SEED DISPERSAL BY GORILLAS IN THE LOPÉ RESERVE, GABON

BEN VOYSEY

Thesis submitted for the degree of Ph.D
The University of Edinburgh
1995

I declare that this thesis was composed by my own hand, and that the work presented in the thesis is my own, except where otherwise acknowledged. The data were collected by myself and Karen McDonald, although Caroline Tutin, Richard Parnell and Rebecca Ham found some of the nest sites, seived many of the dung samples, and undertook the phenology circuits with us.

Ben Voysey

...the sower went forth to sow; and as he sowed, some seeds fell by the wayside, and the birds came and devoured them; and others fell upon the rocky places, where they had not much earth; and straight-way they sprang up, because they had no deepness of earth; and when the sun was risen, they were scorched; and because they had no root, they withered away. And others fell upon the thorns and the thorns grew up and choked them; and yet some seeds were swallowed by a passing group of gorillas...

(with apologies to the sower)

ABSTRACT

The dispersal of seeds of four rain forest tree species by western lowland gorillas (*Gorilla g. gorilla* Savage & Wyman) and the subsequent survival of seedlings was investigated in the Lopé Wildlife Reserve in central Gabon. The species studied were *Ganophyllum giganteum* (Chev.) Haum. (Sapindaceae), *Cola lizae* Hallé (Sterculiaceae), *Dialium lopense* Breteler (Caesalpinioideae) and *Uapaca guineensis* Müll. Arg. (Euphorbiaceae). They are all important fruit foods for gorillas, in that they dominate the diet whenever available, and influence their ranging patterns.

Two elements of seed dispersal were studied: the removal of seeds from fruiting trees, and the survival and growth of seeds and seedlings. The removal of seeds was monitored for a number of focal trees of each species by counting fruit remains under the tree crowns, assigning them to particular classes of treatment by various consumers. The consumption of fruit by gorillas was also studied by means of opportunistic observation and faecal analysis.

The fate of seeds dispersed by gorillas, and the survival and growth of seedlings, was recorded by counting seeds in marked piles of gorilla dung, and monitoring survival and growth for up to two years after deposition. Of particular interest were the seed and seedling "repositories" that are created by the nesting behaviour of gorillas, so most seedlings were monitored in nest sites. The fate of seeds deposited in gorilla dung was compared with that of seeds dropped under the parent tree or scatter-dispersed by the feeding activity of monkeys.

The four tree species showed a range of dispersal strategies. In most cases, gorillas removed a large proportion of the fruit crop of the trees they visited, and sometimes this accounted for the bulk of the seeds produced by the trees that were monitored. Both the survival and performance of seedlings was always highest in a gorilla nest site. The growth of seedlings was negatively correlated with the amount of vegetation cover above them. It would appear that gorillas are important for the effective seed dispersal of these tree species, although they are not the only consumers to disperse seeds. The implications for conservation and management of forests, with respect to the dependence of many plant species on animals for dispersal, is discussed.

ACKNOWLEDGEMENTS

This work was supported financially by a studentship from the Science and Engineering Research Council of Great Britain, to whom I am very grateful. The National Geographic Society of the USA kindly provided an equipment grant.

Liz Rogers was the first to encourage me to get involved in Lopé's ecology, and her support and enthusiasm have been unflagging since those early years. She organised the pilot study from which followed this work, and helped with the initial fieldwork. I particularly appreciated her guidance, encouragement and support as supervisor through times of strife and during the last year writing up.

I am indebted to the Direction de la Faune of the Ministère des Eaux et Forêts in Gabon for permission to carry out research in the Lopé Reserve, and in particular to Alphonse Mackanga-Missandzou, the Commandant of the Brigade at Lopé. The Centre International des Recherches Médicales de Franceville provided financial and logistical support.

Enormous thanks go to Caroline Tutin and Michel Fernandez, who were prepared to share their SEGC home with me. Caroline, my field supervisor, helped me learn many aspects of the forest ecology at Lopé and provided support during the fieldwork and writing stages. To her I say: 'thanks for showing me your Swiss army knife'.

Rich and Reb helped no end during our field days. Rich Pradrell, Ngoya man *sans pareil*, was absolutely smashing, both as helper and friend in and out of the field. His work on the pilot study set this research up. I'm just sorry we didn't get the band off the ground. Brigitte Botaka provided brilliant support and assistance in camp.

Other field workers to whom I extend my warmest thanks include Gilbert, Daniel Mala, André Sinibouré, Jean Toussin, and Lee White.

Many heartfelt thanks go to all family and friends who wrote frequently or otherwise whilst I was in the field; letters are true sustenance. As Tony Collins said, thesis writing is a selfish occupation, so I thank all those that have tolerated my preoccupied state over many months.

My deepest debt, and thus my greatest thanks, go to my 'acclompice' Karen McDonald. She left her job to take on arduous and sometimes tedious field work, and without her help I would still be out there counting seeds in dung. I am grateful too for her fine photography and artwork, some of which is found in this thesis. She has been both breadwinner and sanity retainer in the past year. I cannot thank her enough for her help, support, tolerance, encouragement and love.

This thesis has benefitted from the constructive attention of Alan Longman, Liz Rogers and Caroline Tutin, to whom I am very grateful.

CONTENTS

LIST OF PLATES

LIST OF TABLES

LIST OF FIGURES

Ganophyllum

Cola

Dialium

Uapaca

Chapter 1

INTRODUCTION

1.1 SEED DISPERSAL IN CONTEXT

Seed dispersal is a subject that is now well established within the field of tropical ecology (e.g. Estrada and Fleming 1986, Bawa & Hadley 1990, Wheelwright 1991, Fenner 1992, Fleming and Estrada 1993). The majority of tropical trees rely on animals for the dispersal of their seeds (Jordano 1992) and most research on seed dispersal stems from studies of fruit-eating by animals (frugivory). As a result it is seed removal by animals (zoochory) that has received most attention. Frugivory has been studied for some time (e.g. Snow 1971, McKey 1975), but the emphasis of the research was often on fruit removal and processing by frugivores. Natural regeneration of tropical forests first received anecdotal and practical attention (Aubreville, cited in Brokaw 1985, Richards 1952) and latterly intense study, particularly involving gap-phase regeneration, but the growth of established seedlings and saplings has been the focus for such investigations (e.g. Hartshorn 1980, Brokaw 1985, Hubbell & Foster 1986, Lieberman *et al* 1990). Forging a link between these two aspects of forest ecology is a task that has only more recently been undertaken. Despite the increased momentum of research on seed dispersal, studies of plant-animal interactions that concentrate on the fate of seeds are rare.

Inevitably one is faced with an inherently complex set of interactions to unravel. Studies of the ecological consequences of seed dispersal can provide hypotheses relating to the effects of dispersal on plant populations in time and space. The complexity of the subject poses considerable research problems which, coupled with the obstacles of mortality and time, demand large samples and many years' effort (De Steven 1994). Consequently, information on seed dispersal is sparse, both regarding the particular processes involved and in terms of geographical coverage (Willson 1992). Judging from the published literature, the Neotropics and birds have been more intensively studied than the Old World tropics and large mammals (witness studies from Barro Colorado Island in Panama, Los Tuxtlas in Mexico and Cocha Cashu in Peru). These sites have seen the longest accumulation of consistent research effort regarding frugivory and forest dynamics (Gentry 1990). There has been some work in Kalimantan, Indonesia (Leighton 1990) and on the Indian sub-continent (Dinerstein & Wemmer 1988). As the latter authors point out, large mammals as seed dispersers in African forests have received scant attention (see Alexandre 1978, Chapman *et al* 1993), and the activity of the African great apes as seed dispersers has certainly been little studied (Idani 1986, Tutin *et al* 1991a, Wrangham *et al* 1994).

The ecology of seed dispersal and associated forest dynamics has a direct relevance to our management of forest resources. At its most basic level, there is a requirement to know how tree populations maintain themselves and what degree of interdependence occurs between animals and plants. Given the present degree of physical and biological disturbance of tropical forests caused by humans, the implications for their continued usefulness are clearly sobering. Currently most forests are commercially exploited for exportable timber, with local use often not regarded as part of their economic value (see Peters *et al* 1989), even though most tropical wood use is for local purposes, much of it as firewood or charcoal. If intense harvesting of a certain plant resource depletes animal foods, this may directly reduce the number of seed dispersers, particularly if a 'keystone' (*sensu* Terborgh 1986, and see Howe 1977, Gilbert 1980) food species is affected. The commercial selective extraction of timber not only removes food trees, disturbs soils and disrupts fauna, but is often accompanied by increased hunting of animals for food. Local hunting of animals for immediate consumption, or more seriously for the bushmeat trade, is prevalent in most tropical forests, and can severely reduce the densities of seed dispersers in the area, either temporarily or permanently (Pannell 1989, White 1992). The capacity of a forest to regrow following disturbance will therefore be further diminished, changing its future structure and composition. Even if the target timber species are wind-dispersed, there may be interactions with other fauna and flora that provide links between tree species such that hunting will indirectly affect the timber species.

Most timber extraction has concentrated on very few species. As it proceeds, loggers and local people tend to use more and more species, reducing the species diversity of the forest, which makes conditions for the larger vertebrate seed dispersers more difficult and less stable. Disorganised, careless logging damages juvenile trees of the very species that are being cut, thereby reducing the chance of them being reharvested. Clearly, for the continued use of the forest for local and less local multiple benefits, its broad biological integrity should be retained as far as possible. This includes a maintenance of the diversity of plant species and the presence of seed dispersers. Research on seed dispersal and regeneration can provide clues to the ability of forests to recover from various levels of disruption.

1.2 THE 'NEED' FOR SEED DISPERSAL

Seed-bearing structures that improve the chances of seed removal evolve as a result of the selective advantage to those plants that are able to disperse their seeds: dispersal is seen as benefiting plants (Dirzo & Domínguez 1986). It is the one mobile stage in an otherwise rooted existence. As an alternative strategy to wind, water and external animal dispersal, many tropical trees produce fruits of a shape, flavour and texture that can be consumed as food by animals but which are effectively attractants that maximise the chances for seed transport away from the female parent tree. On a community-wide basis, about 70-90% of tropical forest woody plants rely on animals for dispersal, and this appears to be consistent across different tropical areas, with perhaps the one exception of Dipterocarp forests of south east Asia where most trees are wind dispersed (see Ng 1981, Jordano 1992 and references therein, Mabberley 1992, White 1994b).

Why should seed dispersal be so fundamentally 'necessary'? An individual tree needs to maximise the number of its offspring that may contribute to the next generation. It is not the case that a tree has merely to replace itself with one of its progeny, a concept of group selection (Crawley 1992). At an ecological level, however, on average each tree is replaced by one other as it dies. Elements of an individual's fitness, carried in its seeds, will be favoured or otherwise depending on the fate of flower buds, flowers, developing fruit, seeds and seedlings. If maximising the recruitment of offspring is crucial for the evolutionary gain of an individual and the persistence of a species, there are certain drawbacks to dropping seeds under the parent crown. One is that this seldom allows any colonisation of disturbed ground, or changes in distribution, by a species. Thus dispersal is advantageous as a colonisation mechanism. Seeds and seedlings under the parent may also suffer density- or distance-dependant mortality of one cause or another, so dispersal acts as an escape from these mortality factors. This 'escape hypothesis' was formalised by Janzen (1970) and Connell (1971), and has received support from various field studies (see review by Clark & Clark 1984, Augspurger 1984, De Steven & Putz 1984, Howe *et al* 1985). A third component of dispersal is that it may increase the possibility that some seeds land in a site that is (or will be) favourable for the growth of the young tree: this is the 'directed dispersal' hypothesis (Howe & Smallwood 1982). Over time, a legitimate disperser may satisfy all three hypotheses, in that it behaves randomly (from the plants' perspective) in a patchy and unpredictable environment (Estrada and Coates-Estrada 1986). Tropical forests are very dynamic places, so 'safe sites' as they have been called are unpredictable in space and time. It may not in fact be very far from the parent to a current or future favourable site.

Conditions influencing growth and survival (the suitability of a habitat) will change as the tree grows to maturity, as might the juvenile tree's own requirements or response to local conditions (Augspurger 1983b). Despite the fact that some species' seeds can establish under the parent and one might ultimately replace it, selection forces have shaped (and continue to shape) strategies that: a) aim to transport seeds away from the parent; b) enhance the chances of deposition in a favourable site; c) often exert some control over the time of potential germination by more or less specific fruit ripening times and seed dormancy mechanisms, and d) maintain the viability of offspring. This is a process that operates at both ecological and evolutionary time scales (Howe 1993a), but which is inevitably investigated at an ecological level, usually on a time scale which is a tiny fraction of the fruiting tree's lifespan.

1.3 PLANT OR ANIMAL PERSPECTIVE

The benefits of dispersal to the plant have been outlined above. It is worth stressing that the plant has little control over the actual dispersal event once the ripe fruit or seed is ready for removal. Different adaptations determining fruit structures have evolved among plants to increase the chances of beneficial dispersal and to a large extent they determine "animal acquisition by plants" (Stiles 1992). These fruit 'designs' have developed through interaction with animal morphology and behaviour, and are regarded as dispersal 'syndromes'. They are as much 'choice' over what removes seeds as the plant's evolutionary constraints allow (see below).

As with regeneration strategies or guilds, dispersal syndromes are not distinct classifications but groups within a range of fruiting structures. Broadly speaking, dehiscent fruit with brightly-coloured, lipid-rich arils, and small multi-seeded fruit or berries are thought to attract birds, with monkeys being seed predators or dispersers. Larger fruit with large seeds embedded in a fleshy mesocarp, generally indehiscent and rich in sugars relative to lipids and with varying degrees of protection are fed on essentially by various mammals (e.g. Gautier-Hion *et al* 1985, Janson 1983). These differences in morphology and chemistry can occur within genera (e.g. *Aglaia* Meliaceae, Pannell & Koziol 1987). Big, dull-coloured, often smelly fruits with a fibrous mesocarp and protection against predispersal predation fit the 'ruminant-rodent syndrome'. Theoretically, as suggested by McKey (1975), 'expensive' fruits should attract legitimate dispersers (a kind of specialisation), whereas 'cheap', plentiful fruits can be taken by a range of frugivores with varying degrees of legitimacy as dispersers, which is a more generalist strategy.

Much attention has focussed in the past on the possible coevolutionary links that were thought to exist between plant species and a particular seed disperser or small group of dispersers (see e.g. Gilbert and Raven 1975). However, as Ellen Gryj put it, "La coevolución ha muerto - ¡viva la coevolución!" (Wheelwright 1991). It is generally accepted now that at most there has been a 'diffuse coadaptation' between plants (which cannot depend on the unpredictable behaviour of potential dispersers) and animals (which exert a relatively imprecise selection pressure on plants). Earlier considerations had centered on fruit removal, but the selective pressures on plants will also result from influences that occur before and after removal.

Plants are probably subject to a range of evolutionary constraints that limit the degree or variety of morphological adaptations possible (Herrera 1985). He and other authors have put forward a number of hypothetical constraints that would explain a lack of tight coevolution (Wheelwright & Orians 1982, Howe & Smallwood 1982, Janzen 1983, Schemske 1983, Howe 1984, Herrera 1985 & 1986, Fischer & Chapman 1993). They include: the large differences in generation times, evolutionary and speciation rates between woody plants and their dispersers; the unpredictability of favourable germination sites; the relative strength of selection pressures from non-dispersers such as pollinators and predators or pathogens; the generalist needs of frugivores; the inability of a plant to restrict the number of consumers beyond an assemblage, and the high rates of gene flow among plant populations. The argument is essentially that dispersers exert a relatively weak selection pressure on plants, and the response of the plant will be to the collective pressures from the assemblage of consumers. The observed adaptations may have "been selected for by the dominant coincident pressures persisting through past interactions" (Herrera 1985).

Fruits of any one tree are fed on by a range of animals which vary in their quality as dispersers, including those that are fruit thieves (frugivores that do not remove seeds) and pre-dispersal seed predators, invertebrate as well as vertebrate. Considerable pre-dispersal selection pressures on fruit design may come from the attentions of non-dispersers, particularly pre-dispersal predators. Interactions between large groups of taxa are likely to have existed during evolutionary time (Howe & Smallwood 1982). Plants and invertebrates have existed for longer than vertebrates, and the different groups are thought to have evolved at different rates.

Plant-frugivore relationships are essentially loose (Terborgh 1990), with generalisation the most common strategy that governs the types of fruit structures and seed removal by animals (Herrera 1985). Gautier-Hion and colleagues (1985) were able to recognise two broad guilds in a loose association of fruits and frugivores in northeast Gabon, where there was a large dietry overlap between frugivores (e.g. 22 species feeding on *Trichilia gilgiana* Meliaceae fruit). However, fruit quality and availability may be more important than design for the removal of some fruits by certain species (Estrada & Coates-Estrada 1986).

Specialisation does occur in some interactions, and this seems to be associated with larger fruit and seeds. A close association exists between *Rhinoceros unicornis* and *Trewia nudiflora* (Euphorbiaceae) in Indian floodplain forest (Dinerstein & Wemmer 1988). Elephants (*Loxodonta africana*) are the only legitimate dispersers of a range of fruit in African forests (Alexandre 1978, Chapman *et al* 1993, White 1993), and large-seeded Burseraceae and Meliaceae fruits are closely linked with a small coterie of large hornbills (Bucerotideae) in west Kalimantan, Indonesia (Leighton 1990). The cassowary (*Casuariius casuarius*) is the last remaining disperser of many seeds of Queensland rain forest plants, such as the large-seeded *Beilschmiedia* species (Lauraceae) (Stocker & Irvine 1983). A species of tree may have a different kind of disperser in a different locality. For example, *Virola nobilis* (Myristicaceae) (previously *V. surinamensis*) is dispersed principally by toucans in Panama, and by monkeys in Peru (Howe 1990). Some of the 'ruminant-rodent' fruits in the Mpassa study in Gabon (Gautier-Hion 1990) are likely to be dispersed by gorillas (*Gorilla g. gorilla*), chimpanzees (*Pan t. troglodytes*) and elephants in other areas of the country. A plant that produces fruit risks the attentions of predispersal seed predators and fruit thieves. There has probably been extensive interaction between predispersal predators, especially insects, and plants that has shaped the types of protection found in seeds and fruit (Herrera 1986).

For animals, fruits are food. Frugivory is only ever a partial lifestyle, possibly due to the nutritional imbalance of fruits. Fruit may vary in their importance in any one species' diet, but usually are a source of soluble carbohydrates and/or lipids. Fruit may also be used as a protein source by those frugivores that eat seeds. Fruit is often seasonally available and variable as a food source in terms of reliability and abundance, so its importance in the animals' diets also varies seasonally and annually (Terborgh 1986). Seeds are a digestive obstacle, taking up space in the gut (Milton 1984, Leighton 1990). If the seeds are not eaten (chewed) for their protein and lipid content, they are either dropped, or swallowed and passed out in dung or regurgitated (Corlett & Lucas 1990).

The line between seed disperser and predator is sometimes a tenuous one. In times of ripe fruit scarcity, immature seeds may be eaten by normally legitimate dispersers (Peres 1991, Tutin *et al* 1991b). Some species may even act as both seed predators and dispersers during the same feeding bout (*e.g.* gorillas, pers. obs.). Differences in the treatment of seeds and dispersal legitimacy between equivalent Old World and New World primates have been reported by Rowell and Mitchell (1991). Guenons (*Cercopithecus* spp) were reported to be seed predators or scatter-dispersers by cheek-pouching, whereas capuchins (*Cebus* spp) clump-dispersed seeds by swallowing them and voiding them in dung. The drawbacks of seed swallowing may place certain constraints on smaller mammals and birds in the neotropics (Howe 1993a), but large mammals such as gorillas introduce a slightly different set of parameters in the dispersal equation. Seed mass may be "critical" with regard to the fruit selection or percentage of a crop removed by birds in the neotropics (Howe and Vande Kerckhove 1981), but the mass of most seeds gorillas encounter is unlikely to bother them. Nonetheless, seed size and body size operate as a factor at larger scales in the African context, if we consider chimpanzees, gorillas and elephants and their respective "gape widths" (Tutin & Fernandez 1994, White 1993).

1.4 ELEMENTS OF SEED DISPERSAL

The transition from ripe seed to established seedling is possibly one of the most vulnerable parts of a plant's life cycle, and is thus a narrow mortality "window". As such, research on seed dispersal concentrates on what may essentially be a rare event: the survival of a seed to the stage of established seedling. Inherited characteristics of the species may influence the seed and seedling's ability to survive and grow in a particular environment. These characteristics may be physical (size, mechanical protection) or physiological (chemical defences and germination strategies). However, the largely unpredictable behaviour of the consumer (and possibly the features of its gut) will determine where a seed lands.

The ultimate result of animal-mediated seed dispersal involves several underlying processes. It is a combination of fruit production, seed removal and treatment, seed deposition and mortality, and seedling survival and growth. Chance events feature to a large extent in most of these processes.

1.4.1 Flower and fruit production

Fruit production can only occur as a result of flowering. The flowering event depends on the allocation of resources (Bazzaz & Ackerly 1992), and the phenological rhythms of the species. It comprises flower bud initiation, opening (what is generally thought of as 'flowering') and pollination. Initiation may take place 2 weeks to 9 months before the buds are clearly visible on the tree, and the cues for a switch to reproductive activity are largely unknown (Longman 1985). Flowering patterns in most tropical forests are thought to be linked generally to abiotic factors, principally climate (van Schaik *et al* 1993), although plants may have inherent patterns as well, a result of selective adaptation. These authors suggest that community peaks in new leaf and flower production coincide with the movements of the sun within the Inter-Tropical Convergence Zone, indicating that irradiance has an important influence on plant phenology. The effect of proximate environmental conditions, including possible cues of rainfall or low temperatures that may occur at times unseasonally (e.g. Tutin & Fernandez 1993), may influence the timing of flowering. Habitat conditions can also influence flowering and fruit production, overriding seasonal factors. For example*Miconia centrodesma* (Melastomataceae) trees in treefall gaps in Panama flowered more frequently and produced more fruit than individuals under intact canopy (Levey 1990).

Pollination success is usually a prerequisite for fruit production, and is affected indirectly or directly by factors such as local climate and pollen vector numbers and behaviour (Wheelwright & Orians 1982, Janzen 1983, Appanah 1990). The degree of influence is likely to depend on the type of breeding system of the species. About 30-40% of tropical trees bear separate female and male flowers, and many of these are dioecious (Longman 1985). The pollination success of outcrossing species (particularly those that are pollinated by insects) may be more sensitive to variations in local conditions. There is frequently a loss of a large proportion of the flowers produced on a tree, either by abscission at the bud stage, or after pollination. Water stress and insect attack might be reasons for flower loss, and those flowers fertilised first may prevent fruit set in flowers that were pollinated later (Longman 1985).

Fruit production, as an outcome of the pollination event, often shadows the success of that event, mediated by fruit set, development and ripening. These events can be influenced by: a) maternal effects (Gutterman 1992); b) inherent fecundity of both parents, and c) active abscission or predation of young fruits. Crawley (1992) and Tutin *et al* (1991a) suggest that, in spite of year to year variation, some trees are consistently more fecund than others. De Steven (1994) pointed out that certain individual trees of three species she studied produced more seedlings than others, but this varied annually. Variation in flowering (and subsequently fruit production) between individuals of the same species can be considerable, and it has been reported between clones (Longman, 1985).

Fruit set is likely to be influenced by various little-studied aspects of climate, and fruit development by the activity of fungal or invertebrate pathogens. Fruit availability in most areas is seasonal, sometimes highly so (Leighton & Leighton 1983, Terborgh 1986, White 1994b). According to Terborgh (1990), there seems little evidence that fruiting patterns derive from competition avoidance, although there is some evidence from certain sites (Wheelwright 1985a). As a generality, fruit production in tropical forests varies widely, is generally non-uniform and driven by climate.

1.4.2 Seed removal

Fruiting patterns in tropical forest vary from the long, drawn-out fruiting of some species, sometimes bearing for much of the year, to short, sharply-peaked fruiting periods. Howe (1993a), describing two ends to a continuum, suggested that generalist trees tend to be fed upon by many frugivores, showing a peaked fruiting season whereas specialist species, reliant on a few species for seed removal, may have a long fruiting season. It should be borne in mind that many of these hypotheses and 'paradigms' have been developed from studies on birds and small animals, rather than much larger-bodied animals. Nonetheless it is in the plant's interest to ensure reliable visitation from legitimate, high quality dispersers.

The 'fruiting environment' (*sensu* Herrera 1986) of a tree affects fruit removal. The spatial distribution of fruiting conspecifics and non-conspecifics (and the importance of the latter in the consumers' diets) influences foraging patterns and subsequent visitation to any particular tree (Manasse & Howe 1983, Loiselle & Blake 1993). These authors found that fruit crop size and nutrient content did not account for much of the variation in removal of *Virola nobilis* but the fruiting of conspecific neighbours did. Murray (1987) however, showed that crop size and fruit removal was positively correlated. Competition among animals for the food resource might increase removal rates of fruit from trees. Frugivores can display an intimate knowledge of the location and fruiting schedule of relevant trees (Garber 1987, pers. obs.). Crop sizes vary enormously from tree to tree and from year to year. Some studies have shown that this can influence visitation as a result of foraging decisions (Estrada & Coates-Estrada 1986, Leighton 1990).

Predispersal predation by insects can destroy seeds and make the fruit unpalatable to legitimate dispersers, although some primates may select infested fruit for the additional protein within (Redford 1984, Ham 1994). Removal or destruction of immature seeds as a result of feeding on unripe fruit is effectively waste, as the animal is behaving as a pulp predator or fruit thief.

Predispersal predation can have a considerable effect on a plant's seed crop. Invertebrates in particular may cause severe damage (Crawley 1992), although in tropical forests there are also many seed predators in the form of squirrels, birds and primates. Peres (1991) found that brown capuchin monkeys destroyed almost the entire crop of seeds produced by a sample of 10 trees of the wind-dispersed *Cariniara micrantha* (Lecythidaceae), eating nearly 70% of the seeds and wasting a further 30% by dropping them with the opercula intact, which rendered them inviable. The behaviour of an animal species as predator or disperser is not always predictable, as mentioned above. Gautier-Hion & Maisels (1993) (and see Maisels and Gautier-Hion, 1994) proposed that forest composition, in terms of the degree of fleshy fruit availability, may determine whether animals benefit plants or not. *Cercopithecus wolfi* monkeys in Salonga, Zaire, were predominantly seed predators whereas an equivalent species (*C. pogonias*) in Makokou, Gabon, was largely a disperser of the fleshy fruits that were more abundant in the Gabonese forest. The frugivore community may also determine if animals act as predators or dispersers. Ham (1994) suggests that grey-cheeked mangabeys at a site in Gabon act predominantly as seed predators on those fruits that are favoured by gorillas and chimpanzees in order to avoid competition.

