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Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon

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Abstract: Effects of the elephant gut and elephant dung on seed germination and early seedling establishment/growth were investigated in Banyang-Mbo Wildlife Sanctuary using undestroyed seeds of 14 plant species sorted from fresh elephant dung between 1 June 1994 and 31 May 1995 and similar seeds extracted from fresh ripe fruits fallen on the forest floor within the same period both sown in fresh elephant dung and forest soil. Parameters measured were final germination success, germination time and seedling growth rate. Results indicated that two species, *Panda oleosa* and *Poga oleosa*, did not germinate at all after 365 d irrespective of their sources and media of planting. Germination success observed in ingested seeds was significantly different from that observed in seeds from fresh fruits. Germination success observed in elephant dung was not significantly different from that in forest soil. Mean germination time varied widely between species and treatments but was generally shorter in seeds that passed through the elephant gut than those collected from fresh ripe fruits and these differences in mean germination time were significant in 92% of the species that germinated. Growth rates of seedlings from ingested seeds were higher than those from fresh ripe fruits especially in elephant dung. Growth medium was highly significant to growth in 10 of 12 species (83%) and source was important only to two species (16%) while their combined interacting effects were significant to three of the 12 species (25%). It is concluded that ingestion of seeds by the elephant is important in the germination of some rain-forest species and the elephant dung that contains the seeds dispersed is very important in the rapid growth of the seedlings. On the basis of germination success plant species that are absolutely or exclusively dependent on elephants for dispersal/germination are absent in Banyang-Mbo Wildlife Sanctuary, while *Omphalocarpum elatum* and *Strychnos aculeata* would be on the basis of fruit morphology.

Key Words: Central Africa, dung, endozoochory, forest soil, growth, gut, tropical rain forest

INTRODUCTION

Seed germination and seedling survival have been subjects of much study in tropical rain forests (Augspurger 1984, Bazzaz 1991, Janzen & Vazquez-Yanes 1991, Vazquez-Yanes 1976, Vazquez-Yanes & Orozco-Segovia 1984). Studies of frugivory and the role of frugivores in seed dispersal in the tropical forests (Alexandre 1978, Brahmachary 1980, Feer 1995, Gautier-Hion *et al*. 1985, Howe 1977, Lieberman *et al*. 1979, Merz 1981, Short 1981, Takasaki 1983, Takasaki & Uehara 1984, Wing & Buss 1970, Yumoto *et al*. 1995) indicate that the forest elephant (*Loxodonta africana cyclotis* Matschie) is the largest agent of seed dispersal in African rain forests. It has a digestive system that allows many seeds to pass through it undestroyed. The elephant also moves long (> 100 km) distances (Powell 1998, Short 1983); and may therefore disperse huge numbers of viable seeds over large areas.

Seed germination occurs when seed dormancy has been broken and conditions favourable to germination are met (Canham & Marks 1985, Kozlowski *et al*. 1991). Forest species that are dispersed by passage through the gut of the animals, especially mammals, tend to display less dormancy than fresh seeds or those dispersed by animal regurgitation (Janzen & Vazquez-Yanes 1991). Several studies (Chapman 1989, Estrada & Coates-Estrada 1984, Garber 1986, Idani 1986, Takasaki 1983, Wrangham *et al*. 1994) have tested for differences in germination success between ingested and fresh seeds from fallen fruits. These and other studies, especially Lieberman & Lieberman (1986), focused on primates and primates/birds with few (Chapman *et al*. 1992, Lewis 1987, Lieberman *et al*. 1987) on the forest elephant. Lewis (1987) gave some consideration to the types of medium used for planting,

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while the other studies have either been carried out totally using the forest soil or absorbent paper in Petri dishes and have not investigated the effect of elephant faeces per se. Seeds dispersed by elephants are contained in large dung-piles rich in nutrients. These and the nature of the dung would possibly provide a micro-environment more suitable for seed germination and early seedling establishment.

