seedlings at nest sites was higher than that of seedlings on feeding trails and those growing from dropped seeds ($P > 0.1$ and $P > 0.05$ respectively).

Uapaca. Clumps of *Uapaca* seedlings at site G2/83 (the shadiest site) showed a significantly shorter median duration than those at the other sites ($K = 74.8$, $df = 4$, $P < 0.001$). The heights of seedlings at the nest sites, those from dung on trails, in quadrats and those that were labelled as the first cohort under canopies are shown in Figure 3c. Seedlings at site G2/90 were consistently and significantly taller than seedlings in site G2/84, those from dung on trails, and those in quadrats (all $P < 0.01$). After 21 or 27 wk seedlings away from conspecifics were significantly taller than those underneath ($K = 6.76$, $df = 2$, $P < 0.05$). By the end of the study, seedlings under conspecifics were the shortest of any location. Seedlings at site G2/83 showed significantly slower growth than seedlings at sites G2/81 and G2/90 ($K = 19.48$, $df = 7$, $P < 0.01$).

Vegetation and performance of seedlings

Seedlings in clumps with more herbaceous vegetation cover grew more slowly than those with less herbaceous cover above them. Although vegetation cover was calculated using tree cover as well, it seemed that herbaceous cover had a critical influence on performance. Results were clear for *Ganophyllum* and *Uapaca* but were not significant for *Cola*, although the trend was the same. Data from all locations were pooled, because sample sizes at individual sites were otherwise too small.

Ganophyllum. The density of herbaceous stems around a seedling clump correlated significantly and negatively with the growth rate of seedlings (Spearman's $r_s = -0.611$, $n = 16$, $P < 0.02$, one-tailed test). Seedlings in clumps with cover at ≤ 4 m grew less rapidly than those without ($U = 5$, $P < 0.05$). The survival or maximum height of seedlings did not correlate with herbaceous stem density. Too few seedlings survived in 1993 to investigate any associations with the surrounding vegetation.

Cola. There were no significant associations found between measures of vegetation cover and the performance of *Cola* seedlings. Nonetheless, the trends were clear and consistent, even for what can be regarded as a shade-tolerant species. Seedlings at site G2/19, which was the most open site (scoring the lowest in terms of vegetation cover especially at ≤ 4 m) outperformed seedlings at other locations, with those deposited on feeding trails or growing from dropped seeds usually ranked lowest. Seedlings at G2/19 were the most vigorous, measured in terms of height, length of leaves or number of leaves, as well as rate of growth (see Table 1).

Uapaca. The height of *Uapaca* seedlings was consistently and negatively correlated with vegetation cover ($r_s = -0.560$, $n = 48$, $P < 0.001$), indicating that seedlings with least cover overhead grew the most vigorously. The seedlings without vegetation cover immediately overhead (≤ 4 m) grew significantly taller than those with cover at ≤ 4 m (Mann-Whitney $U = 79.5$, $P < 0.05$).

DISCUSSION

In Voysey *et al.* (1999) we showed that during the study period gorillas were reliable and important consumers of fruits of all three species studied and presented evidence which suggests that they are crucial dispersers of *Ganophyllum* and *Cola* seeds. Their daily ranging (often of several km) affected seed deposition patterns and hence their role as dispersers. Of particular importance was the creation of nest sites, built in a new location each night and usually on the ground, frequently in areas of more open canopy. This paper has highlighted some of the effects of these deposition sites on seed germination and early seedling survival.

Seeds of all three species germinated promptly, as do the majority of tropical tree species studied (Garwood 1983, Ng 1978). Garwood (1983) found evidence that early germination in some cases enhanced survival of seedlings; we found this to be the case for *Ganophyllum*, as promptly-germinating seedlings showed higher survival than delayed ones.

Climate, mediated by other site factors, can have a substantial effect on seed germination. An atypical 6-wk dry period in 1992 affected the germination of *Ganophyllum* seeds deposited in exposed locations. Nest site G2/5 had relatively sparse vegetation, so dung deposited there dried out and much of the seed mortality was due to germination failure, probably a result of desiccation. Seeds in dung left on feeding trails suffered a similar fate. The failure of germinating *Cola* seeds at site G2/22 was also thought to be a result of desiccation. The site was at the edge of an old logging road, and thus exposed to more severe insolation. Additionally, the deposition of seeds at the edge of large nest constructions in some cases meant that germinating seedlings were unable to root adequately.