The dispersal quality provided by a particular animal might then be largely determined by its behaviour. Dispersal quality has been described by Reid (1989) as having two components, effectiveness and efficiency. From only a slightly different angle, Schupp (1993) considered the effectiveness of dispersal as a combination of quality and quantity. The elements that make up the overall contribution of a particular frugivore to seed dispersal include visitation reliability, treatment of seeds, quantity removed, ranging and deposition patterns. An uncommon visitor can be an effective disperser but not an important one if it doesn't remove many seeds (Howe 1990). It would be important, however, if the seeds it disperses are the only ones that survive to adulthood, or those most likely to do so. Conversely, should an animal remove a large proportion of the tree's crop then it is only an effective disperser if those seeds are deposited in favourable sites. For example, in a study by Horvitz & Schemske (1986), ants that rarely removed seeds of a Marantaceae species carried them 12 times the distance away from the plant than ants that were common visitors.

Willson (1992) argued that insufficient attention is given to the fate of these seeds that are at the periphery of the 'seed shadow' (see below). It may be that the bulk of a crop is removed by an ineffective disperser (in terms of deposition), and those seedlings that ultimately survive to adulthood arise from the few seeds that are dispersed by an animal that happens to deposit them more reliably in favourable sites. However, this ecological scenario would possibly be evolutionarily unstable, as there might be selective pressures to reduce the high wastage of parental investment in seed production. An animal that does not always remove seeds of a species when they are presented (i.e. is unreliable) is deficient as a disperser from the plant's point of view. If the feeding methods result in damage to seeds or the dropping of many under the parent, this is effectively waste, and again limits the quality of the dispersal provided. Howe (1980) reported high waste through the dropping of seeds by major consumers and apparently legitimate dispersers of *Tetragastris panamensis* (Burseraceae) in Barro Colorado Island.

The degree to which an animal is beneficial in terms of its treatment of seeds is affected by the size of the animal relative to the seeds, as well as its behaviour (Corlett & Lucas 1990). Threshold fruit or seed sizes have been reported for birds (e.g. Stocker and Irvine 1983, Wheelwright 1985b, Levey 1987), monkeys (Corlett & Lucas 1990, Gautier-Hion *et al* 1985) and African great apes (Tutin *et al* 1994). Garber (1986) reports that south American tamarins (*Saguinus* spp) are important dispersers of relatively large seeds, although the seeds are long rather than wide. Cercopithecine monkeys often fill cheekpouches with seeds and process them later, thus carrying out scatter-dispersal (pers. obs.). Monkeys are more likely to cheekpouch seeds of high-value foods, when competition exists, when there is a risk of predation or when the food requires long processing times (Ham 1994).

Pre- and post-ingestion processing is a balance of costs and benefits for the individual, influenced by body size, metabolic needs, digestive physiology and social factors, as well as the type of food and the energy and risk required to harvest it (Tutin & Fernandez 1994). The separation of indigestible skin and seeds from fruit pulp reduces the quantity of matter in the gut which is nutritionally of poor value, but takes time. Of the two large African apes, gorillas and chimpanzees, it is chimpanzees that carry out pre-ingestion processing more frequently, often by wadging fruit in the lower lip. This in part is due to a social structure which minimises competition, as well as their smaller size (Tutin & Fernandez 1994).

If the animal is not pressured by predation risks or competition to spend as little time in the fruiting tree as possible, then it is more likely to remain in the fruiting canopy and hence void seeds underneath. Frugivorous birds that 'outstay' their useful time in a fruiting canopy become wasteful if it means they regurgitate or defaecate under the crown (Pratt & Stiles 1985). It might be better for some tree species if the animal removes seeds over a series of visits, rather than all at once, as it would reduce the degree of aggregation of seeds in dung. Most frugivores are deficient in one aspect of dispersal or another. The variation from species to species (of animal) and from year to year in terms of favourable dispersal is a factor that probably contributes to the maintenance of diversity in the forest.

For some tree species, not all fruit that falls or is dropped to the ground is wasted in terms of dispersal, for ground-feeding frugivores disperse seeds from under the tree. In fact quite a number of species display fruit syndromes that suggest that they have evolved to be dispersed by large non-climbing, nonvolant frugivores such as elephants (Alexandre 1978, Chapman *et al* 1993, White *et al* 1993) or rhinos (Dinerstein & Wemmer 1988). The species that have evolved large fruits that absciss on ripening and are dispersed primarily by large-bodied frugivores do not necessarily have particularly large seeds, examples being *Nauclea vanderguchtii* (Rubiaceae) and *Omphalocarpum procerum* (Sapotaceae). The large non-volant animals, and ruminants such as duikers, will also 'hoover up' under fruiting trees of other species, providing dispersal from primate or bird waste (Dubost 1984, Bodmer 1991, pers. obs.).

Some seeds taken from under the parent by scatter-hoarding granivores may ultimately escape predation, and in some cases the granivore provides the best dispersal for the species (e.g. Forget 1990). Whelan and Willson (1990), commenting on the often high and very variable levels of seed predation, suggest that it too may be a constraint on coevolved systems, in that a frugivore is unable to deposit seeds in a predictable, reliably safe site given the risks of seed predation.

1.4.3 Deposition and seed shadows

The dispersion pattern of seed fall from a tree has been referred to as the "seed shadow" (Janzen 1971). Although theoretically a valuable concept, the practical difficulties associated with determining precise seed shadows are considerable (Willson 1993). A range of hypothetical types of seed shadow exist. Particular shapes will result from dispersion patterns associated with different dispersers, from manakin to elephant. They are perhaps best described in general terms, with vertebrate dispersal patterns increasing in irregularity with increasing disperser body size as a result of the treatment of seeds, range size and clumped dispersal. The seed shadow may be influenced by the time spent feeding, travel speed, distance moved and retention time (Fleming and Heithaus 1981). These authors had evidence for some colonising species that linked deposition probabilities with seedling distributions. Birds and bats have been described in similar terms as frugivores, but the seed shadows they create may be very different (Fleming & Heithaus 1981, Thomas *et al* 1988).

What happens to a ripe seed when it is removed from the parent tree is largely a matter of chance, although the nature of the fruit influences what treatment it receives. If it is not dropped in intact fruit or spat singly under the parent, then a seed is probably dispersed in one of two ways, called scatter and clump-dispersal by Howe (1989). Larger-seeded species are either spat out singly by birds or mammals under or away from parent or conspecific crowns (the latter being regarded as scatter dispersal), or may be regurgitated or defaecated in aggregations of varying size (Chapman 1989). Repeated use of night roosts can lead to dense aggregations of seeds deposited over time, as demonstrated by Julliot (1992) in the case of howler monkeys. If foraging monkeys deposit seeds in dung away from parents but under fruiting crowns of other species or conspecifics, as reported by Estrada and Coates-Estrada (1986), they are vulnerable to seed or seedling predation by generalists active around those fruiting trees, so the dispersal is perhaps not as effective as removal might imply. Larger mammals may deposit many hundreds of seeds of one or more species in one clump. Howe (1990), familiar with the small aggregations of seeds found in dung of Neotropical dispersers, would be impressed by the "megaclump syndrome" found in African forests populated by elephants, gorillas and chimpanzees.

Seeds deposited in a dung pile have the benefit of manure which may enhance seedling vigour (Dinerstein & Wemmer 1988) and a moist microenvironment to protect seeds from desiccation, but only one can ultimately survive to adulthood at that location. Both inter- and intra-specific competition will occur above and below ground (Loiselle 1990) and in the end most of the seedlings are doomed. Not that they are all strictly wasted, if by aggregation they reduce the vulnerability of an individual. A seed or seedling in a group is less apparent than if it is alone, so in spite of a potential high percentage mortality, the chances of some or one escaping predation (non-zero survival) may be greater than for an equivalent starting number of scatter-dispersed seeds. Clumps of seedlings are something of a bonanza for a foraging herbivore however, although several studies have pointed to similar levels of herbivory on established seedlings under and away from parents (Howe 1993b, Terborgh *et al* 1993, Osunkoya *et al* 1993), suggesting that it is not distance- or density-dependent. On the other hand, single, scattered seeds and seedlings might be missed by predators, particularly invertebrates.

Some benefits to seedling growth resulting from seed aggregation in a clump have been demonstrated (Bullock, cited in Jordano 1992). In that study, biomass and survival were greater for seedlings growing in clumps, and grafting between roots within the clump was evident. Seeds deposited in dung may also undergo secondary dispersal by dung beetles (Estrada & Coates-Estrada 1991, Julliot 1992, Estrada *et al* 1993). The accidental relocation or burying of seeds may afford them some protection from vertebrate predators and desiccation. Dung beetles at Los Tuxtlas are either ball rollers (8 species, 57% of indivduals) or buryers (13 species, 43% of individuals) (Estrada *et al* 1993). Handling seeds from 1.5 to 17.5mm in size, they bury a considerable proportion (41%) of dispersed seeds. Larger seeds are less likely to be handled by beetles. Most (83%) of those buried were at depths of over 2.5cm, which was the limit to which rodents could relocate them in experimental trials (Estrada & Coates-Estrada 1991). Burial may not always be a good thing, as some seeds may be unable to germinate successfully from such depths. Howe (1989) suggested that a species that is adapted to clump dispersal is likely to be resistant to competition, fungal pathogens and insect predators, enabling it also to establish in groups under the parent, and had some evidence to support his hypothesis.

1.4.4 Germination

Tree species exhibit a range of germination strategies, linked to seed morphology and physiology (Osunkoya *et al* 1993, Vásquez-Yanes & Orozco-Segovia 1993). Maturation conditions have an effect on seed characters and germination. 'Maternal effects', related to position and microclimate during fruit development, create variation in germination status within a crop of seeds (Gutterman 1992). Seed size has been shown to be linked to germination pattern and subsequent seedling size (Howe & Richter 1982). Essentially, the main possibilities are that seeds: a) start growing into seedling prior to being shed; b) germinate reasonably promptly after they are shed; c) are prevented from germinating for external reasons (quiescence); d) die without germinating or e) were inviable anyway (A. Longman, pers. comm.). Germination may not greatly limit seedling establishment, except for some large-seeded species in dry conditions (Sork 1985).

Prompt germination is the most common trait among tropical seeds: 65% of Malaysian forest species studied by Ng (1978) germinated within 12 weeks, and 82% of the 185 species in Garwood's (1983) study germinated within 16 weeks. There may be an extended germination period within a cohort, as a result of the differences in seed responses to environmental effects and intraspecific variation in seed morphology and physiology (Vásquez-Yanes & Orozco-Segovia 1993). The term dormancy applies when few or no live seeds germinate within a reasonable time when placed in favourable germinating conditions. A seed may display an innate dormancy, whereby germination does not occur in spite of the appropriate environmental conditions, or be quiescent, in which case a seed does not germinate if a particular environmental condition is missing, such as moisture for hard-coated seeds that dry out on ripening (Murdoch & Ellis 1992).

Dormancy is not a common feature among tropical trees, but 'pioneer' species (i.e. ones that colonise large gaps and severely disturbed ground from seed) more often have dormant seeds. The hard-coated, impermeable seeds among the Caesalpiniaceae are frequently dormant. A cohort of such seeds can display a staggered germination, because different seeds will be in different microsites, particularly important being their contact with moist soil. Other species that fruit just before a season of low rainfall may also display dormancy. It is interesting to consider that a number of Caesalpiniaceae have dry dehiscent pods which ripen and split in the dry season, and accomplish dispersal by ballistic means. As such, it would benefit seeds falling in the dry season to await the rains before germinating.

Staggered germination might be advantageous in an unpredictable environment, in that not all the 'eggs are in one basket'. A delay in germination, or dormancy, spreads the risks of germination over a long time period. Although 'delayed' seeds might lose a possible initial growth advantage, they may avoid density-dependant mortality as seedlings as well as unfavourable climatic conditions. Early germination has been shown in some cases to enhance survival (Garwood 1983, Estrada & Fleming 1986), although Garwood found no peak in germination of understorey and shade-tolerant species. Germination may be sensitive to dehydration, except in seeds with hard coats and a low moisture content. The timing of seed germination coincides with the onset of the rains in some localities (Garwood 1983). The optimal time of germination may be influenced by the timing of flowering, of seed dispersal, or by dormancy mechanisms.

It has been suggested that most tropical forest seed banks are relatively small and their importance has been over-emphasised (Thompson 1992). The role of seed banks in regeneration is likely to depend on the disturbance regime (Martinéz-Ramos & Soto-Castro 1993). Small natural gaps will fill in mostly by seedling and juvenile growth, but large-scale disturbance creates conditions whereby regeneration is from the seed bank, which is largely made up of pioneer species (Thompson 1992, and references therein). Alvarez-Buylla and Martinéz-Ramos (1990) found that for the pioneer species *Cecropia obtusifolia* (Moraceae), seeds less than one year old contributed to recruitment. Seeds of shade-intolerant species are reported to germinate in profusion in dense shade but suffer large mortality, although some seeds may persist in the soil seed bank (Lieberman *et al* 1990).

Vásquez-Yanes *et al* (1990) suggest that the majority of seeds over 1mg in weight have no light requirement for germination. Nonetheless work has shown that the shade light in tropical forests is of a particular quality, rich in the Far Red part of the spectrum, which influences the light response and germination of certain species (e.g. Kwesiga & Grace 1985, Vásquez-Yanes & Orozco-Segovia 1990). The accumulation of leaf litter over seeds that do not germinate immediately further influences light and moisture environments (Vásquez-Yanes *et al* 1990, Molofsky & Augspurger 1992). The physiology of shade tolerance is important in studies of the relative performance of tree seedlings of different species in different sites (e.g. Primack 1990, Raich & Gong 1990, Turner 1990, Osunkoya *et al* 1992), and is discussed further in section 1.4.5.

Gut passage

The effect of gut passage on seed germination has often been investigated (e.g. Estrada & Coates-Estrada 1984, Lieberman & Lieberman 1986, Julliot 1992, Wrangham *et al* 1994). Overall there seems to be no consistent effect of gut passage across plant species under the given experimental conditions. Using a range of 16 plant and 6 animal species, the Liebermans (1986) found that 73% of the 52 plant-animal trials showed no effect of gut passage on time to germination (latency). It was shorter in 12% and longer in 8% of trials. For all trials, there was no significant difference in germination percent (rate) between ingested and fresh seeds. Of 17 species dispersed by howler monkeys (*Alouatta seniculus*) in Guyana studied by Julliot (1992), 7 species showed a lower germination percent and 3 species a higher percent after gut passage.

However, Wrangham *et al* (1994) found that passage through chimpanzee guts increased germination percent and reduced latency in all 10 species examined. In fact for 8 of the ten species, seeds from under the parent did not germinate at all within the time of the trial, which suggests that passage through the chimp gut breaks an innate dormancy. Estrada and Coates-Estrada (1984) discovered that seed passage through howler monkeys (*Alouatta palliata*) in Costa Rica improved overall germination percent of the species studied (9 species representing 95% of seeds), with 5 species showing a significant change. Again, latency studies were less clear: in one species the latency period was shorter and in 2 species it was longer.

Other studies confirm the variability in the effect of gut passage. The transit of most seeds through a cassowary gut did not affect their germination rates (Stocker & Irvine 1983). A 3-7 day ride inside a rhino did not affect the germination of *Trewia* seeds, a species that relies on rhinos for its dispersal (Dinerstein & Wemmer 1988). Janzen (1982, 1983) discovered that horses and cows altered the germination pattern of *Enterolobium cyclocarpum* (Leguminoseae) seeds. Their guts destroyed some of the seeds, this figure being higher for horses than for cows. A seed-eating parakeet (*Brotogeris jugularis*) has been documented as a legitimate disperser of *Muntingia calabura* (Eleocarpaceae), along with Phyllostomid bats, with no discernable negative effects on germination from treatment by either gut (Fleming *et al* 1986). *Balanites wilsoniana* (Balanitaceae) in Kibale forest, Uganda, is apparently only dispersed by elephants, and its seeds germinate much more readily after passage through the elephant gut (Chapman *et al* 1993).

These studies indicate the differing responses of seeds to gut passage in a range of consumers, which mirrors the variation in germination strategies among tropical trees. They also highlight the potential limitations of germination trials of relatively short duration, as some seeds may exhibit a delay in germination beyond the duration of the trial. Certain guts may give seeds a more harsh treatment than others, depending on the relative sizes of gape or teeth, gizzard or gut and the seeds concerned. Physical or chemical degradation of the seed coat in the gut is likely to change the response of seeds to light, temperature or moisture (Vásquez-Yanes & Orozco-Segovia 1986, Jordano 1992). This is not necessarily a good thing if survival or growth are compromised as a result of a seed germinating in adverse conditions. Gut passage may limit the degree of variation in latency among a seed cohort, reducing the advantages of staggered germination. Nonetheless the evolution of animal-dispersed seeds would suggest that gut passage is the 'normal' scenario, and a lack of gut passage (the 'control' in many experimental trials) is the unusual condition, resulting sometimes in retarded germination.

1.4.5 Survival and growth: mortality factors and favourable sites

Seed and seedling predation

Every seed faces a range of hazards once it arrives on the forest floor, hazards whose nature and severity change as the seed germinates. The enormous seed production of most tropical forest trees and the relatively miniscule size of the seedling population of any one species is evidence of major seed and early seedling mortality. Consequently a small percentage change in seed predation can have a large effect on the seedling population (Crawley 1992). Ungerminated and germinating seeds provide food for both rodents and invertebrates and development sites for the latter. Some studies have shown that predation of seeds underneath fruiting canopies is more severe than at distances away from the parent tree.

This seems to be the case particularly for species that suffer invertebrate seed predation. Howe *et al* (1985) found that insects accounted for the huge (>95%) mortality of *Virola nobilis* seeds under parent crowns, which had crops that numbered from 430-31000 seeds. In the first year, mammals accounted for 60% of seed-seedling mortality, and for 90% of the mortality of seedlings growing from the few (<2%) seeds that survived (Howe 1993b). This degree of seed loss under parent crowns has been reported for *Dipteryx panamensis* (Leguminoseae) (De Steven & Putz 1984), with less than 0.5% of its almond-like seeds surviving to seedling stage as a consequence of seed predation. They found that rodents also ate the cotyledons of emerging seedlings. Larger-seeded species are more likely to be able to withstand some predation if only part of the cotyledons is removed (Dirzo & Domínguez 1986, pers. obs.). Insect predation in Howe's study was related to distance from the parent (and density) but this was not so for mammalian predation.

The observation that invertebrate predation is sometimes density- or distance-dependent but vertebrate predation is not has been reported by other workers. Five tree species investigated by Terborgh *et al* (1993) showed a range of susceptibilities to predation. None suffered density-dependent predation by mammals, but one species did show density-dependent insect predation. Three of the 5 species suffered small mammal predation, one was predated by large mammals, one by insects and one species showed no predation losses at all. The losses were not related to the abundance of the different species. Post-dispersal predation was found to drastically reduce seedling numbers of *Gustavia superba* (Lecythidaceae) on Barro Colorado Island, much more so than on mainland areas subject to defaunation through hunting (Sork 1987). When considering the effects of density on predation, the level of scale is important. For *Faramea occidentalis* (Rubiaceae), Schupp (1992) reported that although at the scale of the individual tree seed predation may be density-dependant, when the density of adults is considered, then it was clear that a high density of patches resulted in better survival due to reduced predation.

If rodents locate food by smell (Price & Jenkins 1986), then it is possible that they can find an aggregation of food deposited in odorous dung more easily than scattered individual seeds, although dried elephant dung can in fact protect seeds from predation due to its hard texture (S. Kuroda pers. comm.). Stocker and Irvine (1983) report that seeds in cassowary dung were protected from predation by rodents. In the Los Tuxtlas study by Estrada and Coates-Estrada (1991), rodents rapidly located seeds in dung, even those buried up to 2.5cm, and accounted for the loss of more than 90% of dispersed seeds. Unburied seeds are likely to be more vulnerable to predation than buried ones, and dormant or delayed seeds spend a longer time at risk of seed predation than prompt-germinating seeds. Initial seed density in a clump has not been consistently shown to affect predation rates, survivorship or growth (Willson & Whelan 1990, Whelan *et al* 1991). Janzen (1982b) suggested that seed density in a pile would influence survival due to the effect on rodent searching and predation. Webb and Willson (1985) found no evidence for this in the species they studied in Australia, although they did not use a large range of seed densities. They suggested that large clumps of seeds may face a greater chance of discovery, but survival is greater too, relative to small clumps.

The intensity of seed predation is likely to vary seasonally and annually according to fluctuations in fruit production and (perhaps not unrelated) invertebrate and rodent populations. Schupp (1990) suggested that the community-wide seed production will influence levels of predation, rather than production of one particular species. Webb and Willson (1985) reported that seed predation was less severe in open sites, possibly due to predation risks for the rodents. Schupp and Frost (1989) however, suggested that the dense tangle often found in forest gaps might provide favourable habitats for rodents (including protection), which would explain the greater seed losses in gaps suffered by a palm species (*Welfia georgii*) they studied. It was not clear whether this one palm has a specialist predator (that might prefer gap habitats), or if seeds were taken by a range of generalists.

The predation rate of single seeds reported by Willson and Whelan (1990) varied according to habitat (at micro and macro scales), species, year and season. Overall mortality depended on macrohabitat, species and year. They suggested that seed predation can be high and is certainly very variable, either counteracting or exacerbating habitat-related mortality. The effect of seed predation in the long term on a population is not clear, but if recruitment is not seed-limited then seed loss by predation might not be important (Anderson 1989). The latter author found losses of 95% among four species in southeast Australian woodland, but establishment was site-limited anyway. Even if this is the case, seedling demography is likely to affect overall population demography, because seeds may arrive at a site before it becomes favourable, so predation is another factor contributing to variation and diversity (Dirzo & Domínguez 1986). Seed predation may also contribute to species richness if some species produce more seeds but suffer more intense predation than others (Crawley 1992).

Seedlings suffer predation by invertebrate and vertebrate herbivores. As mentioned above, vertebrate herbivory has largely been found not to be distance or density related, but may be site-related. Vertebrate browsing on seedlings of a large-seeded Bombacaceae studied by Denslow (1980) was not found to be significantly correlated with distance or density, whereas meristem damage by aphids was. Seedlings of a range of species protected from herbivores in an Australian rain forest showed better survivorship (>75%) than unprotected ones (<45%) (Osunkoya *et al* 1992), with survival also related to site factors. Protection did not affect the biomass of seedlings, but did affect the height of some species due to browsing on unprotected seedlings (Osunkoya *et al* 1993).

The loss of seedlings in a growing clump may be more strongly associated with herbivory than with self-thinning (Howe 1990). Suppressed seedlings in the forest understorey are vulnerable to repeated herbivory. Feeding on the leaves or stem of a young plant does not always directly kill it, as it may be able to resprout. Nonetheless it can precipitate mortality if the seedling is growing at light levels close to its compensation point, or if it is rendered more susceptible to fungal pathogens. Established, older seedlings are generally not as affected by vertebrate predation as seeds and early seedlings (Howe 1993b, Osunkoya *et al* 1993, De Steven 1994), possibly due to increased resilience through physical or chemical means (Folgarait & Davidson 1994).

Relatively large changes in vertebrate herbivore densities that persist through time can alter the regeneration pattern of forests (Wright *et al* 1994). Work in Mexico comparing two sites, one with natural densities of herbivores and the other with an impoverished herbivore fauna showed considerable differences in the seedling communities: seedling density was 2.3 times greater in the site with few herbivores, but the site with natural densities of herbivores had a diversity of seedlings 2.9 times greater than the other site (Dirzo & Miranda 1991).

Pathogens, particularly fungi, are causes of mortality for seeds and seedlings. Research at Barro Colorado Island, Panama demonstrated that dispersal away from the parent and more specifically to a gap site reduced the levels of mortality from fungal infections for a range of seedlings, on account of the hotter, drier conditions in gaps used in the study (Augspurger 1982, 1983a,b). Vulnerability to predation and pathogens is likely to vary with site characteristics, and species are likely to display differing resilience to these hazards. Seedling types described by Miquel (1987) and Hladik and Miquel (1990) probably vary in their resistance to predation and pathogens, which may contribute to the maintenence of species diversity.

Overall, the risks facing a seed and seedling are considerable. The chances of discovery, the influence of distance, site and resilience on survival imply a range of interactions between seeds, seedlings and their predators at different stages. Harper (1977) stated that most plant mortality occurs at the seedling stage. There is certainly a population bottleneck at the seed and seedling stage, although the importance at each stage may vary among species. In addition to differences in germination status, species-specific responses to site conditions and hazards may well contribute to the maintenance of diversity in the forest (Miquel 1987, Osunkoya *et al* 1993).

Favourable sites

Although where a seed lands on the forest floor may be a chance event, it nevertheless is critical to survival and growth. A favourable site means different things to different species, depending on their regeneration strategies, or seedling 'syndrome' as Hladik and Miquel (1990) put it. Seedling syndromes are a result of a species' dispersal and germination strategies and size, and are important for success in terms of their ability to cope with adverse conditions and stress. A favourable site can also mean different things to the same species at different stages of growth (Garwood 1986).

Treefall gaps of one description or another are now accepted as important sites for the regeneration of many tropical trees, either providing the right triggers for the germination of seeds, or 'releasing' seedlings that have remained suppressed under an intact forest canopy (Garwood 1986). The importance of the regeneration niche for the maintenance of species diversity (Grubb 1977) is a concept that underlies much of this discussion, and the role of disturbances of this kind in forest dynamics is the focus for much research (see reviews by Clark 1990, Hartshorn 1990).

The main component that is considered to affect survival and more specifically seedling performance in gaps is the change in light regime (Denslow 1987), particularly the amount of light and its quality. Light is the main limiting resource for plants establishing in the forest. In the understorey, typical levels of Photosynthetically Active Radiation (PAR) are 0.5-2%, in small gaps 2-6%, and in large gaps 10-54% of unimpeded sunlight (Chazdon & Fetcher 1984, Denslow 1987, Popma & Bongers 1988, Osunkoya *et al* 1993). Species may vary in their responses to the change in available light, according to their germination status and degree of shade tolerance (Vásquez-Yanes & Orozco-Segovia 1992).

With the increased availability under gap conditions of an otherwise scarce resource, gaps might be expected to be good places for seeds or seedlings to be in. This is not to say that seeds and seedlings in the understorey only receive diffuse light, which is poor in PAR. Sunflecks can provide an important proportion of the total daily light energy, or Photon Flux Density (PPFD), available to plants. This proportion can be in the order of 50% or more, and sunflecks may play an important part in the germination and growth of seedlings (Chazdon 1988). If a seedling is able to maintain a positive carbon balance, then 30-60% of its carbon gain can be from the capture of this resource. The influence of a gap in terms of the light environment it creates extends well beyond the gap 'edge', both in terms of the amount of diffuse light and the frequency and duration of sunflecks in the adjacent understorey.

Most research on the fate of dispersed seeds has been concerned with the effects of distance or site on survival and growth. Schupp (1998) stressed the importance of evaluating the consequences of dispersal to "distinct, definable sites". By using seeds and seedlings under parent crowns, at varying distances away from parents but under forest canopy, and in treefall gaps, the task has been to demonstrate any advantage to dispersal and the persistence of such advantage (Augspurger 1984), especially in terms of 'escape'. The performance of seedlings at different locations has frequently been shown to be influenced by site conditions (Clark 1990). Although only a limited number of species have received detailed investigation, the survival and growth of seeds and seedlings of these species has been found on the whole to be better away from the parent and in gap sites. Survivorship around parents or conspecifics may also vary from tree to tree. Howe (1993), using the fruiting history of the trees, showed that there was a higher proportional survival near more fecund individuals, perhaps related to site conditions.