This study examined the effects of gut-passage and dung on seeds of 14 prominent elephant-dispersed species in the Banyang-Mbo Wildlife Sanctuary (BMWS), south-western Cameroon and its implications for the conservation of elephants using the following research questions. (1) Do seeds that pass through the elephant gut show any differences in germination from seeds extracted from fresh fruits on the forest floor, when both are sown in fresh elephant dung and forest soil? (2) Do seedlings from seeds that have passed through the elephant gut show any differences in early growth rates (vigour) from those of seeds collected from fresh ripe fruits on the forest floor, when grown in either elephant dung or forest soil?

METHODS

Study area

The Banyang-Mbo Wildlife Sanctuary (BMWS) is in south-western Cameroon, Central Africa (Figure 1) and extends from 5°8′ to 5°33′N and 9°29′ to 9°47′E, covering an area of about 66 200 ha.

The climate of the region is hot and humid with distinct but unequal dry and rainy seasons. The rainy season runs from about mid-March to the end of October. However, there is hardly any month completely devoid of rainfall. Weather data collected in Nguti from 1993 to 1997 inclusive show that the heaviest rainfall occurs between May and October. October with mean annual rainfall of 612 ± 109 mm is the wettest month but the months of June to September each have more days of rainfall (almost daily) than others. Annual rainfall ranges from 3498–4739 mm with a mean of 4083 ± 487 mm. Maximum and minimum temperatures in the area do not vary widely and the annual means are 30 °C and 23 °C respectively. Relative humidity and daily temperature in the area are fairly constant throughout the year.

Topography ranges from 120 m asl in the northern part to 1756 m asl in the south-eastern part of the Sanctuary. BMWS is drained by numerous permanent and seasonal streams that rise from the highlands in the south and flow northwards to empty into the Rivers Mbie (Mbu), Mfi or Mor (Figure 1). The vegetation is generally evergreen rain forest and falls within the Guineo–Congolian forest region of White (1983). BMWS has one of the highest plant species diversities in Africa (T. Duncan, *pers. comm.*) and may be the only submontane habitat in Cameroon with a viable elephant population of 200–500 individuals.

Collection of seeds and experimental design

Between 1 June 1994 and 31 May 1995 we searched the section of the BMWS between Rivers Mor in the north-east and Mbie (Mbu) in the west, where elephants were common (Figure 1), for fresh elephant dung less than 48 h old on the forest floor during the first and third weeks of each month and sorted visible (⩾ 2 mm diameter) undamaged seeds. In total, 2387 dung piles were sampled. Seeds found were brought back to our nursery in Nguti (Figure 1) in aerated black polythene bags. The nursery was simple shading with palm fronds 2 m high and was 20 × 50 m in area. These seeds were identified to species (Appendix 1) with the aid of a reference seed collection pre-prepared during the first 3 wk from any plant species that were seen in fruit boom within or around the Sanctuary. Fourteen species were randomly selected for this study from the first 30 most frequent species found in the dung. The collection of seeds of each species was then divided into two equal parts. The number of seeds in each varied from 15 to 50 depending on the abundance of each species sorted from the dung. Seeds of one part were sown at depth varying from 2–8 cm (depending on the size) in fresh elephant dung in polythene pots of 25 × 30 cm. The rest of the seeds were sown at the same depth in pots of forest soil. The dung and soil was carefully searched to ensure that it did not already contain seeds of the study species. Equal numbers of fresh viable seeds of each species extracted from fresh ripe fruits on the forest floor were sown at the same time and depth in further pots of similar elephant dung and forest soil. The forest soil, fresh elephant dung and fresh seeds used were all collected from the same area in BMWS where ingested seeds were sorted from the dung (Figure 1). For the 14 species selected, we randomly picked 10 normal fallen fresh ripe fruits each from 30 different trees not less than 1 km apart for species with three or less seeds per fruit and five fruits each for those with four or more seeds per fruit. Extracted seeds were thoroughly mixed together before randomly selecting the appropriate number of seeds required for sowing. Sown seeds were inspected daily and moistened as often as necessary. In total, 920 ingested seeds and 921 fresh seeds were used as follows; 460 each of ingested and fresh seeds were sown in elephant dung while another 460 ingested seeds and 461 fresh seeds were sown in forest soil.