The deposition of seeds on or adjacent to well-trodden animal paths used frequently by gorillas when travelling, generally limited the success of seeds and seedlings of all three species, largely due to the effects of soil compaction preventing adequate rooting. Seedlings under *Uapaca* trees were vulnerable to trampling by animals feeding on fallen fruit. The effects of trampling and soil compaction were relatively limited at nest sites.

Seed predation, often by rodents, has been shown to be highly variable and in some cases related to deposition site (Schupp & Frost 1989, Willson & Whelan 1990). Janzen (1982) suggested that seed predation was also influenced by seed density in a dung pile. In 1992, predation of *Ganophyllum* seeds (the species most vulnerable to predation) was found to be greater in dung piles left on feeding trails than in nest sites, but in 1993, levels of seed predation were very high irrespective of either the location or size of seed aggregations. *Cola* seeds appeared to be less vulnerable to predation, and rarely were *Uapaca* seeds predated.

The vegetation conditions immediately around a clump of seeds or seedlings influenced the survival and growth of those seedlings. This is consistent with the findings from other studies of the effects of site on seedling growth and mortality (e.g. Clark 1990, Clark & Clark 1984, Denslow 1987). The importance of gap sites, providing release from suppression, is now firmly established for many species (De Steven 1994). There is consistent evidence that seedling vigour or performance is positively associated with gap sites, and the main influencing factor seems to be the change in light regime. A higher growth rate and survival of seedlings of all three species was associated with less vegetation cover, particularly at the herbaceous level (≤ 4 m). Similarly, Dirzo & Domínguez (1986) found that the height, number of leaves and leaf length of seedlings was positively associated with their location in gaps. We noted that seedlings showed different responses to site conditions: *Uapaca* seedlings in the savanna site (G2/81) tended to invest in leaf growth whereas those in the forest interior (G2/90) tended to be taller (Table 1), which corresponds to Popma & Bongers' (1988) reference to 'sun-plant' and 'shade-plant' seedling morphologies. Osunkoya *et al.* (1992, 1993) also found correlations between physiological indicators of performance and site conditions, particularly light.

We have avoided the use of the term 'gap', as the irregularity of the Lopé forest canopy compromises a meaningful attempt at a definition of the term, so we have restricted our interpretation to that of vegetation cover. Indeed, in few dispersal studies is gap ever defined, rather it is used as a relative term and compared to understorey conditions (e.g. Forget 1997, Howe 1980). Precise definitions of gap are more often found in studies relating to structure and regeneration (e.g. Brokaw 1985, Hubbell & Foster 1990). Nonetheless, gorilla nest sites are frequently in locations of more open canopy (Tutin *et al*. 1995; and B. C. Voysey, *pers. obs*.), which is likely to be beneficial for seedling survival and growth.

The three species showed a range of tolerance to shade. *Cola* seemed to be the most shade-tolerant, but even seedlings of this species performed better in more open locations. The large seeds probably provide considerable reserves in their cotyledons for the first stages of growth in shaded sites and *Cola* seedlings are able to persist in the shade of the understorey, perhaps one of the reasons for the species' success in the dense Marantaceae forest at Lopé. *Uapaca* seedlings appeared to be relatively shade-intolerant, and certain shaded nest sites (e.g. G2/83) were disastrous for seedling survival. This might partly explain the abundance of *Uapaca* along the forest margins.

As well as showing a range of responses to site conditions, the factors that influenced mortality varied among the three species. *Ganophyllum* seeds were vulnerable to seed predation in spite of some physical protection, whereas *Cola* seedlings appeared to suffer from repeated herbivory, although they displayed some resilience to browsing. *Uapaca* seemed to be most vulnerable to a lack of light. Miquel (1987) reports that seedlings vary in their responses to predation and pathogens and suggests that this can contribute to species diversity.

Ganophyllum and *Cola* seedlings growing from seeds that were scatter-dispersed away from conspecifics showed similar survival and growth to those growing from seeds dropped underneath conspecifics, implying that there were no detrimental effects from conspecifics. However, *Uapaca* seedlings growing away from conspecifics showed higher survival and growth than those underneath conspecifics, possibly due to the trampling suffered by those underneath the fruiting tree. The *Uapaca* fruit crop is of considerable importance for terrestrial feeders including elephants, most of which provide secondary dispersal of the seeds.