There is clearly a large variation in the range of species responses to differing gap conditions. Augspurger's (1984) research indicated that the colonisation hypothesis was supported by all 9 species studied, and the escape hypothesis by 8 of them. Schupp (1988) found that *Faramea occidentalis* seeds suffered less mammal predation 5m from conspecific crowns than underneath them. Seedling losses however were the same. In gap sites he found that seed predation was no different to that under conspecific crowns, but seedling losses were higher, with better survival in the forest understorey. The overall effect (seed to seedling stages combined) was that survival was better away from conspecific canopies, which suggests that care must be taken when addressing the outcome of one or both stages. The response of *Faramea* seedlings contrasts with Augspurger's (1983) findings with *Platypodium elegans* (Leguminoseae) seedlings, which she found survived better in gap sites because of reduced attack by fungal pathogens. Seed predation on a palm seed (*Welfia georgii*) has been reported to be greater in a gap site than in the forest understorey, away from parents (Schupp & Frost 1989).

The seedlings of *Dipteryx panamensis* studied by De Steven (1988) are apparently dependent on gaps for survival. Greater survival occurred in small gaps than in the understorey, even for seedlings protected from predators. The poorest survival was under parent crowns, and the only measurable growth was in gaps (De Steven & Putz 1984). In a later publication (De Steven 1994) the same author reports on 3 species of shade-tolerant generalists which showed a range of responses to site conditions. Using only established seedlings, she found that release from suppression was important for survivorship and necessary for growth. Performance for all species was better in or at the edge of gap sites. There were also major differences in densities and distribution at the start of the study, as a result of earlier seed and seedling mortality. Each of the species seemed to be more susceptible to one form of mortality than the others, such as fungus on *Tetragastris panamensis* (Burseraceae) or dry season stress and insect herbivory affecting *Quararibea asterolepis* (Bombacaceae).

Sork (1987) found that the survival and growth of the large-seeded *Gustavia superba* was better in gaps, although seedlings were able to survive and grow in the shaded understorey. Seedlings of *Trichilia tuberculata* (Meliaceae) were found by Dirzo & Domínguez (1986) to show better performance (height, number of leaves, leaf length) at the gap edge or centre than under intact canopy, although there were no differences in survivorship. Hladik and Blanc (1987) reported a higher mortality of seedlings in gaps in northeast Gabon, often due to physical damage and rapid change in conditions ("macro-et micro-traumatismes"), although the percent growth in seedling height was 96% in gaps and 41% in the understorey. The increased risks of physical damage to seedlings growing in gaps has also been mentioned by Núñez-Farfán & Dirzo (1988). Howe's (1990) research on *Virola nobilis* has also indicated that seedling performance is better in gaps than at gap edges, where it is better than in the understorey.

One study that shifts the geographical perspective is that by Osunkoya and colleagues working in Australian rain forest (Osunkoya *et al* 1992, 1993a,b). They studied 12 species and found that growth was better in gaps. All species showed a positive response to increased light levels in terms of biomass, although there was considerable variation between them which could be attributed to regeneration status. Larger seeded species producing larger seedlings tended to be less sensitive to low light levels than smaller seeded ones, although whether this persisted beyond a dependence on cotyledons is unclear (their study lasted 15 months). They used both height and biomass as reliable measures of performance. In the Neotropics, work on a range of species by Popma and Bongers (1988) showed that growth was enhanced by the increased light availability of large gaps over small gaps and small gaps over understorey. They reported "sun-plant" and "shade-plant" morphologies of seedlings growing in the different conditions.

It is important to distinguish the different effects of site on seeds and seedlings. Steege and co-workers (Steege *et al* 1994) found that gap conditions reduced the germination success of seeds of *Chlorocardium rodiei* (Lauraceae), but favoured survival and growth of seedlings due to the light environment. Unburied seeds especially were susceptible to the low humidity, temperature extremes and high insolation found in gaps. Seeds of *Vouacapoua americana* (Caesalpiniacaeae) studied by Forget (1990) germinated much better in the understorey than in gap conditions, and burial enhanced germination. Counting all seedlings that appeared on the forest floor on Barro Colorado Island, Garwood (1986) found that more germinated in gaps than in understorey conditions. Of 43 Dipterocarp species studied by Raich and Gong (1990) in Malaysia, only 7 species coped well with understorey, small gap and large gap conditions. Seed germination for most species was reduced or zero in gap conditions, although seedling performance was better in gaps. Blain and Kellman (1991) found that the germination of seeds of three tree species in Mexico (*Brosimium alicastrum* Moraceae, *Cedrela odorata* Meliaceae and *Enterolobium cyclocarpum* Mimosoideae) was more sensitive to watering than was seedling survival over 2 months, and suggested that predation and light availability were more important factors operating on seedlings.

Gaps are often heterogeneous in terms of their microenvironment, with differing conditions for germination and establishment in the different parts of the gap (e.g. Brandani *et al* 1988, Nuñez-Farfán & Dirzo 1988). The effect of microclimatic conditions in gaps should not be underestimated. Fisher *et al* (1991) examined the response of seedlings in gap and understorey conditions to the relief of dry season drought stress. The leaf area of seedlings decreased in both gap and non-gap locations, but biomass and height were greater in gaps whether seedlings were irrigated or not. Seedlings in shade only survived if irrigated. They pointed out that root and shoot growth in the first year can be critical for survival, and that only seedlings in gaps were able to grow enough to cope with dry season stress in the first year. Poor root growth contributed to seedling mortality in a Venezuela study (Flores 1992), and Turner (1990) blamed drought (and some predation) for the higher mortality of seedlings of 3 *Shorea* species growing less well in the shaded understorey in Malaysia. Reduced root growth may be a consequence of defoliation by predators or stress (Fisher *et al* 1991).

In the Australian study (Osunkoya *et al* 1993), defoliation was found to result in reduced root growth, and low irradiance causes greater root growth in cuttings of Dipterocarp species (A. Hamzah, pers. comm.). Seedlings in deep shade are perhaps more likely to allocate resources to root growth, whereas those in light conditions may invest in stem and leaf growth (Osunkoya *et al* 1993). A large root mass can benefit the growth of a suppressed seedling once it is released. The nature of the understorey vegetation (the 'leafing environment'?) can affect seedling survival and growth. Denslow *et al* (1990) found that large-leaved palms (Palmae) and cyclanths (Cyclanthaceae) reduced the chances of seedling establishment of *Inga* spp (Leguminosae) by effectively creating too much shade. Marquis *et al* (1986), however, found no difference in the total number of seedlings or germination and survival over 15 weeks that could be related to differences in understorey vegetation cover. However, their study was of relatively short duration, they used small plots, but more importantly, they lumped all species together, including even understorey palms. In addition, the difference in canopy cover (4.9%, measured by densiometer) was relatively small.

These studies have demonstrated an advantage in dispersal away from the parent for a range of species. Survivorship and growth, certainly of seedlings, are dependent on the type of site a seed encounters. Seeds and seedlings respond in different ways to the sites they encounter, and relative shade intolerance or tolerance can often be recognised. Even 10 years ago, evidence suggested that mortality was associated with density (7 out of 8 studies) or distance (10 out of 12 studies), often related to site conditions (Clark & Clark 1984), even if the specific causes of mortality were not described.

The major limitation to seedling research is the restricted timescale of most studies. At only a handful of sites, principally in the Neotropics, are investigations approaching the time-scales required. Work is also usually limited to one or a few species. It is no straightforward task to evaluate the influence of seed dispersal on the reproductive success of trees and on plant population dynamics within the forest ecosystem. The losses of seeds and early seedlings require huge sample sizes. Nonetheless, even if the majority are lost, then the way in which this mortality is distributed (in terms of site or species) and the performance of the remaining few percent as seedlings, depending where they end up, can indicate some of the processes that link seed dispersal and recruitment. Seedling mortality is usually severe, and the actual population size or distribution of a species is likely to be be affected by later mortality and competition, as well as by the performance of successive cohorts. Nonetheless, the distribution of seedlings, from several cohorts, probably contributes to the future population structure.

Most of these studies, as brief glimpses of a dynamic process, relate to immediate ecological circumstances which are then linked to evolutionary characteristics. Measures are made of physiological responses to a range of conditions, and the assumption is that this in some way is linked to fitness, via survival. The ecological scenario that results in higher survivorship of seedlings is likely to increase the plant's fitness. The effect of dispersal on plant fitness is nonetheless limited by non-disperser selection pressures and an unpredictable habitat. It is only aggregate results from many seasons which might ultimately give us a reasonably coherent picture of the effects of certain dispersal systems on plant populations. Information on the population genetics of forest trees should also provide insights into the structure of their populations, if genetic fingerprinting becomes possible.

1.5 RATIONALE FOR THIS STUDY

Considering the issues outlined above, it was thought appropriate to investigate the plant-animal interactions at a field site in Gabon, concentrating on the role of western lowland gorillas (*Gorilla g. gorilla* Savage & Wyman 1846) as seed dispersers. As will be discussed in the next chapter, gorillas have several attributes as large-bodied frugivores that suggest they may be important seed dispersers. Gorillas in the Lopé forest are seriously frugivorous, consuming over 97 species of fruit (Williamson *et al* 1988, Tutin & Fernandez 1993). The majority of seeds are swallowed and passed out intact in dung. Their nesting behaviour creates frequent seed 'repositories' in the forest which may be favourable sites for seedling growth, leading to seedling banks. For some plant species, gorillas are the major consumers of their fruit from among the frugivore community. In some cases they are in fact the principal dispersal agents. A preliminary study of one species, *Cola lizae*, indicated that gorillas are the only animal that reliably swallows its seeds, and that seedlings survive better in nest sites made by gorillas than elsewhere in the forest (Tutin *et al* 1991a), suggesting a relatively tight dispersal association.

The questions defining our objectives were:

1) Are gorillas major consumers of certain fruit species in terms of the proportion of the ripe seed crop they remove?

2) Is the treatment of seeds by gorillas more likely to result in effective seed dispersal than that by alternative consumers?

3) Do gorillas' ranging and behaviour patterns, in particular the selection of nest-sites, contribute to the quality of seed dispersal they perform?

4) What is the fate of gorilla-dispersed seeds, as opposed to those that are dropped or scatter-dispersed? Can an advantage of gorilla dispersal be demonstrated?

The thesis follows the stages involved in seed dispersal. After a section on the study site (Chapter 2) there is a description of the ecology of the tree species studied (Chapter 3). The removal and deposition of seeds is reported in Chapter 4, and the survival and growth of seeds and seedlings in Chapter 5. Chapter 6 reports the findings of an interaction between gorillas and three plant species of the forest/savanna boundary with very small seeds. A concluding discussion forms Chapter 7.

Chapter 2

STUDY SITE - THE LOPÉ FOREST

2.1. INTRODUCTION

Location, physical characteristics

Gabon straddles the equator at the western edge of central Africa (Figure 2.1). Forest is the natural vegetation of 85% of the country (Caballé 1983), and currently covers an estimated 75% of the land area (Myers 1991). The predominant forest types have been described as "hygrophilous coastal evergreen Guineo-Congolian rain forest' and "mixed moist semi-evergreen Guineo-Congolian rain forest" in a UNESCO classification by White (1983). Although much of the forest has been selectively logged for timber, there still remain considerable areas that have not yet been commercially exploited. The most intensively harvested areas have been in the more accessible coastal zone. The completion of the 'transgabonais' railway across the country in the early 1980's made accessible a large part of the interior for timber extraction.

As a nation with a small human population and a natural resource wealth that does not just consist of timber, conditions in Gabon are such that a sustainable use of its forests could be achieved more easily than in other countries in the region. Sufficiently large tracts of forest exist to furnish multiple benefits on a continuous basis, if logging was done in a way that promoted regeneration. Management could be for timber and other commercial products of local and national value, non-commercial local benefits, the maintenance of biodiversity, as well as offering opportunities for research and education (see Tutin & Fernandez 1987, Pourtier 1989, McShane 1990, Wilks 1990). In his comprehensive review of the status of Gabon's forest ecosystems, Wilks (1990) points out that only 6.7% of the country is in the form of reserves, made up of 5 'protected' areas with a total area of 18000km^2. The legal status of these areas is both vague and neglected and commercial logging takes place unprohibited in all but one small reserve.

In central Gabon lies the 5000 km^2 Lopé Wildlife Reserve (Figure 2.1), the largest of the protected areas in the country. Created in 1962, it is now administered by the Wildlife Department of the Ministry of Water and Forests, and the legal status does not yet forbid timber extraction. Three logging concessions currently operate within the reserve, the impact of which threatens the integrity of the area as a protected zone. Lopé's geology is predominantly Precambrian. The metamorphic rock has weathered to yield poor, shallow sandy or stony soils in the savanna, with slightly deeper, more sandy-clay ferralitic soils under forest cover (Wilks 1990, White 1992 and references therein). Altitudes range from 100-700m above sea level, and a mountainous ridge runs north-south through the middle of the reserve. Most of the reserve consists of semi-evergreen tropical moist

Figure 2.1 Map of Gabon, showing savanna areas (stippled) and the Lopé Reserve (hatched)

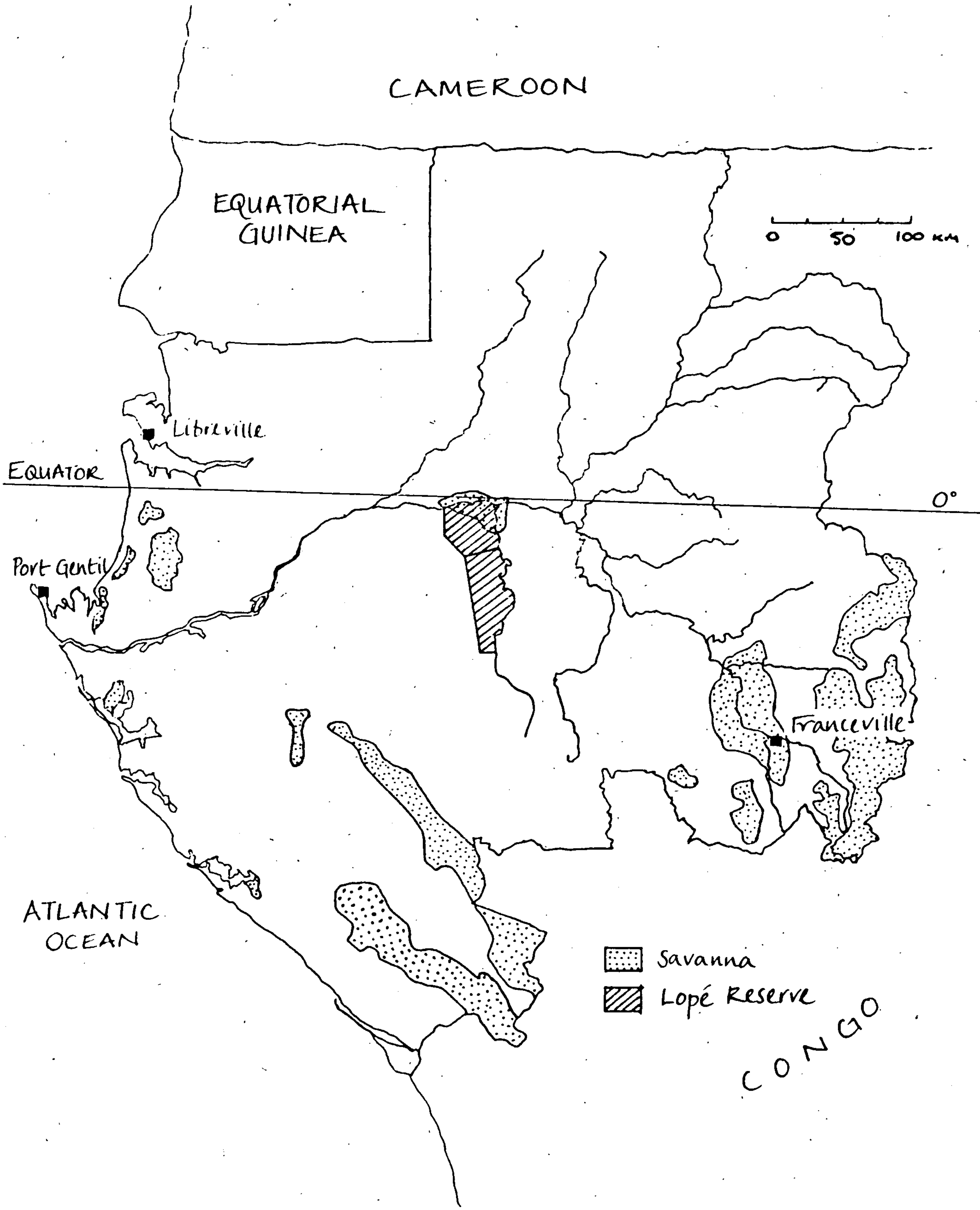


Plate 2.1 a) Hill-top view of the study area, showing savanna-forest mosaïc; b) Marantaceae forest, above the herb layer; c) at seedling level, underneath the herb layer.

a)

b)

c)

forest but in the northern part, bordering the Ogooué river, there is an extensive area (approximately 300 km^2) of savanna interspersed with gallery forest and isolated forest patches, called "bosquets" (Plate 2.1a).

Originally thought to have been the site of an ancient lake, the savannas in the area are considered to be of natural origin. They were probably more extensive during the climate-driven forest reduction of the Pleistocene era, with forest then recolonising areas of savanna as the climate became more humid (de Foresta 1990, White 1994e). Their present distribution and extent are due in part to the human use of fire, areas that are not burned being recolonised by forest. There is evidence that humans have inhabited the area for at least 60 000 and possibly 400 000 years (Oslisly & Fortugne 1993 in Tutin *et al* 1993; Oslisly, in press; Tutin & Oslisly, in press), and numerous old village sites occur within the savanna-forest mosaïc in the study area.

The Station d'Études des Gorilles et Chimpanzés (SEGC) is located at the southern edge of this savanna-forest mosaïc, close to the edge of continuous forest (0°10'S, 11°35'E). The core study area covers approximately 40km^2, most of it within the main forest zone.

Climate

The Lopé is one of the drier regions of Gabon, which sees an average annual rainfall from 1400mm in the southeast to over 3200mm in the northwest of the country (EDICEF 1983). Rainfall at the field site (measured in the savanna 400m from the forest) averaged 1507mm over a 10-year period (1984-1993). Monthly rainfall is shown in Figure 2.2. The climate is characterised by a marked dry season from mid-June to mid-September, although its onset, duration and extent are variable. A reduction in rainfall often occurs from mid-December to mid-January. Cloud cover in the dry season is more or less continuous, resulting in low insolation levels, and temperatures are at a minimum, which probably limits the evapo-transpiration stress on plants. Mean monthly temperatures at the study site range from minima of 20.6-22.3°C to maxima of 27-30.6°C (Figure 2.3), and humidity has not been recorded below 70%. These temperature and humidity records were measured in the forest understorey 10m from the edge of the savanna.

Atypical climatic events occur and can have an important effect on the forest ecology. One such set of circumstances occurred during this study. The last quarter of 1991 was unusually dry, with October-December monthly totals being 149mm, 154mm and 52mm respectively (8-year averages: 270mm; 234mm; 118mm). Although rainfall in January 1992 was more than average at 81mm, February only saw 41mm (average 93mm), and 84% of March's rain of 224mm (average 193mm) fell in the second half of the month. This unusually dry 6-week period had a direct effect on the survival of some seeds (see Chapter 4), and the unusually low temperatures during the dry spell were thought to trigger the flowering of several species that normally do so after the long dry season (Chapter 3, and Tutin & Fernandez 1993a).

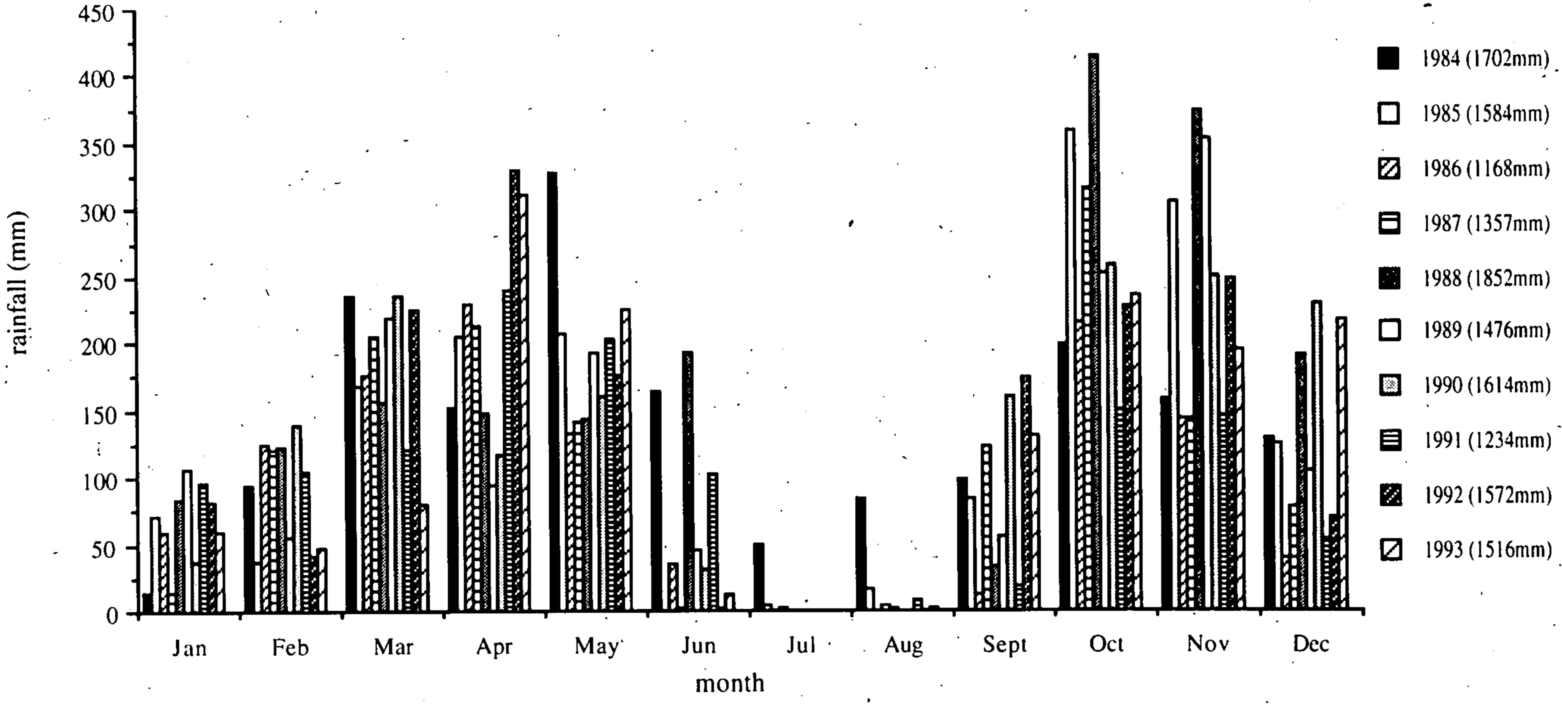
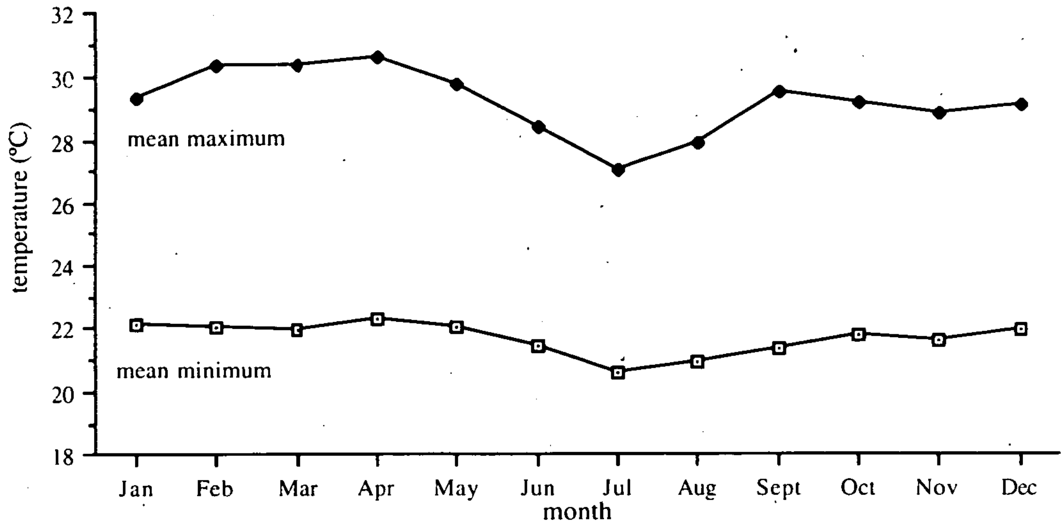


Figure 2.2 Monthly rainfall at SEGC over a ten-year period (annual total shown in brackets)

Figure 2.3 Mean monthly maximum and minimum temperatures at SEGC, 1984-1993



Research history

SEGC was established in 1983 following a nationwide census of gorillas and chimpanzees (Tutin & Fernandez 1984). Research on gorillas, chimpanzees and their forest habitat has been underway since then. Gorilla groups in the study site have not become habituated to close human presence. Efforts have concentrated on studies of the apes' feeding ecology, including diet (Tutin & Fernandez 1985, Williamson 1988, Williamson *et al* 1990, Tutin & Fernandez 1993b, Rogers *et al* 1994), food chemistry (Rogers *et al* 1988, 1990, 1992), food processing (Tutin & Fernandez 1994), ranging and social structure (Tutin *et al* 1991a, Tutin *et al* 1992), their nesting behaviour (Tutin *et al* 1995), phenological patterns of their food plants (Tutin & Fernandez 1993a, White 1994b), the forest vegetation and its history (Rogers & Williamson 1987, White 1992, Williamson 1993, Tutin *et al* 1994, White *et al* 1995), the effects of selective logging (White 1992, 1994c), the mammal community (White 1994d), elephant ecology (White *et al* 1993, White 1994a, White *et al* 1994) and the ecology of sympatric monkeys (Ham 1994). Plant-animal interactions have always been a component of the research at SEGC, and a preliminary study of seed dispersal by gorillas has been carried out (Tutin *et al* 1991b). A pilot study of frugivory was undertaken for 9 months in 1990 by Richard Parnell. It involved concerted observational effort to investigate feeding on the fruit of four tree species (Rogers & Parnell 1991). Some of the elements of the above research are considered in the sections below.

2.2 THE FOREST

Forest structure and composition in the Lopé Reserve is heterogenous, but the two principal forest types that occur have been described as 'Marantaceae forest' (after Letouzey 1968) and 'mixed closed canopy forest' (Williamson 1988, White 1992, Tutin *et al* 1994, White *et al* 1995). In fact many different forest types are represented in a fine mosaïc (White 1992, Tutin *et al* 1994, White *et al* 1995). The myriad of vegetation associations (20 recognised by White (1992)) include forest that is actively colonising savanna, rocky forest, gallery forest, marshes, and different forest compositions related to the degree of transition from Marantaceae forest to mixed closed canopy forest. Marantaceae forest in the Lopé is thought to have colonised savanna relatively recently (Tutin *et al* 1994, White 1994e), and eventually the composition and structure change, giving rise to closed canopy forest. Marantaceae forest is generally less rich in tree species than closed canopy forest, and has fewer trees per unit area (a lower basal area). The forest studies only included trees over 10cm dbh. Table 2.1 (adapted from Tutin *et al* 1994) shows the 'top ten' tree species ≥10cm dbh for each forest type in terms of abundance and basal area. The mode of seed dispersal is also included. White (1994b) found that 75% of the fruit species (n=195 species) he found on fruitfall transects in a range of forest types were adapted for animal dispersal. A total of 676 plant species have been recorded in the SEGC study area to date (Tutin *et al* 1994).