Measurements and records

A record was made of the date the seeds of each species were sown (DS) and the following records and measurements were made during observations: (1) Date of seed-

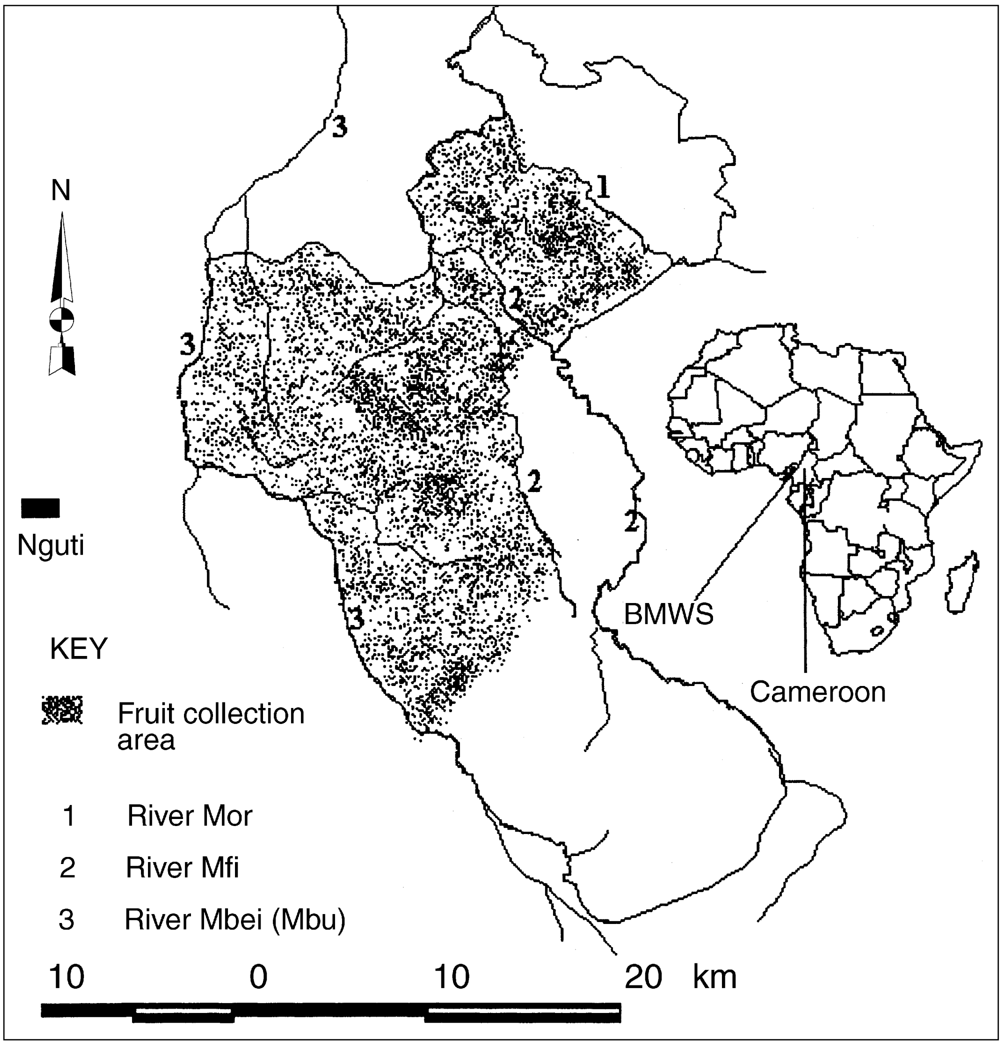

Figure 1. Location of Banyang-Mbo Wildlife Sanctuary in relation to Africa and Cameroon showing fruits collection area and nursery town.

ling emergence (DE) – indicated usually by multiple cracks on surface of the medium. The best measure of seed germination is the emergence of the radicle (Fenner 1985). Under the conditions of this experiment, it was impossible to observe the radicle without destroying or disturbing the seed/seedling. We chose to record seedling emergence rather than germination. (2) Date when first leaves appeared (DFL). (3) Seedling height (mm) when first leaves appeared (HFL). (4) Date when second leaves appeared (DSL). (5) Seedling height (mm) when second leaves appeared (HSL). Once the first leaves appeared, it was assumed that the seedling had attained full germination, established roots, greatly reduced its dependence on parental reserves and started nutrient uptake from the medium and photosynthesizing its own food to continue growth. At the appearance of second leaves, the seedling was considered fully established and observations were stopped.