Seeds dispersed by gorillas are inevitably deposited in aggregations which may consist of many hundreds of seeds of one or more species, and competition will occur above and below ground (Loiselle 1990). Positive physiological effects of clumping have been reported (S. H. Bullock, cited in Jordano 1992). We found no indication of any negative effects of clumping on the growth or survival of seedlings but that growing in clumps increased the likelihood of at least one seedling surviving. Ultimately, only one adult can ever survive from a dung pile, and in nest sites some dung piles may be so close together that only one mature individual could persist. As a seedling bank, or even 'insurance', these aggregations at nest sites are likely to be important to the maintenance of the tree population by contributing to recruitment.

From an ecological point of view, the success of a location can be viewed in terms of the proportion of deposition sites that still contain at least one potential adult. The number of seedlings remaining (the contribution to the seedling bank, or the 'insurance value'), and the number of separate clumps that persist, is an important aspect of seedling survival or performance when the implications for population dynamics are considered. Fragoso (1997) attributes the patchy distribution of a palm in the Amazon forest to the influence of clump dispersal by tapirs. Howe (1989) suggests that a species which is adapted to 'clump dispersal' is likely to be resistant to competition, fungal pathogens and insect predators, which would also enable it to establish in groups under conspecifics, but we did not investigate this experimentally. The fact that gorillas construct new nest sites in a different locality each night avoids the cumulative effects of roosts used repeatedly, such as those made by howler monkeys in some areas studied (Julliot 1997), which may compromise the quality of seed dispersal the monkeys provide. Secondary dispersal by dung beetles was not investigated, although it was observed on several occasions.

There are a number of difficulties associated with studies of the fate of seeds and seedlings, not least of which are the elements of mortality and time. This is the most vulnerable stage in a plant's life-cycle, and most mortality occurs at the stage of seed and seedling (Harper 1977). The scale of mortality means that initial sample sizes have to be enormous, if significant results are to be obtained. The length of time that seedlings can be monitored determines the interpretation of the results and limits the possibilities for generalisation. The myriad factors that influence the probability of a seed germinating successfully and surviving as a seedling create considerable variation within any sample. Chance events feature to a large extent in determining the fate of a dispersed seed. In spite of our problems obtaining a large sample size, this study has provided some clues to the processes that affect the quality of seed dispersal carried out by gorillas.

Our research has shown that, for the three species studied over this period, the highest proportional survival, and the best performance of growing seedlings, was always at a gorilla nest site. The lowest survival and growth of seedlings was under conspecific tree canopies. Not every nest site was favourable for seedling establishment, for such a criterion is unlikely to be part of decision-making by gorillas when they select a site in which to nest. Some nest sites provided better conditions than others, but most appeared to be more favourable sites than under conspecifics, under intact forest canopy or on feeding trails. Some of the nest sites were in gap sites, whereas others clearly were not.

The nesting behaviour of gorillas is a unique feature that sets them apart from other apes and large-bodied seed dispersers. Chimpanzees construct nests, but always in trees so seeds scatter and fall underneath closed canopy. In this respect, gorillas may well contribute more to seed dispersal than their role as consumers might suggest. Their nest sites often were favourable sites that allowed good germination and vigorous early growth, contributing to seedling survival. High mortality of seeds and seedlings is inevitable in any system (Howe 1993b, De Steven & Putz 1984), but for the three species studied at the Lopé (and possibly for other species dispersed by gorillas), a gorilla nest site provided the best chance for the establishment of seedlings, so was the best site for a seed to be deposited.

This suggests that gorillas contribute high-quality dispersal for these species due to their contribution to the seedling bank. In addition, they consume large numbers of seeds, often a substantial proportion of a tree's crop (Voysey *et al.* 1999). They disperse seeds unpredictably over a varied and changing environment, and they create seedling repositories in sites that are often more favourable for survival and growth than the alternatives provided by other consumers, or that result from a lack of dispersal. From the plant's point of view, they are reliable consumers and disperse seeds to favourable sites, two elements of high quality dispersal (Schupp 1993). Over time, gorillas probably satisfy three hypotheses of dispersal: colonisation, escape, and directed dispersal (see Clark & Clark 1984, Howe & Smallwood 1982).

If, as our research has indicated, the improved performance of seedlings at an early stage increases the likelihood of them surviving for at least 2 y, gorillas might promote the recruitment of seeds of the species they disperse into the tree population of the Lopé Reserve. They may well have a similar key role in forest regeneration in any area where they are major consumers of fruit. The crucial role played by gorillas and other seed dispersers in maintaining forest structure (or recreating it) should be taken into account whenever the long-term management of tropical forests is under consideration.

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