Letouzey (1968) described Marantaceae forest as "forêts clairsemées à strate inférieure de Marantacés". At Lopé it is characterised by an uneven and broken canopy typically 25-35m high, a sparse lower storey (10-20m), and a dense undergrowth of herbaceous vegetation, consisting principally of plants in the Marantaceae and Zingiberaceae families. This vegetation provides a major food source for the gorilla and elephant populations (Tutin *et al* 1994, White *et al* 1995), as well as suitable nesting sites and nest construction materials for gorillas (Tutin *et al* 1995). The dominant tree species (in terms of basal area) of this forest type are *Aucoumea klaineana* (Burseraceae) and *Cola lizae* (Sterculiaceae). *Lophira alata* (Ochnaceae), *Xylopia* spp. (Annonaceae), *Diospyros* spp. (Ebenaceae), *Pentaclethra* spp (Mimosaceae) and *Pycnanthus angolensis* (Myristicaceae) are all relatively common (see Table 2.1, Tutin *et al* 1994, White *et al* 1995). The 'top ten' species in this forest type account for 76% of the total basal area and 69% of the tree stems above 10cm dbh (White 1992). The core study area lies within Marantaceae forest.

Closed canopy forest, thought to be an older type in terms of succession (Tutin *et al* 1994, White 1994e), has a much denser lower storey and more continuous canopy. It corresponds to White's (1983) "mixed moist semi-evergreen Guineo-Congolian rain forest". There is an absence of dense herbaceous vegetation, it is more species-rich, and

Table 2.1 'Top ten' tree species in Marantaceae forest (MF) and closed canopy forest (CCF) at Lopé, in terms of basal area and abundance. The mode of seed dispersal is also given.

Species	Family	Dispersal mode*	Rank (basal area) MF	Rank (basal area) CCF	Rank (no. stems) MF	Rank (no. stems) CCF
Aucoumea klaineana	Burseraceae	W	1	2	2	
Cola lizae	Sterculiaceae	A3b	2		1	
Lophira alata	Ochnaceae	W	3		3	
Pentaclethra macrophylla	Mimosaceae	B	4		9	
Dacyodes buettneri	Burseraceae	A1/3	5	1		8
Pentaclethra eetveldiana	Mimosaceae	B	6		10	
Diospyros polystemon	Ebenaceae	A3	7		5	
Hylodendron gabunense	Caesalpiniaceae	W	8			
Xylopia quintasii	Annonaceae	A1	9		4	
Pycnanthus angolensis	Myristicaceae	A1/3a	10			
Trichilia cf. priereana	Meliaceae	A1			7	
Strombosiopsis tetrandra	Olacaceae	A1		7		4
Diospyros dendo	Ebenaceae	A2			6	
Diospyros zenkeri	Ebenaceae	A3			8	
Maprounea membranacea	Euphorbiaceae	A1				10
Scyphocephalium ocochoa	Myristicaceae	?		3		
Centroplacus glaucinas	Pandaceae	A1				1
Xylopia aethiopica	Annonaceae	A1				7
Santiria trimera	Burseraceae	A3		9		3
Coula edulis	Olacaceae	A5		4		5
Augouardia letestui	Caesalpiniaceae	B		5		6
Sindoropsis le-testui	Caesalpiniaceae	B		6		
Strombosia zenkeri	Olacaceae	?		8		1
Cylicodiscus gabonensis	Mimosaceae	W		10		
Dialium soyauxii	Caesalpiniaceae	A2				9

* A: animal (principal dispersers: 1- birds, monkeys; 2 - monkeys, apes; 3 - apes a: chimp, b: gorilla; 4 - apes, elephants; 5 - elephants); B: ballistic; W: wind

has a higher basal area than Marantaceae forest. The major tree species are *Dacryodes buettneri* (Burseraceae), *Aucoumea klaineana, Scyphocephalium ocochoa* (Myristicaceae) and *Coula edulis* (Olacaceae) (see Table 2.1).

Community-wide fruit production at Lopé is highly seasonal, with the highest fruit

Community-wide fruit production at Lopé is highly seasonal, with the highest fruit abundance typically ocurring from November-February (White 1994b) and a distinct fruit scarcity during the dry season. However, a wide range of flowering and fruiting patterns exist among species. These include: asynchronous fruiting within a species, providing fruit year-round; long fruiting periods with sequential ripening; short sharply-peaked fruiting; fruit production every 2 or 3 years (alternate-bearing); or mast-fruiting, in which little or no fruit is produced most seasons but occasional years see major fruit production. There is also considerable yearly variation in the amount of fruit available, with 'good' and 'bad' years of community-wide fruit production (Tutin & Fernandez 1991a). This may depend in part on the weather, pollination success and predispersal predation.

Atypical climatic events can disrupt the flowering and fruiting patterns of some trees. This was the case in 1992 (Tutin & Fernandez 1993b). Eight species from 6 families that usually flower synchronously in September-October and bear fruit in January-May, flowered in March-May in 1992 and many subsequently produced fruit; the following year, 1993, was a'poor' year for these and other species. The minimum temperature during an abnormally dry period in February 1992 (see section 2.1) twice reached 19°C or less. By looking at climatic data and phenology of these species, it was found that a 'critical' minimum temperature of 19°C was a possible trigger for flowering in these species. It explained fruit crop failures in 1984 and 1987 (when temperatures in the dry season remained above 19°C), flowering during a prolonged dry season in 1991, as well as unseasonal flowering in 1985 and 1992. Rainfall patterns, although often associated with minimum temperatures (Figures 2.2 and 2.3) seemed not to influence flowering.

Parts of the study area were selectively logged in the early 1960s, principally for one species of tree, okoumé (*Aucoumea klaineana*). Extraction rates were about 1-2 trees per hectare. Canopy loss from this scale of activity has been estimated to be 10%, although 50% of the canopy is disturbed or changed (White 1994c). The same author reports that, for trees ≥10cm dbh, logging at Lopé caused a reduction of 13% in basal area and 11% of individuals were destroyed. For trees ≥70cm dbh these figures were 21% and 18% respectively. Old logging roads and extraction routes are still obvious in the study area 30 years after the departure of logging teams, and are used by animals and field workers alike.

2.3 THE VERTEBRATE COMMUNITY (mostly large mammmals)

The lack of data on herpetofauna and small mammals makes their inclusion in this section impossible. Similarly, attention has not been directed towards nocturnal primates

Table 2.2 Estimated density and biomass of some of the larger diurnal mammals at SEGC (from White 1994d).

Species	Density (no. km-2) Groups	Indiv	Est. biomass (kg. km-2)
Cercopithecus nictitans	1.76	23.7	80.6
Cercopithecus pogonias	0.38	4.8	10.6
Cercopithecus cephus	0.64	6.2	12.4
Cercocebus albigena	0.46	8.6	35.3
Colobus satanus	1.12	13.6	114.2
Mandrillus sphinx	0.01	1.5	15.3
Gorilla gorilla	0.18	1	78.1
Pan troglodytes	0.28	0.7	27.1
Sub-total: diurnal primates			373.6
Loxodonta africana	1.1	3	5225.1
Potamochoerus porcus	0.05	1.6	99
Syncerus caffer	0.1	0.3	71.3
Cephalophus monticola	0.25	0.3	1.2
Red duikers	2.25	2.5	38.8
Cephalophus sylvicultor	0.91	0.9	51
Hyemochus aquaticus		P	P
Neotragus batesi		P	P
Sub-total: ungulates			5486.4
Squirrels			4.2
Total			5864.2

P: present but not recorded

and carnivores. The larger mammals known to occur in the Lopé Reserve are listed in Appendix A, but the list is incomplete because a full inventory has not yet been done. Of these, about 15 species are frugivorous, and at least 11 species are predominantly seed predators (see section 2.7). The densities and biomass of mammals surveyed by White (1994d) in the main SEGC study area ('Transect 1') are shown in Table 2.2. He reports that Lopé supports possibly the highest mammalian biomass of rain forest areas studied to date. It is clear that elephants make up the majority of the total biomass (89%), whereas primates only account for 6%. Gorillas occur at densities of about 1 individual per km^2, and chimpanzees at 0.7 individuals per km^2. Biomass of gorillas is nearly three times that of the smaller ape at this site. The transect was predominantly in Marantaceae forest, which is favoured by both elephants and gorillas, and may explain the high biomass of these species relative to other sites in Lopé (White 1994d). Figures for closed canopy forest sites showed higher densities of chimpanzees and similar values for biomass.

The extensive avifauna is now covered by a field guide (Christy & Clarke 1994). Many of the forest birds at Lopé are frugivorous, including conspicuous groups such as hornbills (Bucerotidae), touracos (Musophagidae) and pigeons (Columbidae), as well as barbets (Capitonidae), bulbuls (Pycnonotidae) and starlings (Sturnidae). Their activity as seed dispersers is discussed in section 2.7.

2.4 GORILLAS: generalities

The western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman 1847) is one of three subspecies of *G. gorilla*, the other two being the eastern lowland gorilla (*Gorilla g. graueri*) and the mountain gorilla (*Gorilla g. beringei*). The differences on which the divisions are based are largely morphological, although considerable genetic differences exist between the western and eastern subspecies, as well as between populations (Ruvolo *et al* 1993). The important distinction in terms of this study is that mountain gorillas eat little or no fleshy fruit, having a largely foliaceous diet. The current distribution of *Gorilla g. gorilla* (hereafter 'gorilla') is discontinuous but they occur in SW Nigeria, Cameroun, Gabon, Equatorial Guinea, Central African Republic and Congo.

Gorillas display considerable sexual dimorphism, far more so than chimpanzees. Female gorillas (n=3) are typically 42% of the mean weight of adult male gorillas (170kg, n=14) (Jungers & Susman 1984, in Tutin & Fernandez 1994). The large molars are set in relatively huge jaws, and the sagittal crest on the skull provides an area for the attachment of powerful temporal muscles (Dixson, 1981). The gut is long, with a big hind-gut to facilitate the processing of plant foods (Chivers & Hladik 1984), and contains cellulose-digesting ciliates (Collet *et al* 1984). The relative lack of extreme gut specialisation, however, places the gorilla firmly in the band of frugivores rather than folivores among "caeco-colic fermenters", according to Chivers (1989). Typical gut passage times are 36-38 hours (Milton 1984), although some experimental markers were passed up to 84 hours after ingestion, indicating that retention of foodstuffs occurs. That study was done on captive animals; wild gorillas are likely to consume more fibre, which might slow down passage rates.

Gorillas live in relatively stable family groups usually led by one silverback male. Groups at Lopé consisted of 4-15 individuals (median=9) (Tutin *et al* 1992), and White (1994d) found a mean of 5.3 individuals per group. Range size is extremely difficult to assess in some areas due to the difficulties of tracking, terrain or the extent of displacement of gorilla groups. At Lopé, the mean day range was 1172m (n=30, range 320-2600m) but with only 11% of night nest sites found, the mimimum size of the groups' ranges, from 4-14km^2, was probably a very conservative estimate (Tutin *et al* 1992). The ranges of different groups may overlap considerably, and ranges may shift over time. A chance encounter with a known group several kilometres to the north of the study area extended the estimate for that group's range severalfold (C. Tutin, pers. comm.). A bulky diet consisting of high quantities of fibre, and a slow gut passage rate to allow maximum digestion of low quality food, may be associated with a slower lifestyle and a smaller range (Milton 1984). It has been found that during the dry season, a time of fruit scarcity, gorillas at Lopé eat more vegetative plant parts and range smaller distances (Rogers *et al* 1994, SEGC, unpub. data). This may have as much to do with the distribution and availability of the food plants, as with digestive physiology.

2.5 GORILLAS AS FRUGIVORES: the potential for effective seed dispersal

Advantages

The degree of frugivory of lowland gorillas is increasingly well documented, both at Lopé (Tutin & Fernandez 1985, Williamson *et al* 1990, Tutin & Fernandez 1993) and at other sites (e.g. Ndoki Forest: Nishihara 1992, Moutsambote *et al* 1993; Kahuzi-Biega: Yamagiwa *et al* 1992, Yumoto *et al* 1993). At Lopé gorillas consume at least 97 species of fruit and disperse the seeds of the majority of these, generally depositing them intact in their dung. Fruit represented 55% of the known number of plant species in the diet over a 7-year period, and 96% of 4301 dung samples were found to contain fruit remains (Tutin & Fernandez 1993).

The criteria that contribute to effective seed dispersal by a frugivore have been discussed in Chapter 1, and include: reliable visitation to a fruiting tree; removal of many seeds away from the parent; minimal waste; ingestion of seeds and intact passage through the gut; large body size relative to seed size and gentle treatment of the seed by mouth and gut; and perhaps most importantly, the deposition of seeds in a favourable site (Jordano 1992).

For many fruit species of the Lopé forest that gorillas eat, they appear to satisfy all the above criteria. They are certainly large-bodied frugivores, providing a gentle gut passage for seeds. Many fruit species in their diet are eaten whenever they are available. Their reliability as visitors to a particular fruiting tree may be determined in part by their preference for that species, its relative importance in the diet, the distribution and abundance of fruiting trees of that species, the size of the individual tree and the total available fruit crop, the number of other available foods and their abundance and importance, as well as other foraging decisions. These can all vary from species to species and from one year to another. Fruits classed as 'important' are those species that "dominate the diet on a regular or irregular basis and influence ranging patterns" (Tutin *et al* 1991b, Tutin & Fernandez 1993b); 15 such species are listed in that publication. Gorillas at Lopé tend to stay in one small area if ripe fruit foods are concentrated there. They also use uncommon habitats such as gallery forests in response to the seasonal production of fruit crops.

Although gorillas maintain a high degree of foliaceous material in their diets, the quantity and diversity of species whose seeds are found in dung are impressive. A single dung pile may contain hundreds of seeds of one or more species, so a group of gorillas may disperse many thousands of seeds of a species in one fruit season (Tutin *et al* 1991a). The mean number of species per dung sample was 3, with a range of 0-10, over a 7-year period (Tutin *et al* 1991b). During the dry season, when ripe fruits are scarce, gorillas consume more non-fruit plant foods, including some (such as the bast of *Milicia excelsa*, Moraceae) that act as keystone resources (Tutin *et al* 1991b, Rogers *et al* 1994).

Gorillas evidently remove and disperse considerable quantities of seeds. The quantity that they waste is generally low, although it varies depending on the type of fruit and abundance of a particular fruit species. Several of the species they feed on, particularly the more 'specialist' types, have fruit that are firmly attached to the branches and are not easily knocked down by the activity of gorillas in the crown (e.g. *Gambeya africana*, Sapotaceae;*Cola lizae*, Sterculiaceae). As large-bodied animals, there is a direct need to consume bulk amounts of fruit when it is available. They are able to consume fruit without much need for processing, which may be better for the tree in terms of seed treatment and dispersal. They rely on post-ingestion processing, as undigestible ballast does not seem to be a major constraint (Chapter 1.3). In order to satisfy their nutritional demands by feeding on a variety of fruit and vegetative or animal foods, a group of gorillas ranges typically 320-2600m or more on a daily basis (Tutin *et al* 1992), thus covering a varied "habitat template" (Jordano 1992) over which they disperse seeds.

Gorillas deposit seeds in a pile of natural fertiliser (Plate 2.2a). Precise data on defaecation rates are not available, but 4-5 per day is a reasonable figure and is probably conservative (Tutin *et al* 1991a). Much of their faecal output seems to be at nest sites, as they frequently defaecate in the evening and again in the morning before leaving the site. Fresh nests (Plate 2.2b) are built in a new locality each night, so aggregate effects of seed accumulation are minimised. Nests are usually made on the ground (64% of 2435 nests, Tutin *et al* 1995), but this is influenced by habitat type. Nest sites are often found in areas of more open canopy, such as natural treefall gaps, which might favour shade-intolerant species over others that they disperse. Despite the greater abundance of herbaceous material that is sometimes associated with the nest sites, the act of nest building, feeding and playing severely flattens the vegetation and may even kill it.

Dung is usually deposited adjacent to the nest, often in a clear patch of ground with few herbaceous stems around it. Any dung that is not deposited at a nest site either falls from a tree where a gorilla is feeding, or is left as the gorilla moves about the forest. Dung left on elephant paths that gorillas use is often found behind a log or root step, which may afford growing seedlings some protection from trampling (pers. obs.).

Plate 2.2 a) Dung pile of a silverback gorilla, containing 1196 *Uapaca* seeds; b) fresh gorilla nest built of herbaceaous and woody material

a)

b)

Drawbacks

The long gut of a gorilla means that seeds can take some time to pass through it, which could be detrimental to some species. Nonetheless, obstacles such as seeds might be expected to pass through a large, fibre-filled gut unscathed. The evidence from faecal analysis at Lopé suggests that most seeds are passed intact. A number of seeds are destroyed, either accidentally during feeding (possibly the case for *Uapaca guineensis*, Euphorbiaceae) or intentionally when gorillas are acting as seed predators. They regularly exploit the ripe fruit of some species for their seeds (e.g *Treculia africana*, Moraceae; *Duboscia microcarpa*, Tiliaceae), or eat the immature seeds of species they usually disperse, when fruit availability is low (e.g. *Diospyros* spp, Ebenaceae; *Dialium lopense*, Caesalpiniaceae). Another strategy they use is to feed on seeds when fruit is immature but eat the pulp and discard the seeds once the fruit is ripe (e.g. the large-seeded *Pentadesma butyracea*, Guttiferae).

There is no doubt that seeds dispersed by gorillas are deposited in clumps from which only one adult can ultimately emerge. An aggregation of seeds in dung can be a major food resource for granivores, increasing the risks of seed predation. When a 'clump' means tens or hundreds of one or more species, there will inevitably be severe competition between growing seedlings above and below ground. At a gorilla nest site, some seedling clumps will be in such proximity that they too can only yield one adult tree between them in the long run. Despite this apparent "waste", clumps represent a seedling bank which can withstand considerable mortality yet still retain a number of potential adults. Seedling herbivory is a common cause of stress or mortality (see Chapter 1.4.5), and clumps of seedlings may be more easily found by herbivores. Gorilla behaviour may not favour effective dispersal of some seeds, particularly small seeds, or those with specialised habitat or establishment requirements. For example, seeds of some *Ficus* species need to be deposited in the nooks and crannies of a tree crown in order to become adults.

Perhaps the most deleterious effects suffered by some trees whose fruit is eaten by gorillas come from the damage to the crown inflicted by the apes as they harvest fruit. Gorillas readily climb trees to access fruit or other foods, and have been seen feeding up to 40m above ground. Of their fruit foods, 89% are harvested arboreally (Tutin & Fernandez 1993). If the fruit is presented at the edges of the tree crown, gorillas bend or break branches towards them to feed, as they are too heavy to clamber out to the ends of branches. A group of feeding gorillas can inflict a serious amount of damage to a fruiting tree, in rare cases up to 40-50% of the crown of certain species, such as *Uapaca* spp (Euphorbiaceae), *Celtis tessmannii* (Ulmaceae) and *Dialium* spp (Caesalpiniaceae). Branches up to 10cm diameter may be broken. The amount of damage sustained can depend on the manner in which the fruit is presented, the juxtaposition of ripe and unripe fruit, the architecture of the tree and the structural quality of the wood, as well as the behaviour of individual gorillas. Gorillas will sometimes make a nest if they are feeding for a lengthy period in a crown, and the construction of feeding nests in a fruiting crown also contributes to the damage a tree sustains. Structural damage and consequent leaf and stem loss is a cost that the tree has to bear in return for dispersal services carried out by gorillas, a cost which is likely to depend on the tree's size relative to the amount of damage.

If the tree's crown is small, then it will not be able to accommodate an entire group of gorillas. Similarly, if the fruit crop is small, it is less likely to be able to satisfy a whole group. Removal of fruit from a particular tree can be affected if there are nearby trees with larger crops, and if the fruiting trees of a species are relatively abundant. Some individuals of a common species may not be visited at all by gorillas if a high proportion of them bear fruit. When tree densities are quoted, it should be remembered that for dioecious species, only some of them (the females) will bear fruit, and for most species there will usually be a proportion of trees each year that do not fruit.

2.6 OTHER SEED DISPERSERS

Gorillas share the Lopé forest with a range of mammalian and avian frugivores that are also seed dispersers for a range of plants. Most of the fruits gorillas eat are species that are also dispersed by other frugivores. The quality of dispersal provided by the different frugivores varies considerably, depending on the particular plant-animal interaction involved. Differences in external morphology and gut physiology (and fruit characteristics) mean that some consumers may be better for certain plant species than others. I shall briefly point out some of their general traits as seed dispersers in relation to gorillas.

The closest comparison is to be made with chimpanzees, which inhabit the study site at slightly lower densities than gorillas (0.7 individual km^{-2}). They are also large-bodied, although the biomass of chimpanzees in the main study site is considerably less than that of gorillas (Table 2.2). Chimpanzees are more frugivorous than gorillas in terms of the percentage of plant species in the diet whose fruit (pulp, arils and seeds) are eaten: this is 76% for chimps and 55% for gorillas (Tutin & Fernandez 1993). The number of species of fruit eaten is very similar, however: 111 and 97 species respectively. The degree of overlap is considerable: 82% of chimpanzee fruit foods are eaten by gorillas, and 79% of gorilla fruit foods are eaten by chimpanzees. In terms of species diversity per dung sample, the figure for chimpanzees is slightly lower than for gorillas, with a mean of 2.7 species per chimpanzee dung sample (range 0-9). Gorillas eat a wider variety of fruit than chimpanzees for 8 months of the year. Chimpanzees persist in eating fruit even during the dry season, a period of fruit scarcity, when gorillas eat more stems, leaves and bark.

The proportion of species whose seeds are swallowed by chimpanzees is lower than that for gorillas. Chimpanzees are smaller, and have a lower swallowing threshold, so disperse fewer large seeds than do gorillas (Tutin & Fernandez 1994). Chimpanzees tend not to swallow seeds with a volume of 4.2cc or more, whereas gorillas will swallow seeds up to about 7cc in volume. Chimpanzees often carry out pre-ingestion processing, 'wadging' fruit in their lower lips and spitting out unwanted material (seeds, skins and some fibre), which acts to limit the quality of dispersal they provide. It is not just large seeds that are wadged, as fruit that have a high proportion of undigestible material are also treated this way, even if they contain small seeds. For some small-seeded fruit, chimpanzee dung contains more seeds per unit weight than gorillas (e.g. *Dialium*), but faecal output is smaller, so overall the quantities dispersed by the two apes may not be greatly different. Chimpanzees always construct nests in trees, so although clumping effects of seeds dispersed in dung are mitigated by the scattering that occurs as the dung falls to the ground, seeds inevitably land under an intact forest canopy.

The other very large frugivore is the elephant. Attempts have been made to classify it as an honorary ape (White *et al* 1994), given its status as a fruit eater and seed disperser. Quite a number of fruit foods eaten by elephants are also dispersed by other frugivores. They share 71% of the fleshy fruit species eaten by gorillas, for example. Some species are only dispersed by elephants, due to the large size of the seeds (e.g. *Pentadesma butyracea*, Guttiferae; *Irvingia gabonensis*, Irvingiaceae) or the nature of the fruit structure (e.g. *Omphalocarpum procerum*, Sapotaceae). Above the gorilla's swallowing threshold, the elephant takes over as the prime disperser. White (1992) lists 23 species that are dispersed solely by elephants, and an additional 21 species that are dispersed only by elephants and one or both apes. The clumping effect of seeds deposited in elephant dung can be very pronounced. Multi-species 'mini-gardens' of seedlings can frequently be identified as a result of elephant seed dispersal. Elephants have a long gut passage time and range extensively in and beyond the study zone, so may deposit seeds well away from the parent but in a relatively unsuitable habitat. They do provide an escape for seeds from monkey or ape waste for some species (e.g.*Uapaca*) by hoovering up intact dropped fruit, but are unlikely to remove large proportions of the fruit crop this way. Many fruit species that are primarily dispersed by elephants, and/or are important elephant foods, are large, dull-coloured, smell strongly and absciss on ripening.

The study site harbours 5 species of arboreal diurnal monkeys which feed on fruit. *Colobus satanas* is predominantly a seed and leaf eater, acting as predator on most seeds it handles (Harrison & Hladik 1986). *Cercocebus albigena* is also an important seed predator of many species, including favoured ape foods (e.g *Pycnanthus angolensis*, Myristicaceae; *Dialium*), but scatter-disperses others by cheek-pouching behaviour (e.g. *Cola*) (Ham 1994). Very small seeds are likely to be passed out in dung. The three species of guenon, *Cercopithecus pogonias, C. nictitans* and *C. cephus* are all seed droppers, scatter-dispersers or predators of varying degees. All these primates often remove fruit or seeds before maturity, whereas the apes tend to feed only on ripe fruit. Considerable numbers of seeds are dropped under the parent tree by feeding monkeys as they process the fruit prior to ingestion. Although they have much smaller body sizes than apes, the larger group size of monkeys can result in considerable aggregate seed removal from a fruit crop. Mandrills (*Mandrillus sphinx*) pass through the study area on occasion, usually in large bands (>250 individuals), eating immature fruit and predating, dropping and dispersing ripe seeds. By sheer numbers they can have a major effect on fruit crops in an area.

Duikers (*Cephalophus* spp), the small forest antelopes, are also partially frugivorous and may disperse some seeds away from the parent plant if they regurgitate intact seeds after feeding. They, like elephants, remove fallen or dropped fruit, and may be impotant dispersers for large seeds such as *Irvingia* spp (Irvingiaceae). The red forest hog (*Potamochoerus porcus*) is largely a seed cruncher, predating most seeds it encounters on the forest floor or in elephant dung piles. A fraction of those seeds ingested (especially the smaller species) may survive intact and germinate in dung (e.g. *Uapaca*), but *P. porcus* is not a major disperser of seeds.

Fruit bats are uncommon in the study zone and are rarely seen at any time. Their status as seed dispersers is thus unestablished but is unlikely to be of importance for most forest trees at Lopé, apart from one possible exception, *Barteria fistulosa* (Passifloraceae) (C. Tutin, pers. comm.). Civets and genets (Viverridae) also feed on the fruit of some species (e.g. *Uapaca; Vitex doniana,* Verbenaceae). A large proportion of the seeds swallowed by civets end up in middens in the savanna, often on rocks, but some can be deposited in more favourable sites.

Avian frugivores carry out seed dispersal for many species of plant at Lopé, especially species with small fruit and/or small seeds, but are likely to be important in terms of seed removal only in the more limited or specialised plant-animal interactions. The quantity of seeds removed by birds is often far less than by the larger-bodied mammalian frugivores, although this may not represent the quality of dispersal if the seeds are deposited by birds in more favourable sites. Gizzards can provide harsh physical and chemical conditions for seeds. Birds are more likely to scatter-disperse seeds, or drop them under the parent whilst feeding, than are the larger mammalian consumers.