Effects of elephant gut and dung

The effect of gut-passage and medium on each species was evaluated by comparing germination/growth of ingested vs. fresh seeds; germination/growth in dung vs. soil for both ingested and fresh seeds. Germination performance was measured as final percentage of seeds germinated and germination rapidity – estimate of mean time in days for seeds to germinate (i.e. duration between sowing and seedling emergence, DE – DS). Growth performance was measured as the rate of change in seedling height (growth rate) between first and second leaves [i.e. (HSL – HFL)/(DSL – DFL)]. Germination failure was assumed after 365 d of observation before the seeds were dug up and re-examined for viability. This length of time was considered sufficient for most normal seeds to germinate. No seeds were discovered viable during this examination. Seeds were either already decayed or were in the process of decaying.

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Data analysis

All calculations and statistical analyses were performed in SPSS 9.0 (Norušis 1999). Mean germination time of a species was considered only for all seeds that germinated of the species. Mean growth rates were calculated only for seedlings that successfully grew without any external injury (e.g. stems cut off or wounded by insects such as crickets (6%) or rodents (2%, n = 1335)) until second leaves were produced.

Chi-squared tests using 2 × 2 contingency tables (fresh vs. ingested × germination vs. no germination and elephant dung vs. forest soil × germination vs. no germination) with Yate's continuity correction (Little & Hills 1978) were used to compare final numbers of germination in each treatment. The chi-squared goodness-of-fit test (Ludwig & Reynolds 1988) performed on seed germination times showed that these data were not normally distributed. Therefore, the data were log [ln(x)] transformed, and t-tests assuming unequal variance between groups were applied to identify any significant statistical differences in mean germination time of seeds for each species between treatments (ingested seeds vs. fresh seeds and elephant dung vs. forest soil) while the GLM was applied on the log[ln(x)]-transformed data of growth rate to find out the effects and interaction effects of source and medium on seedling growth rates.

RESULTS

Germination of the seed species

Except for two species, *Panda oleosa* and *Poga oleosa*, that did not germinate at all irrespective of source (whether ingested by the elephant or from fallen fresh ripe fruits) and medium of propagation (elephant dung or forest soil) at least some germination occurred in the other 12 species in one treatment or the other (Table 1). Seeds of four species all germinated irrespective of the source and medium of propagation. Germination success of ingested *Anonidium mannii* and *Mammea africana* was similar to that of their respective fresh seeds while that of ingested *Antrocaryon micraster*, *Detarium macrocarpum*, *Duboscia viridiflora*, *Irvingia grandifolia*, *Klainedoxa gabonensis* and *Strychnos aculeata* were each significantly higher than the germination success of the corresponding fresh seeds (Table 2). Germination success of most species in elephant dung and forest soil was similar for both ingested and fresh seeds (Table 2). However, successful germination of fresh *D. viridiflora* and *I. grandifolia* seeds in dung was significantly higher than that in forest soil while germination success of fresh *S. aculeata* seeds in dung was about 24% lower than that in forest soil. Fresh seeds of *D. macrocarpum* in forest soil did not germinate at all compared with 12% successful germination in elephant dung.

Germination time – ingested vs. fresh seeds and dung vs. soil

Mean germination time (Table 3) varied widely between species and treatments. It ranged from 15 d in *Omphalocarpum elatum* to 112 d in *I. grandifolia* for ingested seeds and between 16 d in *Myrianthus arboreus* and 217 d in *I. grandifolia* for fresh seeds. Generally, mean germination time for ingested seeds was less than that for fresh seeds by 13–61% for all species. Student's t-tests (Table 4) indicated that the differences in mean germination times of ingested seeds were reduced significantly compared with seeds collected from fresh fruits for 11 of the 12 species that germinated. Elephant dung significantly hastened germination in 8 and 4 species respectively of ingested seeds and fresh seeds of the 12 species that germinated.

Table 1. Final per cent germination success of elephant-dispersed seed species in Banyang-Mbo Wildlife Sanctuary. Values in parentheses are number of seeds sown in each treatment.