The large blue plantain-eater (*Corythaeola cristata*) is distinctly frugivorous, and regurgitates or defaecates seeds under or away from the parent crown. The smaller green touraco (*Touraco* spp.) is largely confined to understorey, gallery and small-fruited species. A range of sizes of hornbills (Bucerotidae) act as gulpers and regurgitators of seeds, from tiny ones such as figs, to large Myristicaceous seeds. They are likely to be effective dispersers for some of these species, in particular the more 'specialist' fruits (e.g. *Guibourtia tessmannii,* Caesalpiniaceae). Fruit pigeons (*Columba* spp., *Treron australis*) are regularly fruit thieves of some larger-seeded species (e.g. *Uapaca*) but dispersers of small-seeded species. The long time (relative to regurgitation or defaecation rate) spent by some birds in a fruiting crown increases the likelihood of seed waste by regurgitation or defaecation under the crown (Pratt & Stiles 1985). Smaller birds are restricted as dispersers to small-seeded fruit by their gape width and processing limitations. The grey parrot (*Psitticus erithacus*) is an important seed predator of many species of trees in the forest.

2.7 A SHORT NOTE ON ELEPHANTS AND RAIN

The Lopé Reserve is one of the areas of Gabon that enjoys a high density of elephants. White (1993) found an overall mean density of 2 animals per km^2, but this figure was 3 per km^2 on the SEGC transect (see Table 2.2). Seasonal changes in elephant density are marked, and certain habitats see a dramatic concentration of elephants at particular times, usually related to fruit supply (White 1994a). During the 11 years of continuous fieldwork at SEGC, elephants have become habituated to human presence in the forest. This has certain drawbacks for field workers if the dense nature of the forest understorey is considered. It is possible to be 5m from an elephant and not actually be able to see it. If elephants have not detected an approaching human (and the human is unaware of the elephant), and remain silent or immobile, there exists a potential for stressful encounters, especially if there are females with young involved. Equally, elephants may detect a human and remain still and silent, which from the human's point of view is just as disturbing.

A scenario that is occurring more frequently is when elephants intimidate, charge or actually chase the human(s). There have been several serious chases by elephants at the study site, and our experiences with these highly intelligent animals show that it is not wise to generalise about their character or behaviour. For this study, in the 9 months of fieldwork in 1992, elephants disrupted on average 1 in 3 of all field days. During the 11 months of study in 1993, this figure was 1 in 4 days. By "disrupted", I mean that access to the site of work was not possible, a change of itinerary and route had to be made, work at a particular location was interrupted, or a long delay occurred as a result of waiting for elephants to move away.

Heavy rainfall, which was often preceded or accompanied by violent winds, prevented fieldwork. The noise of the rain in the canopy meant that animals could go undetected and sudden contacts could prove stressful for animal and observer alike, or even dangerous. The risk of falling branches in such conditions was also very real, so fieldwork was usually abandoned under these circumstances.

2.8 SUMMARY

1. Gorillas are likely to be effective seed dispersers for the species they eat, as they appear to satisfy most if not all the criteria for high quality dispersal for many tree species, on account of their morphology, treatment of seeds, ranging and nesting

behaviour. This is particularly the case for those species that are classed as "important" foods.

2. The main drawbacks to dispersal by gorillas are the clumping effect of seed deposition, and the damage inflicted to the crowns of fruiting trees.

3. The building of nests in light gaps, with most dung deposited at nest sites, may favour shade-intolerant species, but are likely to be favourable for the growth of seedlings of most species.

4. The alternatives to gorilla-mediated seed dispersal for some species are probably no better and often may be worse, with the possible exception of dispersal by chimpanzees. These other agents do not provide consistently satisfactory dispersal for a range of plant species in terms of visitation or seed treatment. The size of many seeds limits the chimpanzee's, and any smaller animal's, effectiveness as dispersal agent. Those seeds that are within both apes' swallowing capacity are likely to be dispersed in larger quantities by gorillas. Elephants are important for those seeds beyond the swallowing threshold of gorillas.

Listed in Table 2.3 are tree species whose seeds are removed in considerable quantity by gorillas. The table mirrors Table V in Tutin & Fernandez (1993). Their fruits are all "important" gorilla foods (see above), the seeds of which are swallowed by gorillas. Ten of the 15 important fruit foods listed by Tutin & Fernandez (1993) are represented in the table. The other ones are either herbs or shrubs, or have seeds that are too large for gorillas to swallow. Alternative consumers that are possible dispersers, and their treatment of ripe seeds, are also listed. The species that were chosen for study are shown in bold text. Species in brackets are those for which some alternative consumers are also potentially important as dispersers, in terms of the quantity removed. Monkeys are separated into two groups, 1) those which mostly predate seeds (*Colobus* and *Cercocebus*) and 2) those which generally do not (*Cercopithecus* spp).

Table 2.3 List of tree species for which gorillas are potentially important dispersers (see text for selection criteria). Species in bold are those chosen for study. Brackets indicate that some other consumers remove many seeds.

Species	Family	Other consumers	Treatment
Celtis tessmannii	Ulmaceae	chimpanzee	swallowed
		elephant	most destroyed
		monkey (1)	dropped or pouched/spat
		monkey (2)	predated
		?birds (hornbill)	dispersed
Cola lizae	Sterculiaceae	chimpanzee	dropped or wadged/spat
		monkey (1&2)	dropped or pouched/spat
Dacryodes normandii	Burseraceae	chimpanzee	swallowed
		elephant	'hoovered' & swallowed
(Dialium lopense)	Caesalpiniaceae	chimpanzee	most swallowed
		monkey (1)	dropped or pouched/spat
		monkey (2)	predated
		parrot	predated
Diospyros dendo	Ebenaceae	chimpanzee	swallowed
		elephant	'hoovered' & swallowed, minor drop
		monkey (1)	dropped or pouched/spat
		monkey (2)	predated
Diospyros polystemon	Ebenaceae	chimpanzee	swallowed
		elephant	'hoovered' & swallowed, minor drop
		monkey (1)	dropped or pouched/spat
		monkey (2)	predated
Gambeya africana	Sapotaceae	chimpanzee	swallowed
		elephant	hoovered & swallowed
Ganophyllum giganteum	Sapindaceae	chimpanzee	swallowed
		monkey (1&2)	dropped or pouched & spat
Santiria trimera	Burseraceae	chimpanzee	swallowed
(Uapaca guineensis)	Euphorbiaceae	chimpanzee	swallowed
		elephant	'hoovered' & swallowed
		monkey (1&2)	dropped or pouched & spat
		birds (plantain eater)	dropped or swallowed

1) those which mostly predate seeds (Colobus and Cercocebus)

2) those which mostly do not (Cercopithecus spp)

Chapter 3

THE FRUITING TREES:
predispersal characteristics and regeneration strategies.

3.1 INTRODUCTION

This chapter describes aspects of the ecology of the four tree species that were selected for study that are relevant to the dispersal of their seeds. The species chosen were *Ganophyllum giganteum* (Chev.) Haum. (Sapindaceae), *Cola lizae* Hallé (Sterculiaceae), *Dialium lopense* Breteler (Caesalpiniaceae) and *Uapaca guineensis* Müll. Arg. (Euphorbiaceae). Generally, they will hereafter be referred to by their generic name alone. They are all listed in Table 2.3 (see previous chapter) as species that are important fruit foods for gorillas. They were chosen for study for a range of reasons:

1. They are important gorilla foods which influence ranging and habitat use, and are eaten whenever available;
2. Their seeds are swallowed in considerable quantity by gorillas;
3. They represent a variety of fruiting patterns, fruit and seed types, and attract a range of consumers and seed treatments;
4. They have a range of regeneration strategies and seedling types;
5. Their fruiting seasons rarely overlap, placing relatively even demands on research effort;
6. They occur at densities which facilitate study;
7. It has been suggested that gorillas are the principal dispersers of *Cola* seeds (Tutin *et al* 1991b), and this warranted further investigation, especially as it is an endemic species with a limited geographical distribution and yet the commonest tree in the study area;
8. Two of the four species have only recently been described scientifically, adding to the interest of investigating their ecology. These are *Cola lizae* (Hallé 1987) and *Dialium lopense* (Breteler 1994).

3.2 DESCRIPTIONS OF THE TREES

Note: Information on all the four species is given in Table 3.1, and includes density in the study area, tree size, fruit and seed characters and seedling types. Additional data can be found in Appendix B.

		Ganophyllum				*Cola*				*Dialium*				*Uapaca*			
														forest			edge
Density* (trees/km2)	≥10cm dbh	80				7460				280				20			13600
	≥70cm dbh	20				8				2				10			
		mean	S.D.	n	range	mean	S.D.	n	range	mean	S.D.	n	range	mean	S.D.	n	range
Dimensions (means, fruiting focal trees)	ht(m)	25.8	3.9	13	17-32	23.9	3.4	25	16-30	27.2	2.7	10	22-31	20.3	3.4	27	14-28
	dbh(cm)	75.4	25.7	13	47-136	46.9	16.2	21	26-89	50.6	15.6	14	19-81	60.7	18	26	32-90
	lowest branch (m)	10.8	2.8	13	4-15	14.6	4.3	24	5-22	14.7	3.1	10	10-20	5.9	2.3	23	2-10
Season of ripe fruit		Jan (Feb)				(Feb)Mar-Apr(May)				May-June				Oct-Dec			
Normal flowering		annual				annual				biennial				annual			
Fruit characters																	
colour (ripe)		bright orange				crimson				dark brown (no change)				russet yellow			
distribution		on cymes at terminal twigs				groups of follicles on twigs				on terminal panicles				clustered on terminal twigs			
dehiscent/abscising?		no				no				no				no/when very ripe			
skin		thin, tough				thick, rubbery				brittle capsule				thin			
part discarded		skin				skin & fluid				capsule				(skins)			
No. seeds/fruit		1				5-8				1(2)				3			
		range	mean	n		range	mean	n		range	mean	n		range	mean	n	
Fruit dimensions	l (mm)	20-30**				50-80		24		ND				ND			
	w (mm)	10-15				45-75				ND				ND			
	wt (g)		1.73	18			92	7			0.84	59			7.6	67	
		mean	S.D.	n		mean	S.D.	n		mean	S.D.	n		mean	S.D.	n	
Seed dimensions	l (mm)	18.5	0.7	10		30.8	3.7	40		9.5	0.71	10		16.5	1.1	10	
	w (mm)	10.2	0.4	10		16.7	1.6	20		7.2	0.63	10		9.7	1.4	10	
	vol(cc)	0.8				4.75				ND				0.45			
	wt(g)	0.94		36		4.76*°				0.54 (immature)				0.5		32	#U13
										0.23 (ripe)				0.83		38	#U9
Seed weight (% of whole fruit wet weight)	processing	seed	skin	pulp	n	seed	skin	pulp	n	seed	skin	pulp	n	seed	skin	pulp	n
	human	53	31.2	15.6	16	31.2	43.4	11	7	25	49	26	58	24	41	35	10(U13)
	monkey	54.3	25.4	30.3	50	(fluid=13.6%)								24	33	43	12(U9)
Seedling type		epigeal, fleshy cotyledons				epigeal, fleshy cotyledons				epigeal, fleshy cotyledons				epigeal, leafy cotyledons			

Table 3.1 Summary of some ecological characteristics of the four study species. Data from focal trees; fruit samples from one or more trees, or from other sources where indicated. ND: not determined. (Sources: *Tutin *et al* 1994; ** Fouilloy & Hallé 1973; *°Tutin *et al* 1991a)

3.2.1 *Ganophyllum giganteum* (Chev.) Haum. (Sapindaceae)

The name stems from the Greek *Gano*, meaning 'shining', and *phyllum* ('leaf'), from the appearance of the tree's bright green canopy. Originally it was a monospecific genus, with one species (*G. falcatum*) from south-east Asia. *G. giganteum* was described from material named *G. africanum* collected in Cameroun and the Central African Republic (CAR) and from earlier misidentified material from Gabon. It is known also from Congo and Zaïre. There is apparently little difference between the two species (Fouilloy & Hallé 1973).

The previous name used for this species at SEGC was *Zanha golungensis* (e.g. Rogers *et al* 1990, Williamson *et al* 1990), due to misidentification. A canopy tree of moderate size (Plate 3.1a) occurring at low densities, *Ganophyllum* has a clumped distribution, which results in it being locally common. It is dioecious (individual trees produce either female or male flowers) and flowers open in November. There is a relatively short period of fruit set and a sharp, peaked fruiting season. The occurrence of ripe fruit over a period of 7 years is shown in Figure 3.1 for a sample of 6-10 trees. The techniques used to obtain the phenological data are fully described in Chapter 4. The 'theoretical maximum' would be when each tree in the sample scored the highest value for ripe fruit. Only ripe fruit is included because it is more obvious to the eye and thus more reliably assessed, and because it is the production of viable diaspores that reach the dispersable stage that is the main interest for this study. Ripe fruit are available for only a few weeks in January to February each year, although the amount varies considerably between years. The percent score may appear low; this is due to depletion of some of the crop once it is ripened but before the next (monthly) assessment, and also to the fact that it is rare that every tree in the sample produces a 'maximum' crop in any one year.

Considerable variation in fruit production is evident between individuals as well as from year to year, as shown by the individual production of fruit on individual trees shown in Figure 3.2. Some individuals appear to be consistently more fecund than others (e.g. trees #6 and #11), although there is an overriding effect of particular years, either favourable for fruit production by most trees in the sample (e.g. 1987, 1990), or not at all (e.g. 1988 and 1991). The crop failure in 1988 might be attributed to climatic events, particularly the absence of a 'critical minimum temperature' in 1987 to trigger flowering (Tutin & Fernandez 1993a, Chapter 2). During fruit set, *Ganophyllum* trees usually suffer severe defoliation by a species of caterpillar as yet unidentified, which makes the ripe fruit more visible (Plate 3.2b). A new complement of leaves grows after fruiting.

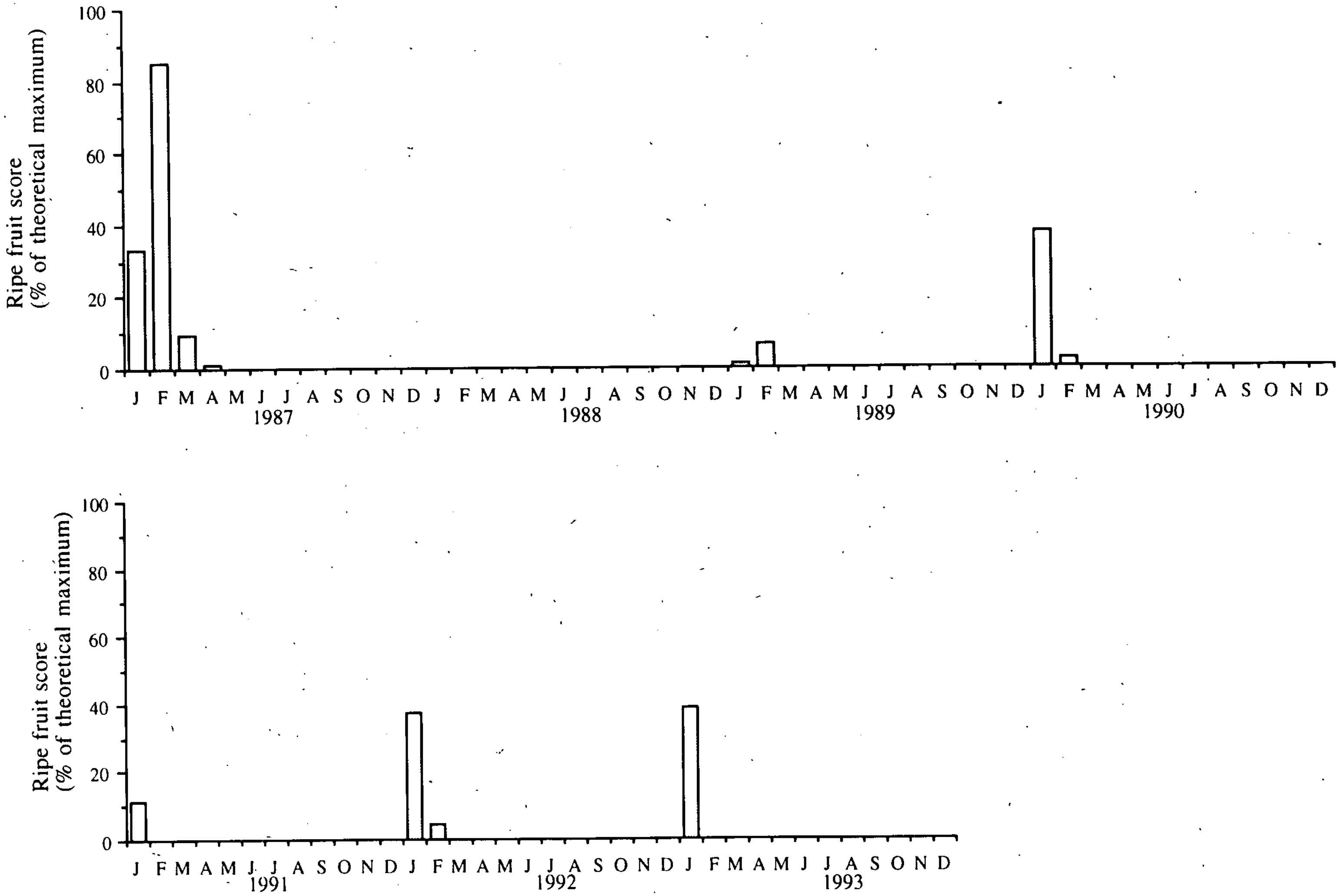
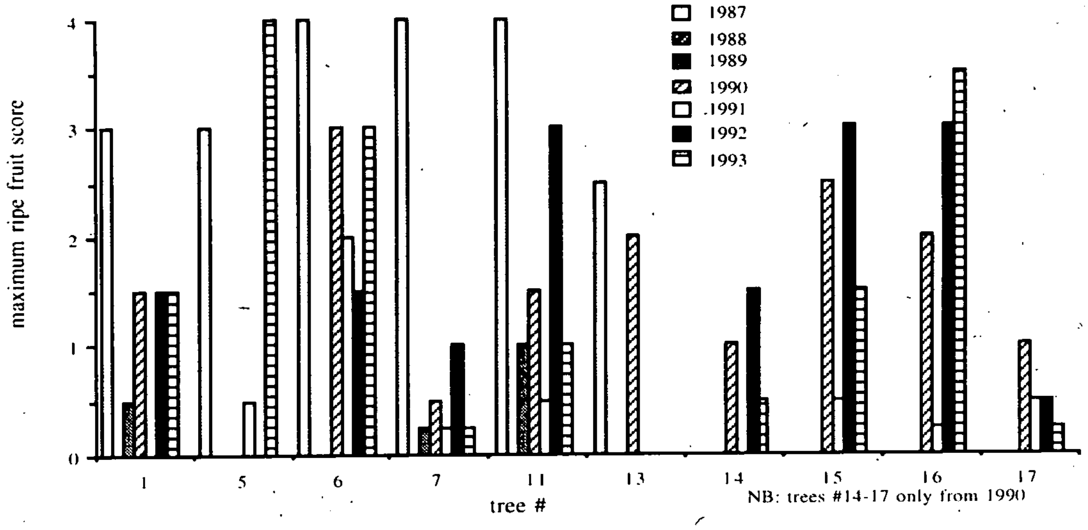


Figure 3.1 Production of ripe *Ganophyllum* fruit on a sample of 6-10 trees over 7 years

Figure 3.2 Ripe fruit production by individual *Ganophyllum* trees, 1987-1993

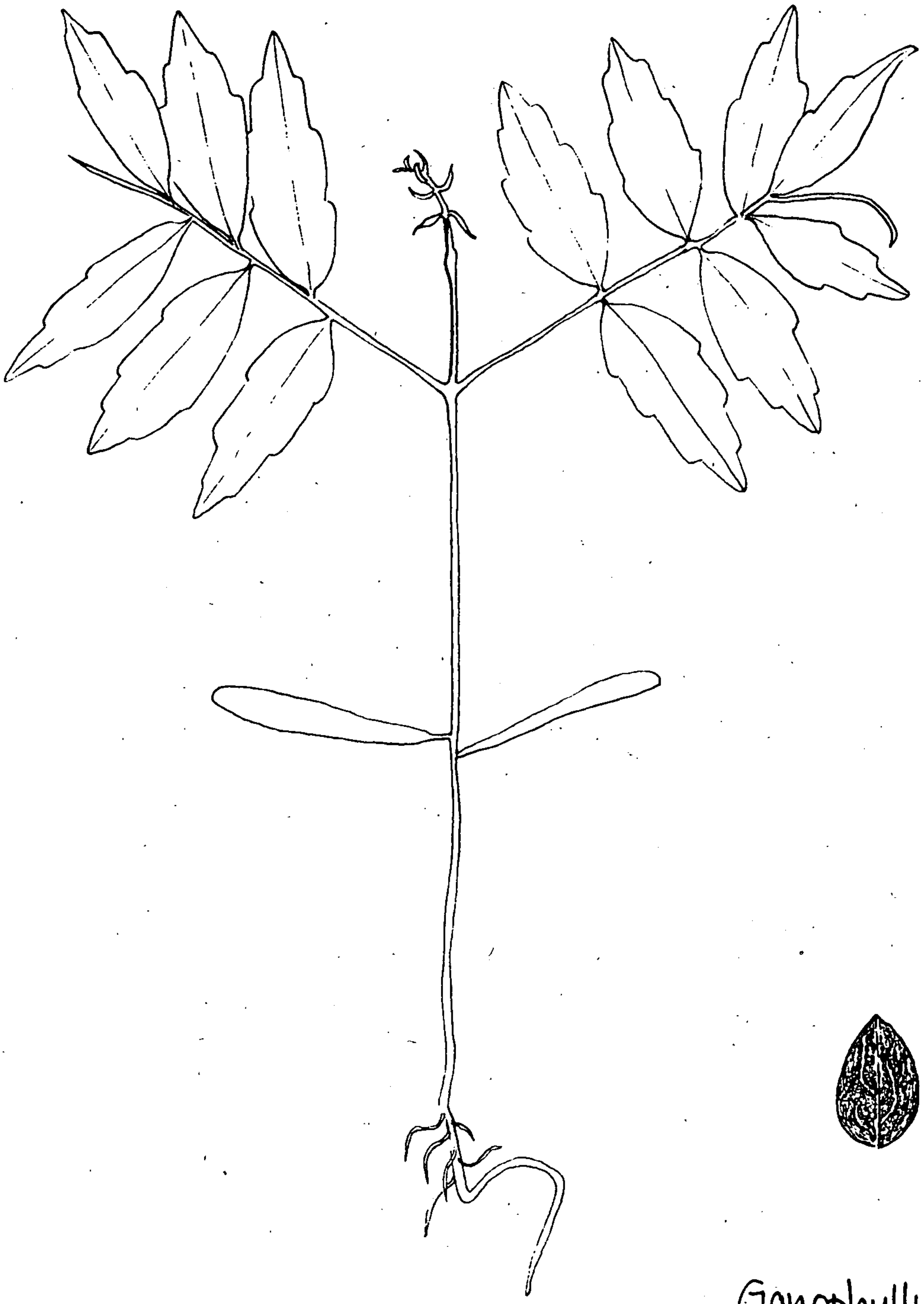


NB: trees #14-17 only from 1990

Fruits are single-seeded drupes typically measuring 20-30mm long and 10-15mm wide (Table 3.1, Plate 3.2c). The seed, which has a hard coat, is firmly embedded in a sweet, succulent mesocarp, high in water-soluble carbohydrates (Rogers *et al* 1990), and with a thin, tough outer skin. Bright orange when ripe, fruits are borne in ramified infructescenses (cymes) at the terminal ends of branches, with 7-19 fruit on each cyme. Seeds represent about 53% of the wet weight of fruit, but no data are available on their chemical composition, so far as I am aware. They measure typically 18.5mm by 10mm, weigh nearly 1g and have a volume of 0.8cc. Seeds usually germinate promptly (in 1-3 weeks), but a small proportion display a delay in germination of about 8 weeks. Seedlings are epigeal, with fleshy cotyledons unprotected by the seed coat (phanerocotylar); that is, "Type 2", *sensu* Miquel (1987), Hladik and Miquel (1990) (Plate 3.2d-e).

Seeds are eaten both when immature and ripe by arboreal squirrels (e.g. *Heliosciurus* spp), and once fallen or deposited, are food for other rodents. Ripe fruit is eaten by the Cercopithecine monkeys *Cercopithecus nictitans, C. cephus, C. pogonias* and *Cercocebus albigena.* They rarely swallow seeds, and more usually process fruit in the tree, dropping seeds beneath the parent. Only for *C. albigena* did we obtain evidence that they occasionally swallowed seeds (pers. obs.). Some scatter dispersal by monkeys occurs, as they put fruit in their cheekpouches and transport them up to 80m from the

Plate 3.1 *Ganophyllum*: a) trunk, showing reddish shaggy bark; b) canopy with ripe fruit; c) ripe fruit and leaflet; d) clump of seedlings at *c.* 12 weeks; e) (overleaf) seed, and seedling at *c.* 12 weeks (full size)



Ganophyllum giganteum
SAPINDACEAE

parent to process them in another tree or fruiting conspecific (pers. obs.). Seeds treated like this are likely to end up beneath the canopy of whatever adult tree is used when processing the fruit. Cheekpouching is particularly an activity of *C. albigena*, the subject of a study in the same area (Ham, 1994).

Gorillas feed extensively on *Ganophyllum* fruit, often humming as they do so. This kind of "non-syllabic close call" in chorus has been associated with feeding bouts where gorillas are in prolonged close proximity as a means to maintain "cohesion and coordination" (Harcourt *et al* 1993). There is no reason why it might not reflect the degree to which gorillas favour the fruit and the excitement this generates. If necessary they break terminal branches to gain access to the fruit, which are then plucked off with their lips or fingers. The only seeds they drop are those in intact fruit that are not eaten. Seeds are usually swallowed and voided undamaged. Chimpanzees also eat the fruit and swallow seeds intact. We had no observation of chimpanzees feeding on *Ganophyllum* in the two seasons of the study, and seeds were found in chimpanzee dung only during the fruiting season in 1993. This would indicate that chimpanzees do not favour *Ganophyllum* fruit to such an extent as gorillas. Elephants do not eat the fruit that drops beneath the canopies. Hornbills (Bucerotidae) have occasionally been seen feeding on fruit (C. Tutin, pers. comm.), although none were seen to do so during this study. Fruits are not easily detached from the cyme, even once they are ripe.

All consumers discard the skins, which have to be split open and detached from the rest of the fruit. Skins are said to 'burn' human mouths, which might explain their rejection by consumers, and the fact that elephants avoid them (C. Tutin, pers. comm.). The skins probably account for the high levels of secondary compounds found by Rogers *et al* (1990), since flesh and skins were processed together for chemical analysis. Thus it would appear that gorillas and monkeys (all species, but particularly *C. albigena* with associated groups of *C. pogonias*) are the only reliable visitors to *Ganophyllum* trees. Both groups act as dispersers but only gorillas swallow seeds and transport them any great distance from parent trees. Chimpanzees disperse seeds in their dung but are less reliable visitors, possibly influenced by alternative food sources.