	Ingested seeds		Fresh seeds	
Species	Elephant dung	Forest soil	Elephant dung	Forest soil
Anonidium mannii	100 (15)	100 (15)	100 (15)	80 (15)
Antrocaryon micraster	100 (35)	97 (35)	45 (35)	31 (35)
Detarium macrocarpa	96 (50)	74 (50)	12 (50)	0 (50)
Dovyalis zenkeri	100 (15)	100 (15)	100 (15)	100 (15)
Duboscia viridiflora	100 (50)	100 (50)	38 (50)	4 (50)
Irvingia gabonensis	100 (40)	100 (40)	100 (40)	100 (40)
Irvingia grandifolia	100 (50)	100 (50)	56 (50)	12 (50)
Klainedoxa gabonensis	96 (50)	70 (50)	12 (50)	10 (50)
Mammea africana	72 (25)	100 (25)	100 (25)	92 (30)
Myrianthus arboreus	100 (30)	100 (30)	100 (30)	100 (30)
Omphalocarpum elatum	100 (50)	100 (50)	100 (50)	100 (50)
Strychnos aculeata	100 (50)	100 (50)	44 (50)	60 (50)
Panda oleosa	0 (50)	0 (50)	0 (50)	0 (50)
Poga oleosa	0 (50)	0 (50)	0 (50)	0 (50)

Table 2. χ^2 comparison for germination success of elephant-dispersed species in various treatments.

Species	Ingested vs. fresh seeds		Ingested seeds in dung vs. in soil		Fresh seeds in dung vs. in soil	
	χ^2	P	χ^2	P	χ^2	P
Anonidium mannii	1.40	0.05	–		0.371	< 0.05
Antrocaryon micraster	55.7*	< 0.001	0.00	< 0.05	0.965	< 0.05
Detarium macrocarpa	123*	< 0.001	7.84*	< 0.01	4.43*	< 0.05
Dovyalis zenkeri	–		–		–	
Duboscia viridiflora	127*	< 0.001	–		15.4*	< 0.001
Irvingia gabonensis	–		–		–	
Irvingia grandifolia	139*	< 0.001	–		7.09*	< 0.001
Klainedoxa gabonensis	101*	< 0.001	10.21	< 0.01	0.00	< 0.05
Mammea africana	1.95	< 0.001	5.98*	< 0.02	0.521	< 0.05
Myrianthus arboreus	–		–		–	
Omphalocarpum elatum	–		–		–	
Strychnos aculeata	107*	< 0.001	–		2.43	< 0.05

* Significant differences occur in germinations between treatments; –, comparison unnecessary.

Table 3. Mean time (in days) for seeds to germinate.

Species	Ingested seeds		Fresh seeds*		
	Elephant dung	Forest soil	Elephant dung	Forest soil	Gabon†
Anonidium mannii	20	20	51	47	30
Antrocaryon micraster	56	52	102	96	10–200
Detarium macrocarpa	101	123	206	–	65
Dovyalis zenkeri	18	25	25	23	–
Duboscia viridiflora	18	15	41	41	25
Irvingia gabonensis	40	46	60	67	15
Irvingia grandifolia	67	137	213	238	45
Klainedoxa gabonensis	78	56	193	135	180
Mammea africana	48	69	144	117	90–189
Myrianthus arboreus	16	15	15	17	15
Omphalocarpum elatum	13	17	28	49	37
Strychnos aculeata	55	22	38	48	–
Panda oleosa	–	–	–	–	300

*, –, Not available or germination failure; † Germination data from Miquel (1987) in Makokou–Gabon probably from fresh seeds in forest soil

Table 4. Student's t-test* (P = 0.05) for germination time between treatments for some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary.

Species	Ingested vs. fresh seeds		Ingested seeds in dung vs. in soil		Fresh seeds in dung vs. in soil	
	t	df	t	df	t	df
Anonidium mannii	2.821	55	1.959*	27	2.094	25
Antrocaryon micraster	3.009	97	2.867	66	2.646	25
Detarium macrocarpa	2.389	89	2.937	35	–	–
Dovyalis zenkeri	2.546	58	2.067*	28	2.217	28
Duboscia viridiflora	2.693	119	3.296	98	2.896	18
Irvingia gabonensis	3.902	156	2.774	74	2.867	78
Irvingia grandifolia	3.562	115	2.472	98	2.180*	15
Klainedoxa gabonensis	4.425	92	2.093	81	4.671	9
Mammea africana	2.337	89	3.413	41	2.657	46
Myrianthus arboreus	1.704*	118	1.234*	58	1.845*	58
Omphalocarpum elatum	2.180	199	2.014	98	2.064	99
Strychnos aculata	3.599	134	3.420	98	2.096	34

* Not significantly different; –, comparison not applicable.

Effects of ingestion and growth medium on seedling growth

Seedlings of all species grew more rapidly in elephant dung than in forest soil (Table 5). Additionally, more than 60% of the seedlings originating from ingested seeds showed more rapid growth than those from fresh seeds in the same medium.

The general linear model indicated that the interaction between source and medium was significant in the growth of *M. africana* (F = 14.4, df = 72, P < 0.05), *K. gabonensis* (F = 4.3, df = 130, P < 0.05) and *O. elatum* (F = 66, df = 190, P < 0.05). That of growth medium alone was significant for all species except *D. macrocarpum* (F = 0.4, df = 89, P = 0.05) and *D. viridiflora* (F = 1.6, df = 115, P = 0.5), and that of source was only significant for *A. mannii*

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Table 5. Mean growth rate (mm d^{-1}) of seedlings of species dispersed by elephants in Banyang-Mbo Wildlife Sanctuary. Values in parentheses are number of seedlings that survived from germination to production of second leaves.

	Seedlings from ingested seeds		Seedlings from fresh seeds	
Species	Elephant dung	Forest soil	Elephant dung	Forest soil
Anonidium mannii	2.8 (12)	0.5 (14)	1.5 (15)	0.3 (12)
Antrocaryon micraster	1.7 (35)	0.5 (34)	1.3 (16)	0.1 (10)
Detarium macrocarpa	0.6 (49)	0.3 (37)	0.1 (6)	–
Dovyalis zenkeri	1.4 (15)	0.4 (15)	0.9 (15)	0.3 (13)
Duboscia viridiflora	0.1 (50)	0.6 (49)	0.1 (18)	0.1 (2)
Irvingia gabonensis	1.7 (37)	0.3 (40)	1.7 (40)	0.1 (3)
Irvingia grandifolia	0.8 (50)	0.4 (50)	0.2 (14)	12 (50)
Klainedoxa gabonensis	0.5 (45)	0.4 (34)	1.3 (50)	0.1 (5)
Mammea africana	2.2 (18)	0.6 (14)	1 (25)	0.6 (19)
Myrianthus arboreus	0.9 (30)	0.3 (30)	1 (30)	0.2 (30)
Omphalocarpum elatum	0.7 (50)	0.1 (50)	0.9 (44)	0.1 (50)
Strychnos aculeata	0.1 (50)	0.1 (45)	0.1 (11)	0.1 (17)

–, germination failure.

(F = 13.2, df = 49, P < 0.001) and *I. grandifolia* (F = 13.4, df = 160, P < 0.001).

DISCUSSION

Based on germination success, Chapman *et al.* (1992), Lieberman *et al.* (1987), Martin (1989) and Voorhoeve (1965) have pinpointed plant species that are absolutely or almost exclusively elephant-dependent for dispersal/germination. This study has been unable to identify with certainty any such plant species in BMWS. However, the dispersal/germination of *O. elatum* and *S. aculeata* based on fruit morphology appears to be elephant-dependent. *Strychnos aculeata* has a large woody berry of about 15–19 cm diameter with seeds buried in a soft pulp enclosed within a hard shell. *Omphalocarpum elatum* on the other hand has a large hard drupe of about 12–22 cm diameter with seeds buried in a hard woody pulp. We found no seedlings or saplings under parent plants of 56 *S. aculeata* and 27 *O. elatum* inspected opportunistically between January 1994 and December 1995. Rather, intact fruits of various age classes ranging from fresh falls to about 2–3 y old of both species were found, some with borer holes and enclosed seeds all destroyed. In this experiment, we manually extracted the seeds from ripe fallen fruits for germination trials of both species and recorded germination success of 100% both in ingested and fresh seeds of *O. elatum* and some *S. aculeata*. Though frugivory in mammals (small and large) is yet to be studied in the BMWS, neither species seems to have dispersers other than elephants. An elephant can use its trunk to hit these fruits against other hard objects to break them open before grinding the hard shell or pulp with its massive teeth. Though it could be inferred from Emmons (1980) that rodents and large arboreal squirrels may be playing a role in their dispersal.