3.2.2 *Cola lizae* Hallé (Sterculiaceae)

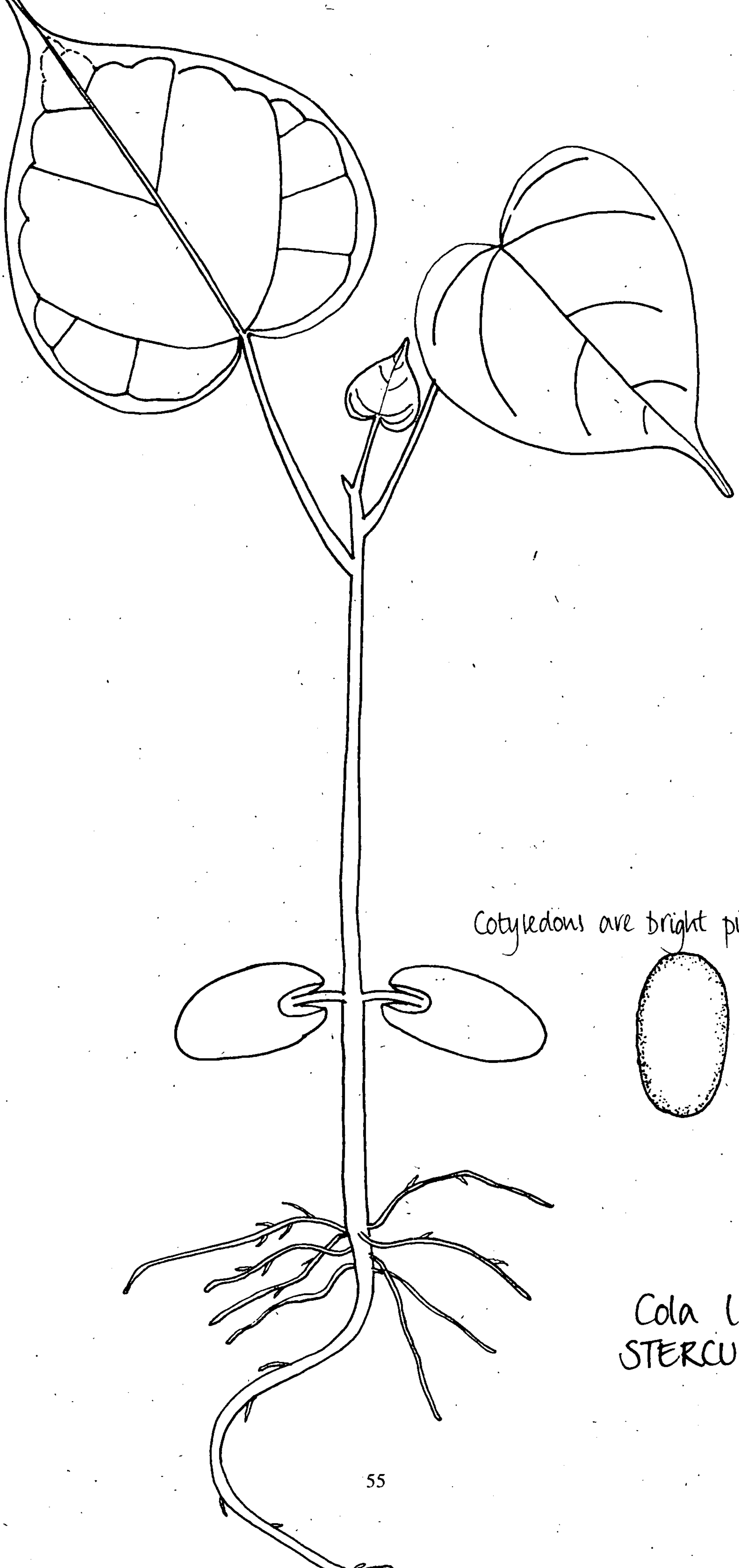
Cola is a large African genus with about 140 species and at least 34 occur in Gabon (Hallé 1961). *Cola lizae*'s closest congener is *C. lateritia* K. Schum., known since 1899, but it is not yet known if these two species occur together. Two aspects that make *C. lizae* 'remarkable' according to Hallé (1987) are the size of its leaves (the largest of the genus) and its abundance at the Lopé study site, where it is gregarious. The other species recorded from the Lopé are *C. mahoundensis*, which occurs in closed canopy forest rather than Marantaceae forest (Tutin *et al* 1994), and *Cola* SEGC #332, which is very rare: only a few individuals are known in the study area.

Plate 3.2 *Cola*: a) mature tree; b) intact ripe follicle; c) clump of seedlings at *c.* 12 weeks; d) (overleaf) seed, and seedling at *c.* 12 weeks (full size)

a)

c)

b)



Cola lizae
STERCULIACEAE

Cola lizae is the commonest tree in the study site, both in terms of density and basal area (Williamson 1988, White 1992, Tutin *et al* 1994, and see Table 3.1). It is endemic to Gabon, where it has a limited geographical range (Hallé 1987). Leaves are simple and huge (up to 125cm by 100cm; Tutin *et al* 1991b). The local name given to it by the Saké is "Poukoupoukoué", referring to the similarity between the shape of the leaves and a large freshwater ray found in the Ogooué river (Hallé 1987). *Cola* trees are of moderate height (the mean height of focal trees was 24m) and most have diameters less than 70cm at breast height (Plate 3.2a). From transect data (see Chapter 4), the smallest trees bearing fruit were 18.5cm (n=1) and 20cm dbh (n=2), so it was assumed that only trees larger than 15cm dbh can produce fruit. The proportion of trees ≥15cm dbh that bore fruit in 1992 varied from 12-46% among 6 linear transects (mean=24.3±13.5%). Trees are monoecious, bearing separate male and female flowers in August-September, which are eaten by *Colobus satanas* monkeys.

Ripe fruit generally occurs from February until the end of April (Figure 3.4). There is a reliable peak of fruit production, usually in March, but annual and individual variation is evident. Figure 3.5 shows the ripe fruit scores for individual trees over a 7-year period. In spite of general yearly effects, some individuals tend to produce more fruit, and/or more frequently, than others. The absence of a ripe fruit score for some trees in some years (e.g. trees #2 and #11) does not necessarily mean that no fruit was produced, but any fruit that was produced did not last until it ripened. Again, the fruit crop failure in 1988 might have been a result of climatic conditions affecting flowering in 1987. *Cola* was disrupted by the unusual climatic events in early 1992 that triggered flowering after the fruit crop had just finished, and there was some fruit set from this event. Perhaps as a result of this, flowering was poor at the usual time (Sept-Oct), so there was very little fruit in the 1993 season.

A single fruit consists of four follicles. Each follicle is bright crimson when ripe, remains closed and is firmly attached to the branch by means of a stout stalk (Plate 3.2b). The seeds (typically 5-8 per follicle) are a pair of unprotected cotyledons with a thin integument, covered by a sugary mesocarp with a thin pale "skin". They are bathed in a fluid within the thick, rubbery walls of the pod, both of which are discarded by consumers. Ripe *Cola* mesocarp had one of the highest values for water-soluble carbohydrates (58% dry matter) of 47 fruit species analysed by Rogers *et al* (1990).

The mean length of a sample of 40 seeds collected under one tree was 30.8mm (SD=3.7mm, range 26-38mm). The sizes of seeds in samples from other trees and from gorilla dung fell within that range. The individual volume of seeds, at 4.75cc, is to all intents and purposes too large to be swallowed by chimpanzees, although *Cola* seeds have been found in chimpanzee dung on rare occasions. Chimpanzees wadge the seeds to obtain the mesocarp, and spit them out singly or in clumps. They are one of the largest seeds to be swallowed in quantity by gorillas (Tutin & Fernandez 1994).

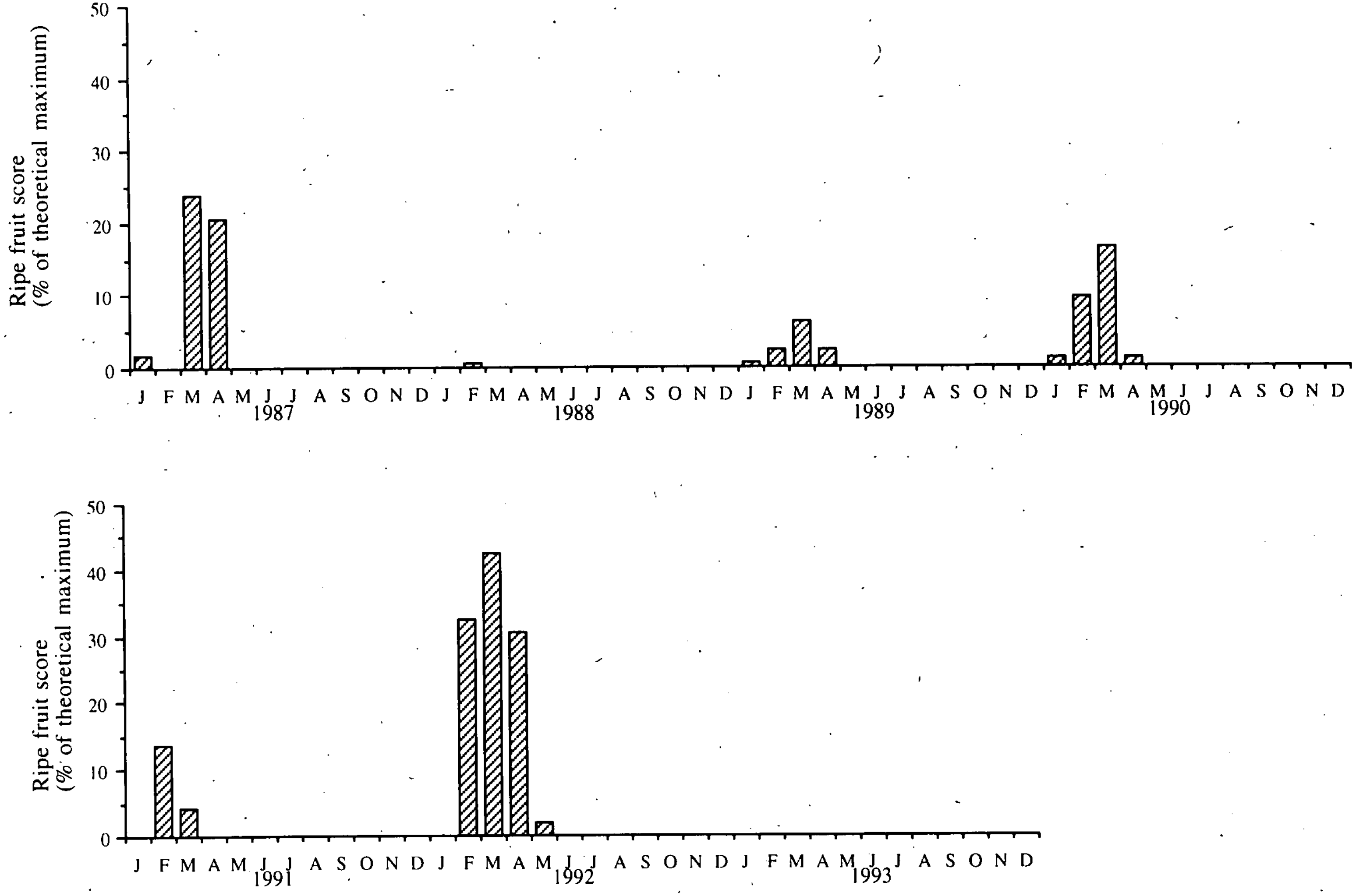
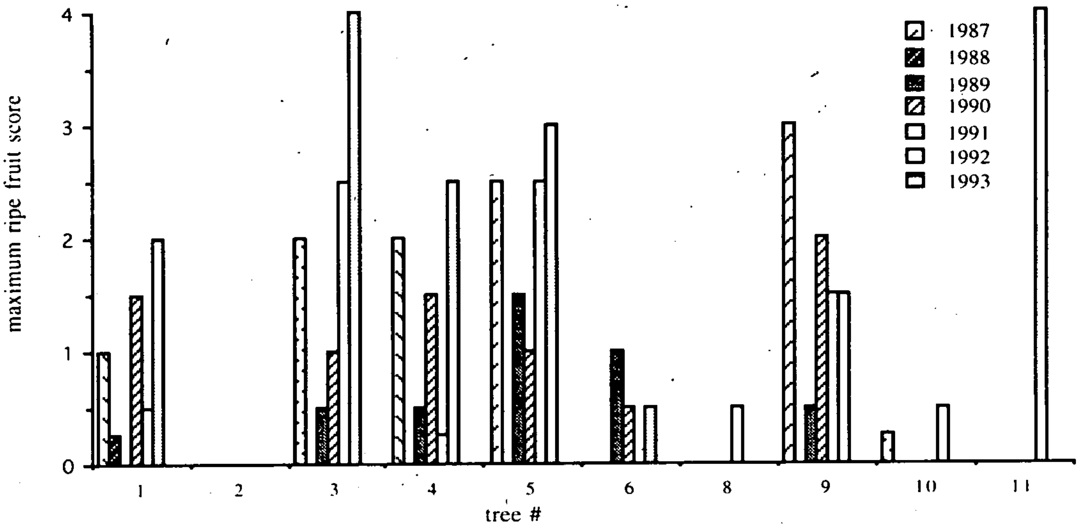


Figure 3.3 Production of ripe *Cola* fruit on a sample of 10 trees over 7 years

Figure 3.4 Ripe fruit production by individual *Cola* trees, 1987-1993



Elephants do not eat *Cola* fruit, possibly because of the thick pod and unpleasant fluid within the fruit. No birds or bats are known to feed *Cola* either. Monkeys other than *Colobus* scatter-disperse the seeds by transporting some in their cheekpouches for later processing, but most are dropped under the parent canopy (pers. obs.). They also eat the fruit immature, when the mesocarp contains appreciable amounts of condensed tannins, but is nonetheless quite sugary (Rogers *et al* 1990). Insects also eat the fruit and seeds. Fruits found under the canopy were often infested by an unidentified weevil (Curculionidae) which damaged the seeds. These intact fruits were marked with a borehole, suggesting that eggs are laid inside the young fruit on the tree, and the larvae develop inside the fruit. There is little apparent vertebrate seed predation, perhaps due to chemical protection. *Cola nitida* seeds are an important commercial crop in West Africa because of the chemical compounds found in them, and it would not be surprising if *C. lizae* seeds also contained similar compounds.

Seeds germinate rapidly, usually within a few days, and even from fallen and rotting fruit. Seedlings are epigeal with fleshy cotyledons (Plate 3.2c-d), the "Type 2" described by Miquel (1987). Interestingly, she (and see Hladik & Miquel 1990) described other species of *Cola* (*C. acuminata* and *C. rostrata*) in north-east Gabon as having hypogeal seedlings, whereby the cotyledons remain at ground level. The dispersers of these species were undetermined.

3.2.3 *Dialium lopense* Breteler (Caesalpiniaceae)

Although a pantropical genus, most *Dialium* species (about 36 of them) are to be found in Africa. The Neotropics have one species and Asia five. The richest zone for species is rain forest; 12 species are known from Gabon and Cameroun, and others have been recorded from Congo and CAR. *Dialium lopense* is another plant species from the Lopé that has only recently been described scientifically (Breteler 1994). The other *Dialium* species recorded from the Lopé (*D. dinklagei, D. pachyphyllum, D. soyauxii*) all occur predominantly in closed canopy forest (Tutin *et al* 1994). *Dialium lopense* is a locally common species, growing close to or at the forest-savanna edge and in gallery forest, and to a lesser extent within the Marantaceae forest interior. A sample of 19 fruiting trees had diameters of 19-81cm at breast height, and were typically 25-30m high (Table 3.1).

Flowering of this dioecious species occurs usually every year, in December, but individuals flower at best every other year. Often it is only a very small proportion of trees that flower in 'interim' years. Figure 3.5 shows that ripe fruit is usually available during May and June, and shows the general biennial pattern of fruit production. Some trees in the sample did produce fruit in the 'poor' years, but it was all removed immature (see below). Disruption of flowering in some individuals by climatic events, as described for *Cola*, has been recorded (Tutin & Fernandez 1993b). In 1992, most trees flowered atypically in early April, but very few bore fruit. Most had flowered in 1991 (normally) as well, so it is possible that only a few were physiologically capable of flowering in October-November 1992, since an individual flowers normally every 2 years. Consequently there was very poor fruit production in 1993, the second season in this study, with nearly all the trees in the main study site failing to flower or set fruit. However, a small number of trees several kilometres to the west did bear fruit, but they were all eaten immature. The production of fruit by individual trees in a shifting sample of ten trees (due to mortality of focal trees) is shown in Figure 3.6.

Although no quantitative data are available, it appears that a majority of the adult trees in the study area flower, and they bear fruit at the outer and upper edges of the spreading crown (Plate 3.3a). Fruit are small capsules, typically 25mm by 19mm and weighing about one gram. Dark brown and with a velvety texture, they are distributed on terminal panicles (Plate 3.3b). The capsule is brittle, containing one, rarely two, small seeds in a soft, moist and powdery mesocarp tasting of sherbet, the least sugary of the four species considered here (Rogers *et al* 1990). Externally, fruit do not change colour as they ripen, but the capsule becomes fatter and the mesocarp turns from white to pale orange. The fruit remains closed and firmly attached to the panicle.

Plate 3.3 *Dialium*: a) mature tree; b) empty and intact capsules after gorilla feeding (note broken branch); c) seedling at *c.* 12 weeks; d) (overleaf) seed, and seedling at *c.* 12 weeks (full size)

a)

b)

c)

Dialium lopense
CAESALPINIACEAE

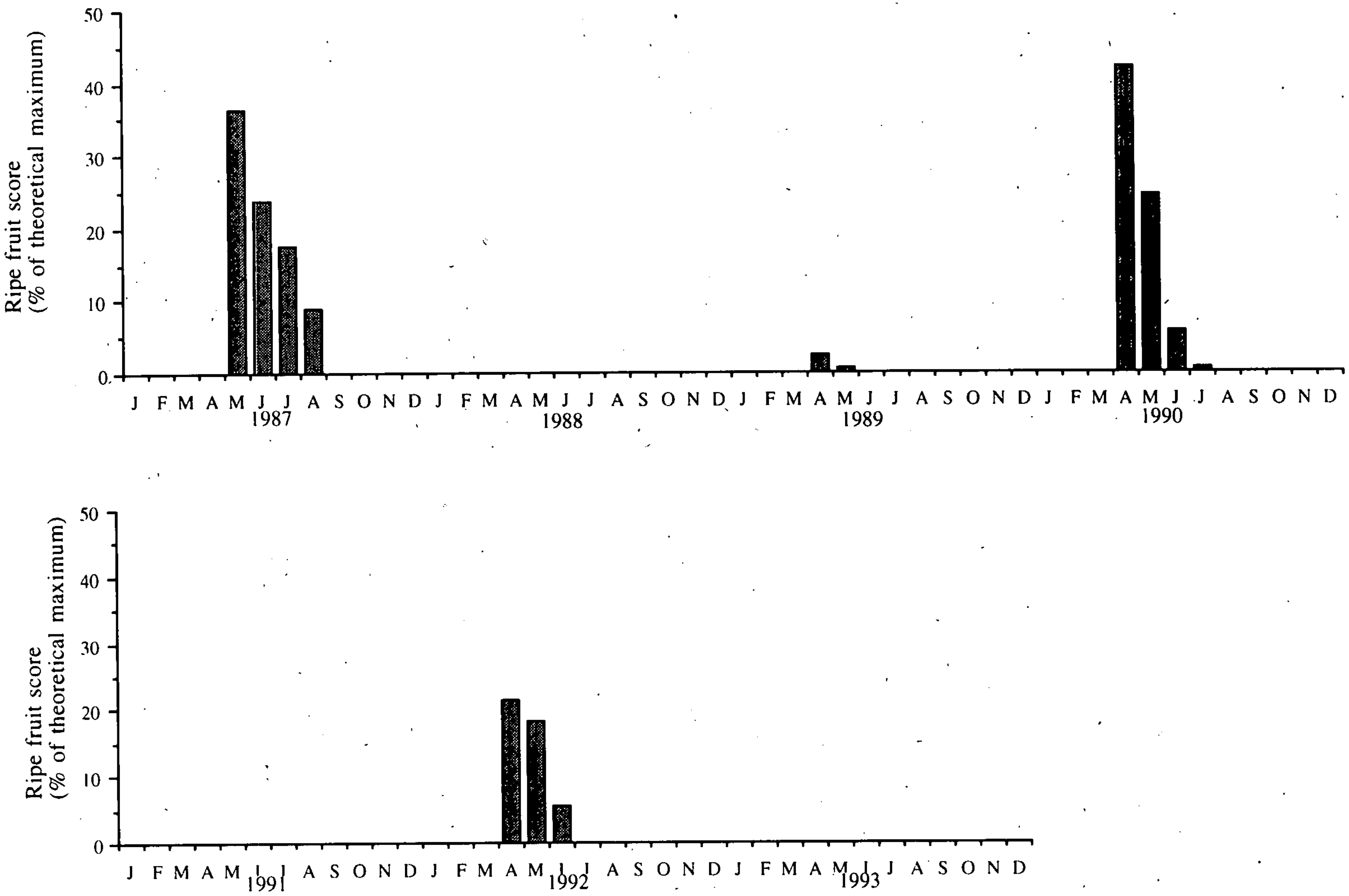
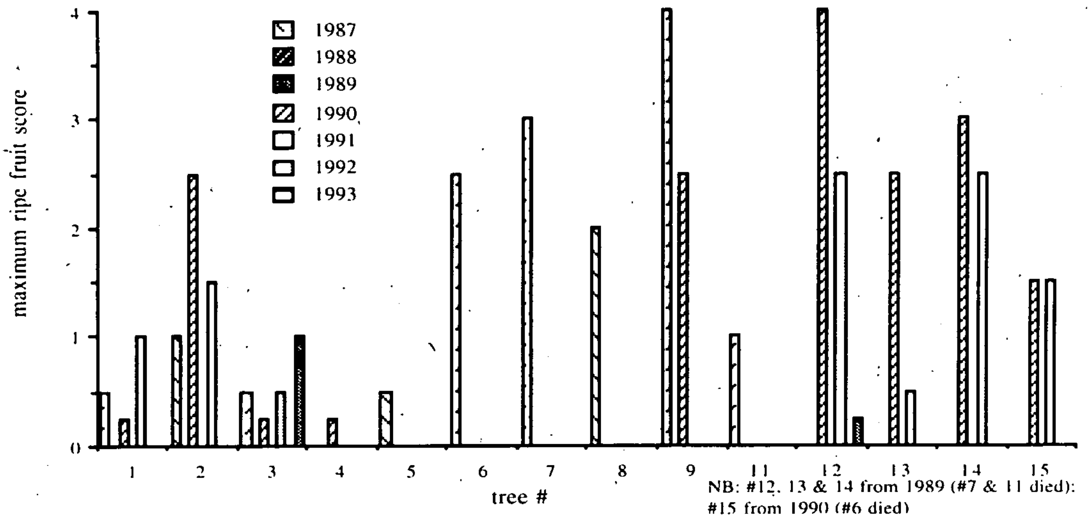


Figure 3.5 Production of ripe *Dialium* fruit on a shifting sample of 10 trees over 7 years (note different scale of y-axis)

Figure 3.6 Ripe fruit production by individual *Dialium* trees, 1987-1993



Immature seeds are soft and swollen, and some fail to dehydrate as they ripen and remain in the ‘imbibed’ state. These weigh about 0.54g and germinate immediately on deposition, but are vulnerable to fungal pathogens. Most ripe seeds, however, are extremely hard and typically weigh 0.23g. The mean size of 10 seeds was 9.5mm by 7mm (Table 3.1). Seeds have very high levels of crude protein (18% dry matter), second only to fruit of *Milicia excelsa* (Moraceae) in the study by Rogers *et al* (1990). All hard seeds remain dormant or quiescent during the dry season (June-September), then display a staggered germination. Ungerminated seeds may be incidentally buried by dung beetles, or simply be incorporated into the leaf litter. Seedlings are epigeal, phanerocotylar, with fleshy cotyledons (“Type 2” in Miquel 1987) (Plate 3.3c-d).

Gorillas and chimpanzees are very fond of the mesocarp, and swallow the seeds intact. Both apes also predate some seeds by splitting them to eat the cotyledons, often at the end of a feeding bout. Immature fruit may be eaten in February-March if there is little alternative fruit available. A considerable amount of damage is often inflicted by feeding gorillas on *Dialium* canopies as they break branches to access the fruit (Chapter 2.6). Gorillas indulge in considerable coprophagy when *Dialium* seeds occur in their dung. This may be to re-ingest soft seeds, or to eat hard seeds that might have been softened by gut passage, to obtain the high levels of protein in them. Three monkey species, *Cercocebus albigena, Colobus satanas* and *Mandrillus shpinx*, discard the mesocarp and split the seeds to eat the proteinaceous cotyledons, thus acting as seed predators. The three guenon species (*Cercopithecus nictitans, C. cephus* and *C. pogonias*) eat the mesocarp and drop or swallow the small seeds. Parrots are important seed predators (R. Parnell, pers. comm.) of *Dialium*. Seeds were not observed to be dispersed by animals other than the great apes during this study, although guenons do (C. Tutin, pers. comm.). White (1992) recorded intact seeds in less than 1% of elephant dung piles in one month of the year during his study. These may have been incidentally swallowed when elephants fed on foliage dropped by apes.

3.2.4 *Uapaca guineensis* Müll. Arg. (Euphorbiaceae)

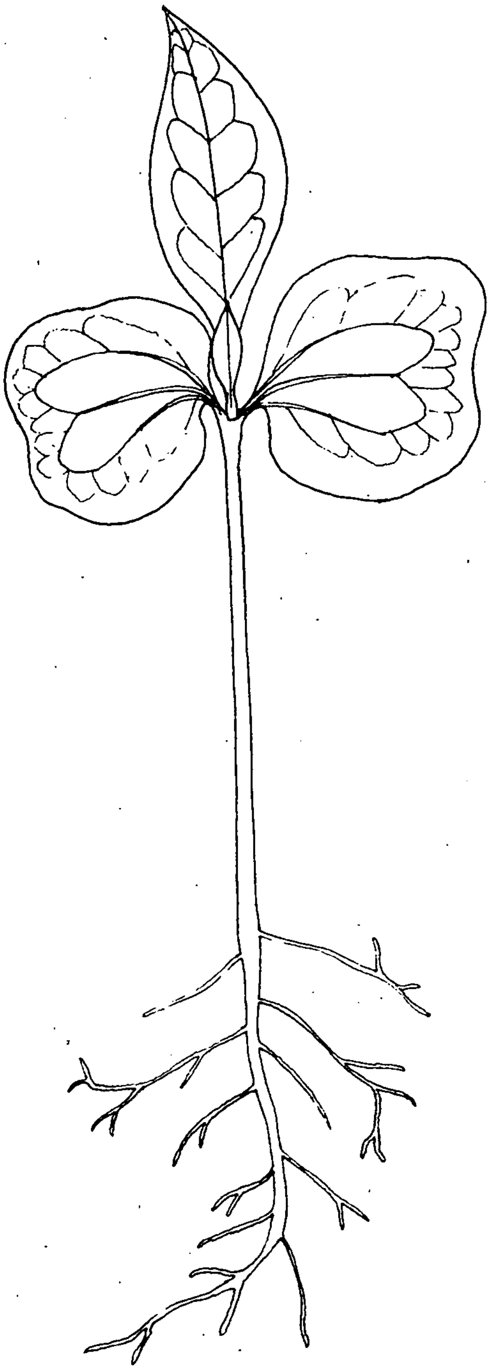
Other *Uapaca* species that have been recorded at Lopé are *U. heudelottii, U. paludosa, U.* aff. *togoensis* and *U. vanhouteii.* Only the last species overlaps with *U. guineensis* to any extent in Marantaceae forest in the study area.