Variation in germination time between species observed here is normal, arising from innate variation of dormancy in the species while within-species variations observed are due to factors considered in the experiment. However, irrespective of the treatments, among the 14 species studied here, there are similarities (Table 3) in germination time with an earlier study from Gabon (Miquel 1987), except for two species, *I. grandifolia* and *D. macrocarpum*, with respectively only 45 and 65 d in the previous report instead of the 217 and 206 d (mean time) in the present study.

Panda oleosa and *Poga oleosa* failed to germinate under all conditions in this study after 365 d. This is similar to the report of Lieberman *et al.* (1987) who observed germination failure after 196 d for both *Panda oleosa* seeds that were ingested by elephants and those collected from fresh fruits. However, Alexandre (1978) reported that *Panda oleosa* germinates slowly without specifying how long it took to germinate, while Miquel (1987) in Gabon reported that it took 300 d to germinate and de la Mensbruge (1966) in Côte d'Ivoire reported that it took *Panda oleosa* 1095–1460 d (3–4 y) to germinate. Though no study has been reported previously for germination of *Poga oleosa*, it has characteristics similar to *Panda oleosa* and has exhibited similar germination failure in this study. It is therefore difficult to conclude from this study whether ingestion by elephants enhances or influences the germination of either species since our observations lasted more than the mean germination time reported from Gabon though less than the time reported from Côte d'Ivoire. If it took these species 3–4 y to germinate but they were observed to be inviable after 1 y in our study, then some other factor(s) that we are unable to account for might have interfered with the seeds during our study. However, considering the wide difference in the two previously reported germination times for *P. oleosa*, it may be worth investigating further the germination time for these species.

In other instances, both seeds that passed through the elephant gut and those collected from ripe fallen fresh fruits germinated but there were greater and faster germination successes in the former. Alexandre (1978), Chapman *et al*. (1992) and Dinerstein & Wemmer (1988) obtained similar results in germination between seeds ingested by large mammals and seeds collected from ripe fallen fresh fruits. Lieberman & Lieberman (1986) also reported differences in germination between seeds ingested by other animals (including birds) and fresh seeds from fruits though did not report whether ingestion hastened or retarded germination of forest seeds. Delayed germination in most mature viable tropical seeds is usually due to impermeable seed coats that prevent imbibition of water, permeability of gases and the hard seed coats that provide mechanical resistance to growth of the embryo (Kozlowski *et al.* 1991). Mechanical abrasion from the massive teeth during chewing and partial digestion of the impermeable testa layers by various enzymes and stomach acids, coupled with the heat action during the stay of seeds (3–5 d, Powell 1998) in the elephant gut, would probably have removed the impermeability of the seed coats to water and gases as well as soften the hard seed coats, thus alleviating mechanical resistance to the growth of the embryo. The net effect is the rapid imbibition of water and exchange of gases that activate the various enzymes to hydrolyse the food reserves of the cotyledons, mobilize and transfer growth hormones to the radicle for growth resumption leading to the rapid germination and germination success observed in ingested seeds compared with the fresh seeds. It could be concluded that passage through the elephant gut is not absolutely essential for germination but increases the germination potentials of the seeds through the physical and chemical treatment received during their passage and stay in the gut of the elephant and enclosure in the elephant dung.

More germination occurred in elephant dung than in soil for both ingested and fresh seeds. This suggests that dung imparts some chemical treatment and other requirements on seeds, assuring germination success even if it is not rapid.

Growth rates of seedlings from ingested seeds were higher than those from fresh seeds. Additionally, growth was more vigorous in elephant dung than in forest soil. This would have been enhanced by the vigour that seeds acquired during the physical and chemical treatment received in the elephant's gut during the passage period. The elephant dung may also have provided a medium richer in nutrients than ordinary forest soil.