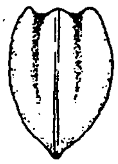
Although forest transects indicate a low density for this species (Tutin *et al* 1994, and Table 3.1), *Uapaca* is in fact common in the study area because it occurs in high densities along the forest-savanna edges and in gallery forest (Ham 1994), habitats to which it is largely confined, although it does occur in the forest interior close to water courses. If data from linear transects along the forest edges (5m wide) are used (see Chapter 4), then a typical value for *Uapaca* densities in this forest/savanna boundary habitat is 13600 trees/km^2. Stem diameters have to be measured above the abundant stilt root systems of most trees. They are not particularly tall trees, and bear their short-stalked fruit crowded in tight clusters at the terminal ends of branches (Plate 3.4a).

Uapaca is dioecious. After flowering in January-March, ripe fruit is usually available from October to December, but some trees in 1992 and 1993 displayed an abnormal flowering pattern, and hence ripe fruit may be available for a large proportion of the year. Fruit set normally occurs before the dry season but fruit remain immature until the coming of the rains in late September-October. Figure 3.7 shows the annual crop of ripe fruit for a sample of trees from 1987 to 1993. Individual crops of ripe fruit for this period are shown in Figure 3.8. Inter-annual and inter-individual variation in ripe fruit crops is evident. The proportion of trees with fruit each year of this study was in the order of 30-50%, which represents a high proportion of female trees if there are similar numbers of males and females. Fruits undergo a slight colour change as they ripen, from green to a dull yellow. They also soften considerably, and teeth marks on discarded immature fruit indicate that texture may be a criterion used by primates in the selection of fruit. Fruit fall from the tree easily once they are fully ripe.

Each ripe fruit contains three, rarely four, seeds that are encased in a succulent sweet pulp (Plate 3.4b), although the flesh also contains some secondary compounds, particularly condensed tannins. Immature fruit are particularly high in these secondary compounds (Rogers *et al* 1990).

Plate 3.4 *Uapaca*: a) mature tree showing branches with fruit, broken by gorillas; b) immature fruit on twig (ripe fruit removed); c) clump of seedlings at *c.* 44 weeks; d) (overleaf) seed, and seedling at *c.* 12 weeks (full size)





Uapaca guineensis
EUPHORBIACEAE

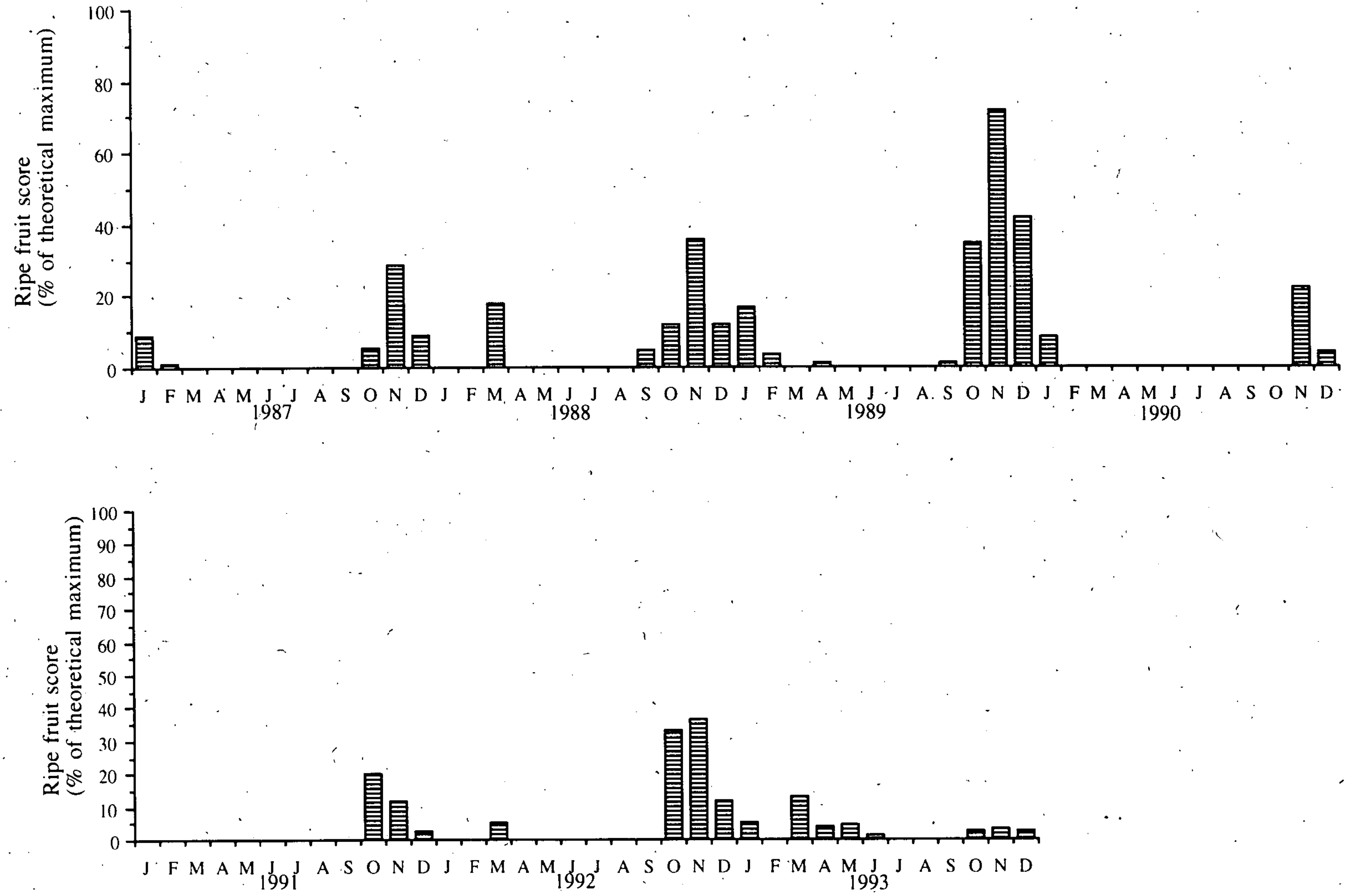
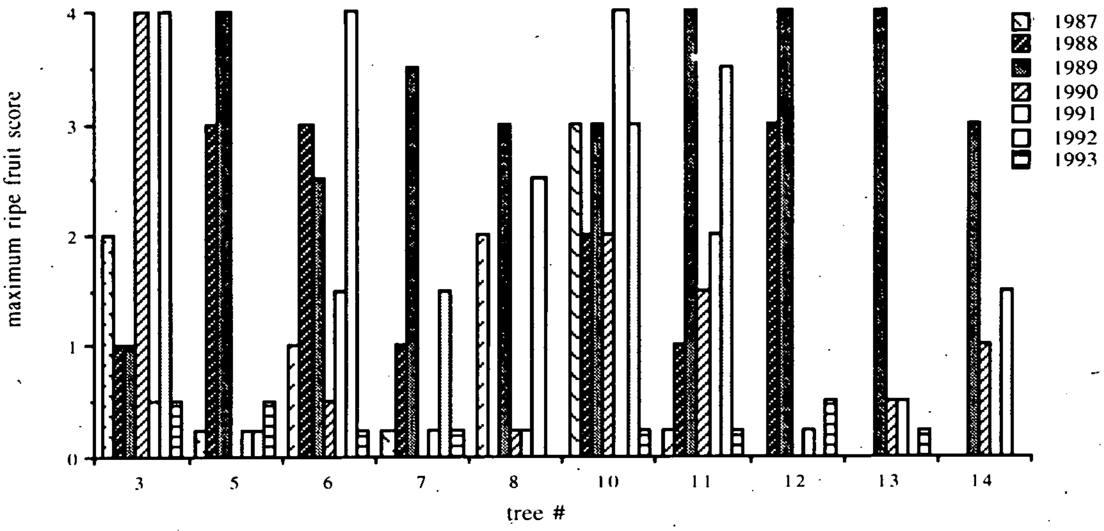


Figure 3.10 Production of ripe *Uapaca* fruit on a sample of 10 trees over 7 years

Figure 3.8 Ripe fruit production by individual *Uapaca* trees, 1987-1993



Fruit sizes vary between trees, but the almost spherical whole ripe fruits measure about 3cm across and weigh 6-11g (n=67, Table 3.1). Skins are thin and not tough when ripe but are generally discarded by primate consumers, possibly because they contain more secondary compounds, although gorillas swallow some skins. Seeds are protected by a hard, ridged coat and they do not seem to suffer from high levels of predation.

During faecal analysis, some seeds were found to float in water and were empty when opened: there were no embryos within the tough case, such empty inviable seeds accounting for a third of all seeds. This proportion was the same for a sample of seeds gathered under 7 different trees and for seeds from 50 gorilla dung samples. The furrowed seeds weigh 0.5-0.8g (n=211 from 4 trees), accounting for 24% of the wet weight of whole fruit. They measure typically 14-23mm by 10-15mm, with an individual volume of 0.45cc (Tutin, unpub. data). Germination is rapid but staggered: most seeds germinate within three weeks but some germinate up to 8 weeks after deposition. Seedlings (Plate 3.4c-d) have leafy cotyledons and are epigeal (i.e. 'Type 1', *sensu* Miquel 1987), apparently a characteristic of more shade-intolerant species (Fenner 1985).

Uapaca fruits are eaten by a wide range of arboreal and terrestrial animals, including brown-cheeked hornbills (*Bycanistes cylindricus*), touracos (*Touraco* spp, *Corytheola cristata*), fruit pigeons (*Treron australis* in particular), civets (e.g. *Nandinia binotata, Viverra civetta*), monkeys (Cercopithecidae, including mandrills) except black colobus (*Colobus satanas*), gorillas, chimpanzees, elephants, forest hogs (*Potamochoerus porcus*) and duikers (*Cephalophus* spp). Apes and elephants disperse large quantities of seeds in their dung, and most arboreal consumers generally drop seeds under the crown. Some seeds are dispersed in dung by civets, through cheekpouching behaviour by monkeys or regurgitation by touracos and probably duikers. Fruit pigeons peck at the flesh and do not remove seeds (pers. obs.). Forest hogs predate the seeds but a small proportion may escape crushing and germinate in dung (pers. obs.). Feeding gorillas can cause severe damage to *Uapaca* trees, as they break even large branches to facilitate feeding. Some of the broken branches may be used to construct feeding nests during a feeding bout. There have been cases when gorillas have broken branches which carry mostly immature fruit but do not feed, returning some days later to eat the fruit which has been 'force-ripened' by the breakage (C. Tutin, pers. comm., and pers. obs.).

3.3 SUMMARY

These four species comprise an interesting group for studying plant-animal interactions in tropical forest. Distributions and densities are markedly different, with *Cola* densities impressive (7460 trees ≥10cm dbh km^{-2}), *Ganophyllum* and *Dialium* relatively rare, and *Uapaca* largely restricted to a particular habitat in which it is very abundant. The breeding systems vary between the four species, as do their fruiting patterns. *Ganophyllum* has a short, sharply-peaked period of ripe fruit availability, with a 'ripen all at once' system, and most trees fruit most years. *Uapaca* lies at the other end of the range, with sequential ripening over several months. *Cola* too has an extended fruiting period with sequential ripening, and a relatively small proportion of trees bear fruit each year. These fruiting strategies are possibly related to the species' distributions and abundance and the types of legitimate consumer they attract (see Chapter 7). Fruits of *Cola* are mechanically difficult to process, providing protection for the seeds which are themselves chemically resistant to predation. *Ganophyllum* relies on a hard case to protect the seed, as does *Uapaca*. *Dialium* seeds are very hard as well, but suffer predispersal predation by primates that are able to split the two cotyledons apart using relatively powerful jaws, something humans at SEGC have failed to do.

Although they show a wide range of fruit types and especially seed sizes, from the small *Dialium* to the large *Cola* seed, all four species are major foods for gorillas. The degree to which they depend on gorillas for seed removal also varies. *Uapaca* seems to have a very generalist strategy with a wide coterie of consumers, whereas *Cola* might be regarded as more specialist, perhaps with an "ape syndrome", as its fruit has features from both 'bird-monkey' and 'ruminant-rodent' syndromes (Gautier-Hion 1990). Gorillas are thought to remove a considerable porportion of each of these species' seed crop, thus indicating at least a potentially important role as seed dispersers. The species' germination strategies are different, and the seed and seedling types differ, which might influence how they respond to gorilla-mediated dispersion and deposition patterns. Taken together, the abundance, fruiting pattern, fruit type, seed and seedling type, germination strategy and 'target consumer' make up what can be regarded as a dispersal strategy for each species. The task was to pin down whether these species do in fact rely on gorillas to any extent for seed dispersal of a higher quality than that provided by other consumers.

Chapter 4

STUDIES OF SEED DISPERSAL I: SEED REMOVAL AND DEPOSITION

4.1 INTRODUCTION

Two of the components that are thought to contribute to high quality dispersal of seeds from the parent tree are reliable visitation and the removal of large numbers, or a large proportion, of ripe seeds by consumers (see Chapter 1.4.2). These aspects may operate successfully in evolutionary time, or over a long period of time in an ecological framework, but may not be evident in the short term. Equally, effects may be evident at larger (i.e. population) scales that are not clear when a small sample is considered. Consequently information from one or two fruiting seasons may be difficult to interpret with any certainty. This chapter details the removal by gorillas, and where possible by other consumers, of ripe seeds from a sample of fruiting trees of each of the four study species. The objective of this part of the study was to establish whether indeed gorillas *are* the major consumers of these species, the degree of variation in crop removal, and the alternatives to seed removal by gorillas provided by other consumers. The methodology was, on the whole, common to all four species so they are treated together for that section. The way fruit crops were scored and the selection of focal trees are described. Seed removal by gorillas and other principal consumers is assessed, in terms of the proportion of each focal tree's crop taken, and the treatment and deposition of seeds by gorillas and other consumers is described.

4.2 METHODS

4.2.1 Prior to fruit removal

Selection of focal trees

The criteria for selecting individual trees to monitor varied slightly for each species, but were based upon the dispersion of the trees, areas of the forest or individual trees known from previous experience to be favoured by gorillas, and individual tree crops. From the results of the pilot study of frugivory (see Chapter 2.1), it was evident that the choice of trees had to be made to maximise the likelihood of gorillas visiting them, because otherwise there was a risk of failing to obtain data (Rogers & Parnell 1991). Static, long-duration tree watches were not used, because during the pilot study they had been found to be inefficient and frustrating, in terms of the amount of data they yielded (R. Parnell, pers. comm.). It was impossible, with the number of observers available, to watch a sufficiently large sample of trees to give sufficient data on fruit consumption by gorillas.

Previous casual observation had indicated that gorillas were more likely to visit trees with larger fruit crops; hence this criterion was included in the selection of individuals. The assumption that gorillas' feeding patterns are influenced by patch size (i.e. dense aggregations of fruit, as a result of large crops or closely-spaced groups of fruiting trees) is based on anecdotal evidence and has yet to be tested, but this behaviour has been reported for the Asian great ape, the orangutan (Leighton 1993). In the event, some of the focal trees of three of the four species were not fed in by gorillas, so data on the fate of the fruit crop from such trees were collected, providing an indication of the probable scenario for the population as a whole.

Trees also had to be chosen in a pattern that would make it efficient to carry out repeated visits on a circuit to assess fruit removal. A minimum of ten individuals of each species was chosen. This was the smallest sample size acceptable for analyses whilst still remaining logistically feasible to study. For common trees, this number is unlikely to be representative of the population in the study area, a frequent problem for field research of this nature. At least some of the individuals chosen had a known phenological history as they had been monitored on the monthly phenology circuits, sometimes from 1986 (see below).

The clumped dispersion of *Ganophyllum giganteum* allowed 13 of 26 known fruiting trees in a relatively small core area to be monitored in 1992, and most of the others were checked periodically. In 1993 only ten trees were monitored as focal fruiting trees, two of which had not been used as focal trees the previous year. The abundance of *Cola lizae* presented more of a problem, since it was impossible to monitor even a small proportion of the population of fruiting trees. Three groups of fruiting *Cola* trees which had overlapping canopies were chosen, in addition to 4 individuals adjacent to them, and 12 other trees, a total of 26 individuals which were treated as 19 patches of *Cola* fruit. Ten *Dialium lopense* trees were selected in an area of the study zone where this species is locally common. *Uapaca guineensis* trees are dispersed predominantly in a linear way along the edges of the main forest block and gallery forests. Ten trees were chosen in 1992, in areas likely to attract gorillas, but with the proviso that other trees would be used if the gorillas fed elsewhere. Three *Uapaca* trees inside the main forest block with good fruit crops were included in the sample. Eleven individuals, in addition to a clump of three with overlapping canopies, were monitored in 1993, the choice of trees being largely determined by gorillas' ranging patterns.

Long-term monitoring of phenology

During the first days of each month, a circuit was walked to monitor leaf, flower and fruit production of 600 trees of 63 species known to be foods for primates in the Lopé community. These included all trees whose fruit are frequently eaten by gorillas, so at least 10 individuals of each of the four study species were represented in the sample. Each tree was examined through 10 x 40 binoculars and scored for the relative abundance of new, mature and senescing leaves, flowers, immature and ripe fruit. A graded scale was used, from 0 (no detectable presence of a particular category) to a maximum of 4 (a full complement of flowers, or fruit, or a full crown of leaf categories). This provided a consistent indication of the food availability in the forest with a high degree of observer reliability. Relative fruit availability could thus be expressed as a percentage of a theoretical maximum of 40 for the ten individuals monitored. For example, if the 10 trees had a combined fruit score of 25, then this was equivalent to 25/40=62.5% availability. Data have been collected like this since 1984 (Tutin *et al* 1991).

Tree dimensions, crop sizes and nearest fruiting conspecifics

For each focal tree the following measurements were taken: diameter at 1.3m above the ground or above buttresses or stilt roots, measured with a diameter tape (dbh, diameter at breast height); the height of the lowest branch and the overall height (both estimated to the nearest metre); two crown diameters measured on the ground using visual estimation of the crown edge, one across the widest part of the crown and the other perpendicular to the first; and crown depth (estimated to the nearest metre). The approximate shape of the crown in horizontal and 3-dimensional aspects was noted in order to allow the calculation of fruitfall area, crown volume and surface area. The mean value of the two horizontal areas, calculated from the two crown diameter measurements and the appropriate crown shape, was taken as the fruitfall area. Figure 4.1 is a diagram of the measurements taken at each focal tree.

For *Ganophyllum* and *Dialium* focal trees, and the three *Uapaca* trees in the forest interior, transects were run out from each individual along the four cardinal (compass) directions to record the presence of fruiting conspecifics. They were intended to provide some information on the 'fruiting environment' of a particular tree (see Chapter 1), based upon the area a feeding primate might be expected to see from the crown without obstruction. Transects were 100m long for *Ganophyllum*, the first species to be studied, but not all conspecifics in a 100m radius from the tree were detected by humans scanning as far as they could see, so a transect length of 50m was used for the other species. Fruiting *Diospyros polystemon* (Ebenaceae) and *D. dendo* trees around focal *Dialium* trees were also recorded, as they provided food for gorillas at the same time.

Due to the high densities of *Cola* trees in the study area (7460 stems ≥10cm dbh/km^2), 6 linear transects along animal paths that included slope, ridge and valley were used to record the proportion of trees ≥10cm dbh with fruit. The first 50 trees within 10m of both sides of the path were sampled, irrespective of linear distance, which gave a total of 300 trees. The number of adults (≥15cm dbh) without fruit between each fruiting tree was used to indicate the proximity of fruiting individuals. The number of *Uapaca*

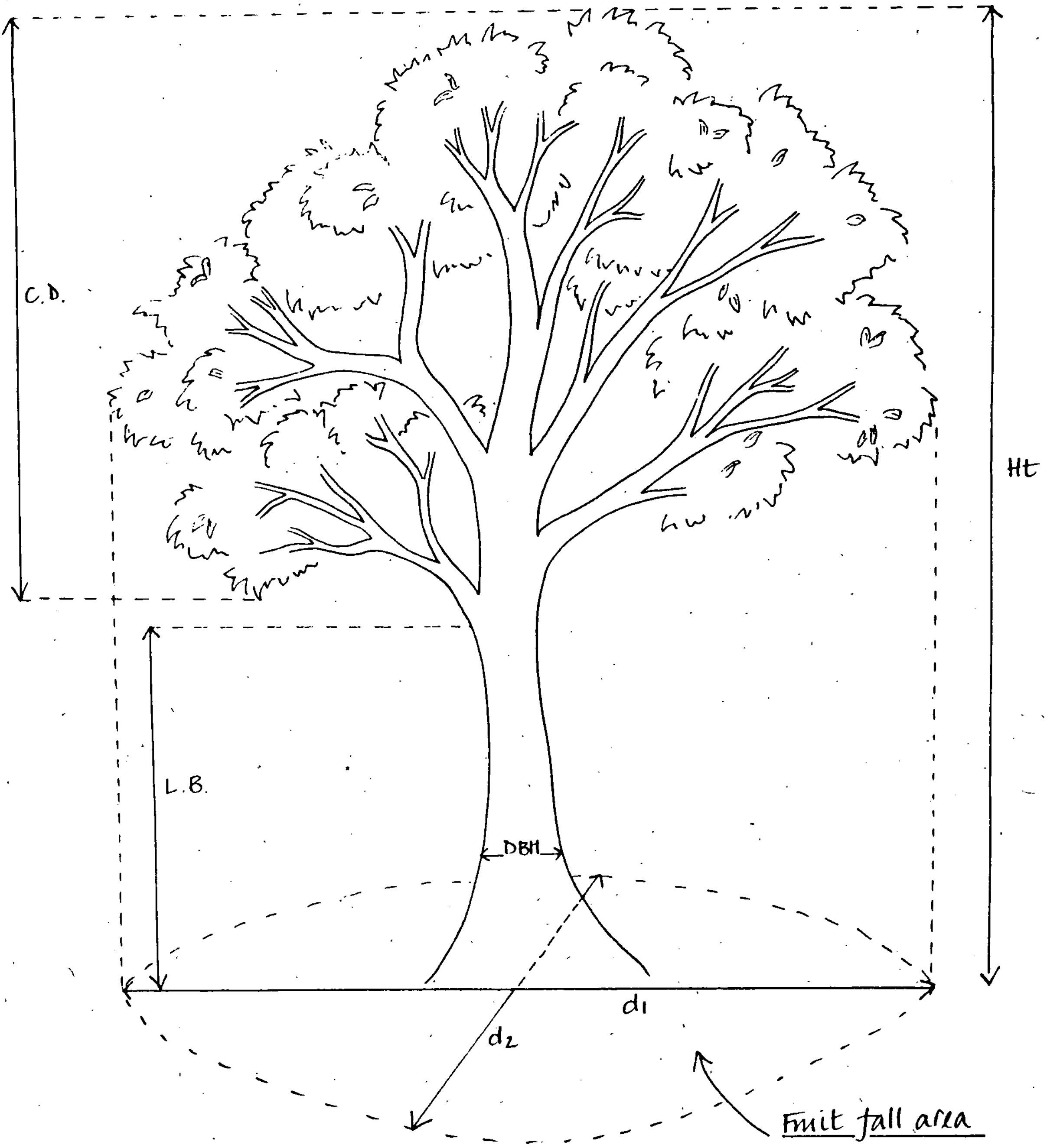


Figure 4.1 Diagram of the dimensions recorded for focal trees. Ht: height; CD: canopy depth; LB: lowest branch; DBH: diameter at breast height; d1, d2: two crown diameters.

trees with and without fruit was recorded along 3 linear transects totalling 1715m of gallery forest and forest edge, and in this case the mean distance between fruiting trees was recorded to give the proximity of fruiting conspecifics. Fruiting *Uapaca* trees nearby that were further in from the forest edge, or that were on the other side of a narrow gallery, were not sampled.

Estimation of crop size and preparation of fruitfall strips

To assess the possibility of counting fruit crops, an attempt was made to estimate the numbers of fruit on focal *Ganophyllum* trees using a 10-40 x 60 telescope. Of the four species, *Ganophyllum* has the most easily visible fruits. The number of fruit on a sample of 10 cymes was counted, then the number of cymes in a visible section of the crown and, using an estimation of the proportion of the fruit-bearing crown that was visible, counts were extrapolated to give a final figure (Leighton 1993), which was very time-consuming and difficult. This method was also tried for *Cola* fruit, but they are well hidden behind the huge leaves (Tutin *et al* 1991a), and *Dialium* crops are also difficult to count (R. Parnell, pers. comm.). Thus the relative sizes of fruit crops on focal trees for all species was assessed using the phenology scoring system. The initial crop size was eventually estimated in a 'post-hoc' fashion, by multiplying the total number of fruit found on the fruitfall strips (derived from feeding remains and natural fruit fall) by the appropriate proportion of the fruitfall area sampled by the strips. Intact (whole) fruit removed from the crown, and any taken from under the tree, were consequently missed.

Fruit removal was recorded from fallen remains on "fruitfall strips" under focal tree canopies. To prepare the fruitfall strips, the ground was cleared of leaves and other debris along two or more strips 0.5m wide, perpendicular to each other and running under the entire width of the crown. The orientation of the strips was not always related to principal compass points, as had been planned, due to the dense nature of the herbaceous vegetation. Instead, the first strip was cleared under the longest crown diameter and the other strip made perpendicular to the first, as for the crown diameter measurements. The even distribution of the fruit in the crown of each species, and the use of all areas of the crown by consumers, meant that using these strips was probably a reliable way of sampling feeding remains. Fruitfall traps were not practical in a forest with high densities of elephants and other large mammals, but they have in any case been shown to give unreliable estimates of fruit crop size (Chapman *et al* 1992 & 1994). Strips sample a larger area but must be monitored often to minimise the disappearance of fallen fruit and feeding remains.

4.2.2 Period of frugivory

Measuring fruit removal: tree circuits

Fruit removal from trees when the crop was still immature was not assessed systematically. At the first appearance of ripe fruit, focal trees were visited every two or three days, even daily in the case of the short fruiting period of *Ganophyllum*. Trees were approached quietly, and any animal seen feeding was observed and recorded. If gorillas were encountered anywhere, attempts were made to stay and observe them, or to prolong the contact without unduly disrupting them. Every effort was made not to disrupt their natural ranging or feeding behaviour. Sometimes it was possible to follow them, or anticipate their direction of travel and move to a position to monitor their feeding activity, but this was rare. The gorillas in the study zone were unhabituated, which meant that observation and contacts were usually brief and infrequent.