We conclude that ingestion is important for rapid and successful germination while dung is important for growth. Therefore elephants eating fruits give a double enhancement to seed and seedling success in addition to dispersal. The conservation of elephant to ensure the success and perpetuation of species they disperse is crucial especially in the BMWS area where law enforcement is very weak and elephants are frequently poached.

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Appendix 1. Plant species with seeds ≥ 2 mm found in elephant dung in BMWS.

Species	Family	Form	Number of dung piles containing species	Fruiting period
Duboscia macrocarpa	Tiliaceae	Tree	819	May–September
Strychnos aculeata	Loganiaceae	Vine	719	Year round
Omphalocarpum elatum	Sapotaceae	Tree	713	July–December†
Klainedoxa gabonensis	Irvingiaceae	Tree	638	May–August*
Panda oleosa	Pandaceae	Tree	631	March–December†
Detarium macrocarpum	Caesalpinioideae	Tree	541	November–March
Picralima nitida	Apocynaceae	Tree	507	Year round
Irvingia gabonensis	Irvingiaceae	Tree	463	May–August
Uapaca guineensis	Eurphorbiaceae	Tree	437	November–April
Irvingia grandifolia	Irvingiaceae	Tree	397	June–August
Anonidium mannii	Annonaceae	Tree	321	April–July
Treculia africana	Moraceae	Tree	308	February–September
Dovyalis zenkeri	Flacourtiaceae	Tree	289	November–March
Mammea africana	Guttiferae	Tree	282	January–March
Massularia acuminata	Rubiaceae	Shrub	254	Year round
Myrianthus arboreus	Moraceae	Tree	208	June–August
Angylocalyx zenkeri	Papilionoideae	Shrub	193	April–August
Antrocaryon micraster	Anacardiaceae	Tree	154	September–October
Desplatsia dewevrei	Tiliaceae	Tree	137	Year round
Tetrapleura tetraptera	Mimosoideae	Tree	136	December–April
Poga oleosa	Rhizophoraceae	Tree	107	June–August
Pycnanthus angolensis	Myristicaceae	Tree	96	February–July
Theobroma cacao‡	Sterculiaceae	Shrub	76	August–December
Gambeya africana	Sapotaceae	Tree	59	December–March
Ricinodendron heudelotii	Euphorbiaceae	Tree	56	May–August
Xylopia aethiopica	Annonaceae	Tree	49	Year round
Trichoscypha accuminata	Anacardiaceae	Tree	47	March–June
Pachypodanthium staudtii	Annonaceae	Tree	44	January–April
Diospyros mannii	Ebenaceae	Tree	41	July–August
Megaphrynium spp.	Marantaceae	Herbs	38	November–February
Rattans	Arecaceae	Vines	37	July–September
Canarium schweinfurthii	Burseraceae	Tree	35	May–September
Trichoscypha arborea	Anacardiaceae	Tree	28	March–April
Telfairia occidentalis	Cucurbitaceae	Vine	27	February–April
Landolphia mannii	Apocynaceae	Vine	24	Year round
Cogniauxia podolaena	Cucurbitaceae	Vine	21	November–March
Staudtia kamerunensis	Myristicaceae	Tree	19	June–January
Artocarpus communis	Moraceae	Tree	17	October–December
Tetracarpidium sp.	Euphorbiaceae	Vine	16	July–September
Mangifera indica‡	Anacardiaceae	Tree	14	March–July
Citrus spp. (oranges)‡	Rutaceae	Tree	13	September–November
Coffea spp.‡	Rubiaceae	Shrub	13	November–January
Celtis tessmannii	Ulmaceae	Tree	11	July–August
Aframomum spp.	Zingiberaceae	Herbs	10	December–April
Psidium guajava‡	Annonaceae	Shrub	9	Year round
Vitex doniana	Verbenaceae	Tree	9	June
Baillonella toxisperma	Sapotaceae	Tree	8	June–August
Citrus paradisi‡	Rutaceae	Shrub	7	December–March
Vitex ciliata	Verbenaceae	Tree	5	September
Dacryodes edulis	Burseraceae	Tree	4	July–August

* Fruit available at least for 9 mo of the year on forest floor; † fruits available year round in the forest floor; ‡ cultivated exotic species.

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