If no animals were present in the crown of a focal tree, then the prepared strips were examined for feeding remains. All remains were counted and assigned to various categories: intact ripe and immature fruit; discarded ripe skins; whole (spat) seeds; and insect-damaged fruit. The classes used for each species depended to a certain extent on the morphological characteristics of the fruit and the manner in which they were processed by consumers. It was usually possible to determine when gorillas had made a visit, as a result of the nature and quantity of the remains, the damage to the tree, feeding trail around the base of the tree, or dung or urine underneath the crown. *Cola* pods for example are broken open in a particular way by gorillas. A high proportion of skins of *Uapaca* fruits are left intact by chimpanzees whereas gorillas tend to leave more separated half-skins. Large numbers of broken terminal branches were usually a result of a gorilla visit. Larger branches, up to 12cm in diameter in the case of *Dialium* or *Uapaca*, may also be broken, a sure sign of gorilla feeding. Chimpanzees break some smaller branches but on a more limited scale.

Consequently most feeding remains could be attributed to gorillas or other primate consumers (chimpanzees or monkeys). It was impossible to distinguish between monkey species from their feeding remains. As they forage in mixed species groups, and treat seeds of three of the species in a similar manner, classing them as a group was sufficient for the purposes of this study. For *Dialium* some monkey species (colobus and mangabeys) eat the seeds whereas others (the guenons) eat the mesocarp and discard the seeds, but the remains could not be reliably attributed to a particular consumer (see below). Mandrills were treated separately because they forage in such huge groups and can have a major effect on fruit crops. The difference between the number of seeds found on the strips and the number of empty fruit (and seed locations) was used as an estimate of the number of seeds removed. The prepared strips were cleared as the remains were counted. Evidently intact fruit that was removed from the crown without leaving any sign would not be recorded. This was known to occur to some extent for *Cola* (monkeys take whole fruits away to process), *Dialium* (chimpanzees take small branches away) and *Uapaca* (gorillas can consume whole fruit including skins).

Often it was not possible to check under a tree immediately following a gorilla feeding bout, because they may have visited earlier in the day or during the previous one. The additional fruit remains left by monkeys or other consumers visiting after the gorillas, if not distinguishable from the gorillas' feeding remains, would have been included in the counts of gorilla feeding remains. This amount of "pollution" was not thought to detract from the overall picture when hundreds or thousands of fruit were involved. Extrapolation of the counts of different categories from the fruitfall strips allowed an estimation of the removal of fruit and seeds by the various consumers from the crown as a whole.

Other fruiting conspecifics were noted if they were known to have been fed in by gorillas. Circuits were continued until the crops were finished. Largely opportunistic observations and circuits to check a number of trees meant that shy, inconspicuous and infrequent feeders were likely to be under-represented, but a complete list of all possible consumers was not one of our objectives. Similarly, the proportion of feeding remains that were a result of non-primate consumers was thought to be relatively small for these species, and would affect equally the counts attributed to apes or monkeys. This was probably a safe assumption for the three species other than *Uapaca*. Only rarely have birds been recorded feeding on *Ganophyllum*, no consumers other than primates have been recorded for *Cola* and the only birds to feed on *Dialium* are parrots, which predate seeds (Rogers & Parnell 1991). A variety of avian and other non-primate consumers feed on *Uapaca* fruit (see Chapter 3.2.4), but the quantity handled by canopy feeders other than primates is relatively small (R. Parnell, pers. comm., and pers. obs.). Although evidence of the passage of elephants or duikers could usually be noted, it was not possible to measure the quantity of fruit they removed from under the crown. This was a potentially important influence only for *Uapaca*, whose fruits elephants hoover up readily. Elephants do not eat *Ganophyllum* nor *Cola*, and only rarely *Dialium* (see Chapter 3.2).

Samples of ripe fruit were collected in order to record their dimensions, the weight of component parts, and seeds. Results are included in Chapter 3 (Table 3.1). Chemical analyses of these foods have already been done (Rogers *et al* 1990).

Some problems with Dialium

Some difficulty was encountered with the assessment of *Dialium* fruit remains, as a result of the fruit characteristics and the type of treatment from the different consumers. Attributing all feeding remains with absolute certainty to particular consumer species was not possible. The small brown capsules were often shattered by monkeys or broken open but left *in situ*, although panicles were sometimes detached and dropped by them. If a gorilla was then to eat other fruit on the panicle, and drop it, it was not clear how many were taken by each consumer. Thus branches that had been broken and dropped by gorillas may contain remains of capsules from previous monkey visits as well as their own feeding. However, apes tended to ‘pop’ capsules open with their lips, so the half capsules remaining on the panicles were most likely to be from ape feeding. To minimise this confusion, only fresh-looking empty capsules were counted as gorilla feeding remains.

A further complication with *Dialium* was the fact that the light, very branched panicles that gorillas dropped could get caught in the crown, only to be dislodged sometime afterwards, even several days after the event. This possibly inflated some of the counts that were attributed to monkeys (see below). If monkeys shattered capsules, leaving little or no trace, and panicles were left in the crown even by apes, then estimates for seed removal by the different consumers are likely to be inaccurate. The numbers of seeds removed by monkeys might have gone largely unrecorded, resulting in underestimates. For this reason it was thought best to display the removal of seeds in terms of absolute quantity estimated fom fruitfall, rather than the proportion of the estimated total crop.

Nonetheless the order of magnitude differences were clear, especially as they were corroborated by some quite precise counts made immmediately after observing feeding gorillas. More importantly, only the apes disperse the seeds in any quantity, so the estimates from their feeding were the more relevant in terms of dispersal. For most feeding bouts by apes in *Dialium* trees, counts of empty capsules were done by means of sampling, counting the number of capsules on 10 fallen panicles on each strip, then counting the number of panicles on the strips.

Seed deposition: nest sites and dung piles

During the fruiting period, searches were made for fresh gorilla nest sites (see Chapter 2). This was usually done by following feeding trail back to or on towards the nests. Gorillas may range extensively during the day (Tutin *et al* 1992), and feeding trail can often be sparse, especially when ripe fruit is abundant, so efforts to locate nests from trail were not always successful. The unhabituated nature of the gorillas in the study zone compounded these difficulties. Nest sites were sometimes located by spotting a tree nest and going to investigate, or purely by smelling them nearby. Some of the nest sites found during each fruiting period were set up to monitor the fate of seeds and seedlings (see Chapter 5).

Dung samples were also collected for routine analysis. In this case they were put in a plastic bag where found and marked with the date, location and age class. Samples were kept sealed for up to 10 days before they were weighed and washed through a 1mm mesh sieve in a stream close to camp. The number of seeds of different species was recorded for larger seeds. The relative quantities of smaller seeds were assessed using a 4-point ranked abundance scale. The classes used for ranking were rare, few, common or abundant (see Tutin & Fernandez 1993). The relative proportions of leaf fragments and fibre, as well as any insect remains, were ranked in the same way. When possible at least 50 samples per month were collected.

Other fruit foods

The number of other tree species with ripe fruit consumed by gorillas was recorded each month, and the fruit availability derived from the phenology scores. Additionally the species of large seeds found in the dung during analysis were also recorded. This was done to gather information on the preference for the focal species, as well as seed mixing in dung and potential inter-specific seedling competition.

Most of the statistical tests used were non-parametric in design, because of the small sample sizes and large variations in the data. Tests are 2-tailed except where stated otherwise. Sources were Siegel and Castellan (1988), and Fowler and Cohen (1990).

4.3 RESULTS

Dimensions and fruit crops - all species (Table 4.1)

A summary of the crown dimensions and estimated fruit crops for all four species is shown in Table 4.1, but are discussed in each section below. Additional information and details of individual trees are given in Appendix B.

Availability of ripe fruit and consumption by gorillas - all species (Figures 4.2, 4.3 & 4.4)

The pattern of availability of ripe fruit for each of the four species during the study period is shown in Figure 4.2. There is usually little overlap in availability of the species. 1992 was a relatively typical year, but in 1993 the fruiting of all but *Ganophyllum* was disrupted. *Uapaca* was available in small qauntites for much of 1993, instead of the normal 3-4 months of availability. *Cola* and *Dialium* crops failed almost entirely in 1993, for reasons discussed in Chapter 2. Table 4.2 shows the number of species of tree with ripe fruit eaten by gorillas in each month, and the rank availability of the study species (based on phenology data). This further emphasises the peak of production of the four study species, as well as their importance in terms of the quantity of available fruit foods.

Figures 4.3 and 4.4 show the consumption of these four species by gorillas, in terms of the percentage of dung samples collected that contain seeds of each species (Figure 4.3), and the median number of seeds of each species in the dung samples (Figure 4.4). Together they firmly illustrate that gorillas fed on these fruit whenever they were available. The peaks in occurrence of seeds in dung as well as their abundance coincide precisely with the peaks in ripe fruit availability (Figure 4.2). Further comments appear in each section below.

		Ganophyllum		*Cola*		*Dialium*		*Uapaca*	
		diameter 1	*diameter 2*	*1*	*2*	*1*	*2*	*1*	*2*
crown diameter (m)	mean	20	14.93	11.07	9.12	18	14.5	15.86	13.3
	SD	3.02	4.3	2.57	2.37	2.8	1.67	4.54	4.4
	range	16-24	7-21	6-16	5-15	14-23	11-16	9-24	7-21
	median	19	15	11	9	18	15	14	12.5
	n	15	15	21	21	10	10	29	29
		1992	*1993*	*1992*		*1992*		*1992*	*1993*
Fruitfall area	mean	211.98		82.5		202.1		198.67	147.7
(m2) (FFA)	SD	78.95		40.6		53.86		118.42	83.29
	range	110-396		30-189		107-289		71-383	75-381
	median	225.5		75		191.5		189	128
	n	15		21		10		15	14
% FFA sampled	mean	8.09	8.37	28.1		8.29		9.23	9.72
by strips	SD	3.52	3.34	10.3		2.19		4.8	4.44
	range	4.1-17.2	4.1-17.2	13.5-39.8		5.97-13.08		3.2-20	4.9-15.4
	median	6.95	8.7	29		7.84		9	8.26
	n	15	15	21		10			
estimated	mean	11114	19551	6966		46351		65266	42481
seed crop	SD	7518	16814	7162.0		32143.6		19264.0	11850.0
	range	2048 - 24197	830 - 50034	341 - 21488		4596 - 94125		5639 - 81916	9247 - 54946
	median	8005	13195	3276		48567		69715	41135
	n	13	10	17		10		7	12
								distance (m) between fruiting trees	
no. of fruiting	mean	1				1		38.1	29.5
conspecifics ≤50m	SD	1				0.47		41.7	26.7
	range	0-3				0-2		0-167	5-115
	median	1		(0-7)a		1		22	20
	n	15				10		27	26
period of ripe fruit availability	weeks	5	5	16	n/a	16	n/a	18+2 (12)b	21+12 (9)b
proportion of trees in fruit		most females	most females	24.8%c (n=254)		most	none	37.8%d (n=98)	34.5%d (n=84)

a) no. of non-fruiting conspecifics between fruiting trees: range of medians from 6 transects

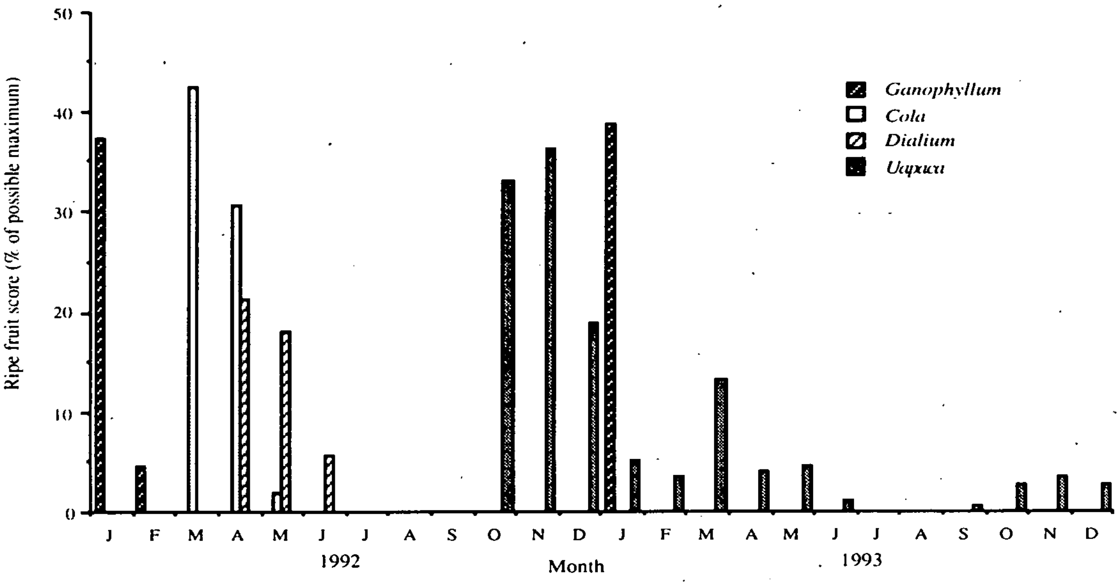
b) peak period in brackets: additional weeks 'out of normal season'

c) % of trees ≥15cm dbh

d) % of all trees (males & females)

Table 4.1 Crown dimensions and estimated crop sizes of the four study species

Figure 4.2 Ripe fruit production by the four study species in 1992 and 1993

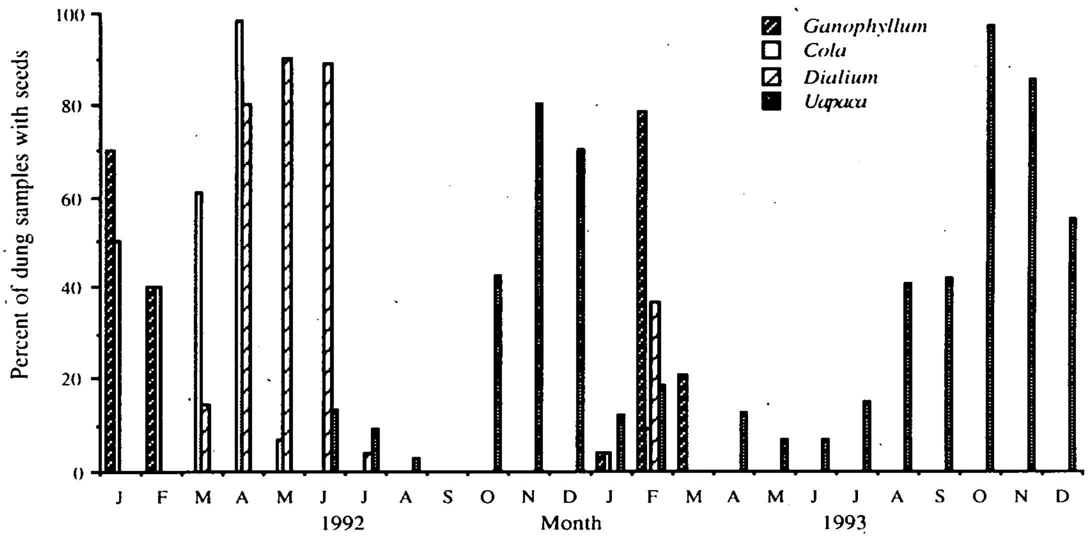


		1992												1993											
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Ganophyllum	a	14	16											16											
	b	3	11											1											
Cola	a			15	19	11																			
	b			2	2	11																			
Dialium	a				19	11	11																		
	b				5	5	5																		
Uapaca	a										15	19	16	16	10	12	13	10	4			10	16	17	
	b										2	2	4	11	8	7	10	6	3			8	13	13	

a: number of available ripe gorilla fruit species (trees)
b: rank availability derived from phenology scores - see text

Table 4.2 Rank availability of the four study species and the number of other available ripe fruit species

Figure 4.3 Percent of collected gorilla dung samples containing seeds of the four study species in 1992 and 1993.



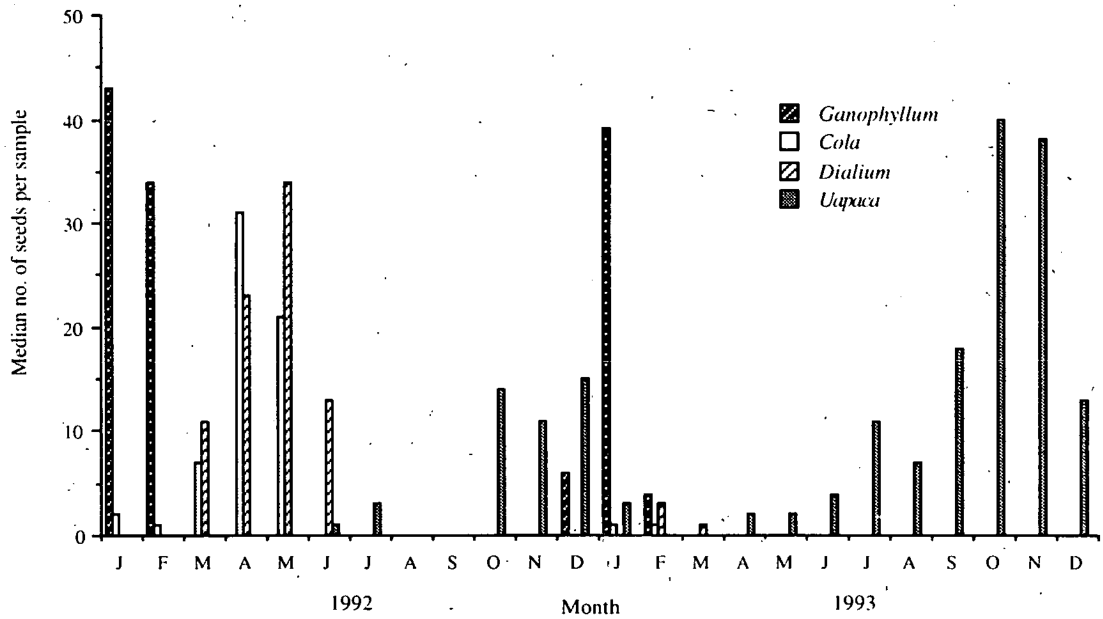


Figure 4.4 Median number of seeds of the four study species per dung sample each month in 1992 and 1993

4.3.1 *Ganophyllum giganteum*

Dimensions and fruit crops (Table 4.1)

Ganophyllum crowns had a typical fruitfall area of $225m^2$, elliptical or circular in shape (Table 4.1). The fruitfall strips sampled on average 8% of the fruitfall area. Fruit crops varied widely, with focal trees in 1992 producing between 2000 and 24000 seeds (median = 8000). In 1993, this range was estimated to be 830 to 50000 seeds (median = 13200). It was not always the larger trees that bore more fruit, although trees with larger crown surface areas have a physical capacity to produce more fruit than smaller trees. There was no significant correlation between crown surface area or volume, and crop size, but dbh did correlate significantly with crop sizes of 1992 (Spearman's r_s=0.713, P<0.02, n=13), but not with those of 1993 (P>0.1). Nor did trees that bore many fruit one season necessarily have smaller crops the following year, although this did occur for several trees (see Appendix B). From casual observation, it was apparent that most females in the study area produced fruit each year, but some did not produce any, or very little, in one of the two seasons of the study. Fruiting trees had on average one other fruiting conspecific within 50m. In terms of availability, *Ganophyllum* was ranked third out of 14 gorilla fruit foods in January 1992 and first out of 16 foods available in January 1993 (Table 4.2).

Seed removal (Figures 4.5 & 4.6)

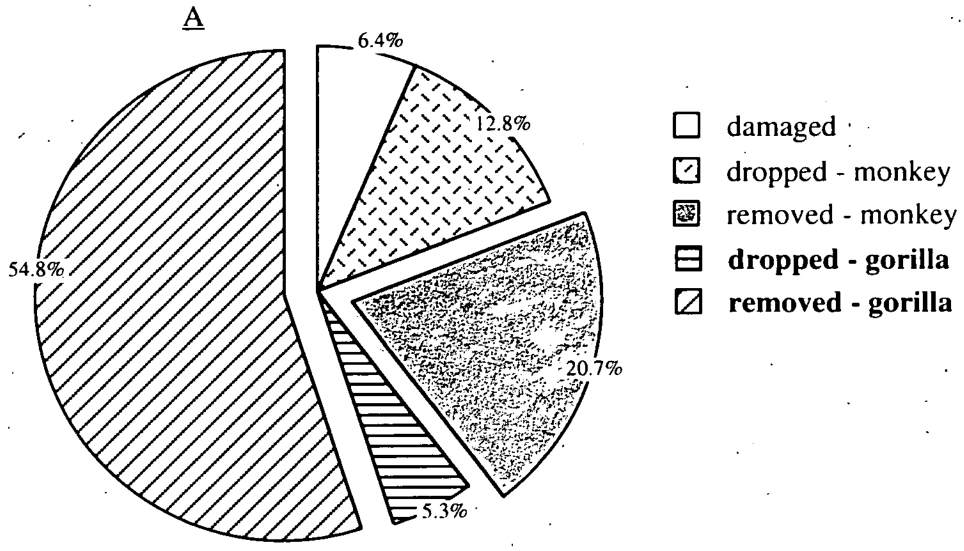
Figure 4.5 shows the proportion of the seed crop removed in (A) 1992 and (B) 1993, using data summed from the 13 and 10 focal trees, respectively. The fate of the seed crops of individual trees is shown in Figure 4.6A (1992) and B (1993). The categories shown were defined as follows:

'removed'	- seeds taken away from the parent canopy;
'dropped'	- seeds dropped in intact immature or ripe fruit, or spat out after processing;
'damaged'	- seeds rendered inviable by the activity of invertebrate predators, or seeds eaten by squirrels.

Where possible I have attempted some degree of consistency with the labelling throughout the chapter. Generally, seeds handled by gorillas are represented by diagonal or horizontal stripes, monkey treatment is stippled or hatched and damaged fruit is clear. The number of confirmed visits by gorillas is the circled value adjacent to the appropriate segment. The segments that correspond to seed dispersal (movement away from the parent) are shown detached from the circle.

Those that were dropped were not necessarily wasted, as ripe seeds may germinate and establish under the canopy. Gorillas rarely spat out seeds: most of those included in

Figure 4.5 The fate of seeds from the estimated crops on a sample of *Ganophyllum* trees. A: 1992 (n=13); B: 1993 (n=10)



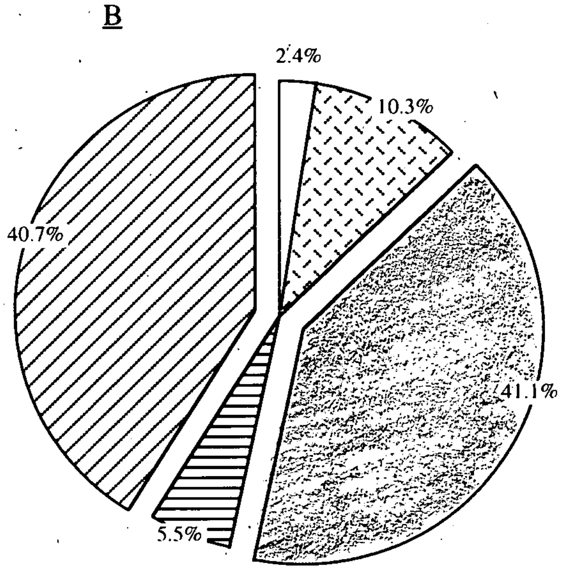


Figure 4.6A The fate of seeds from 13 *Ganophyllum* trees in 1992. Number of gorilla visits circled. (Continued overleaf).

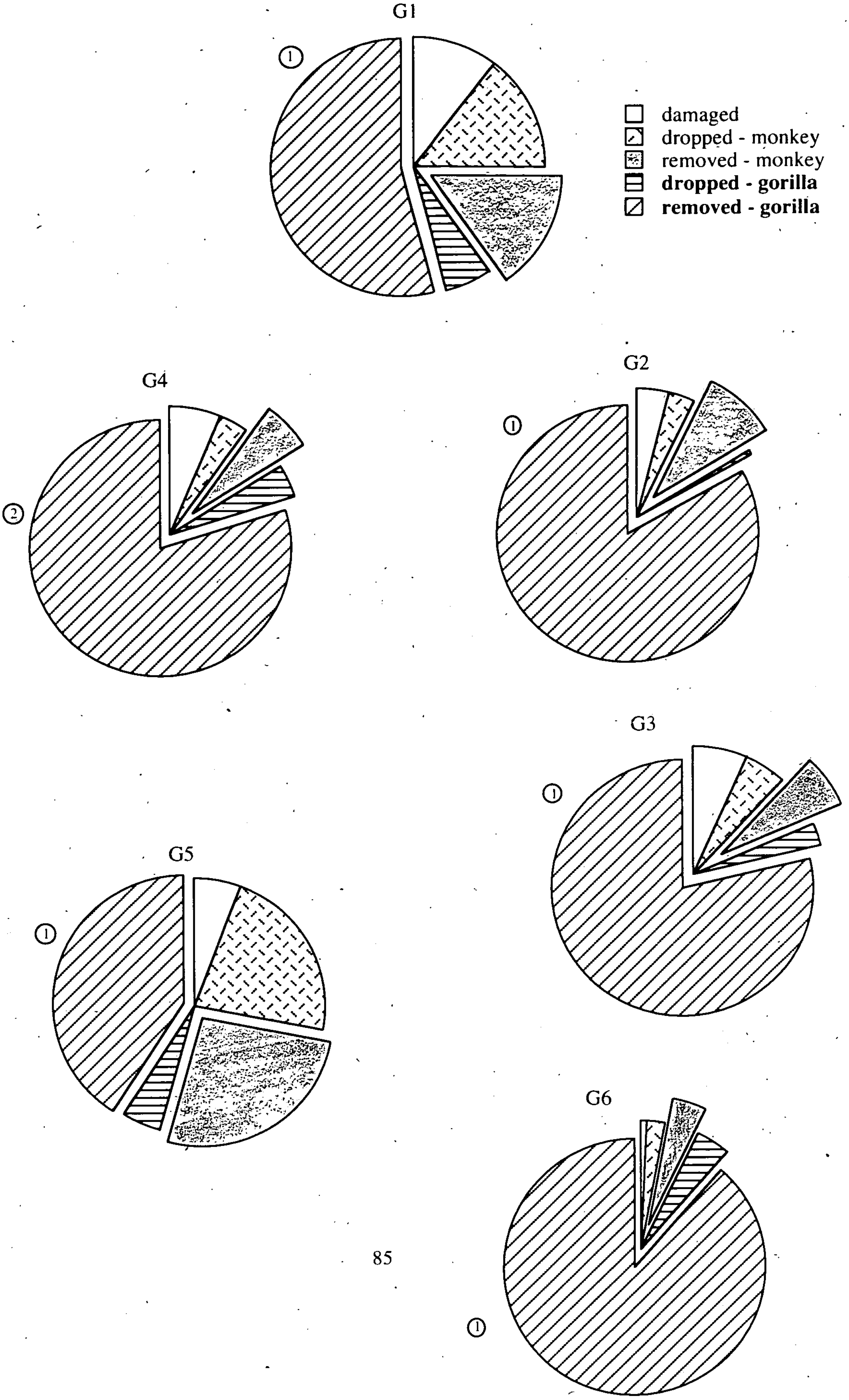
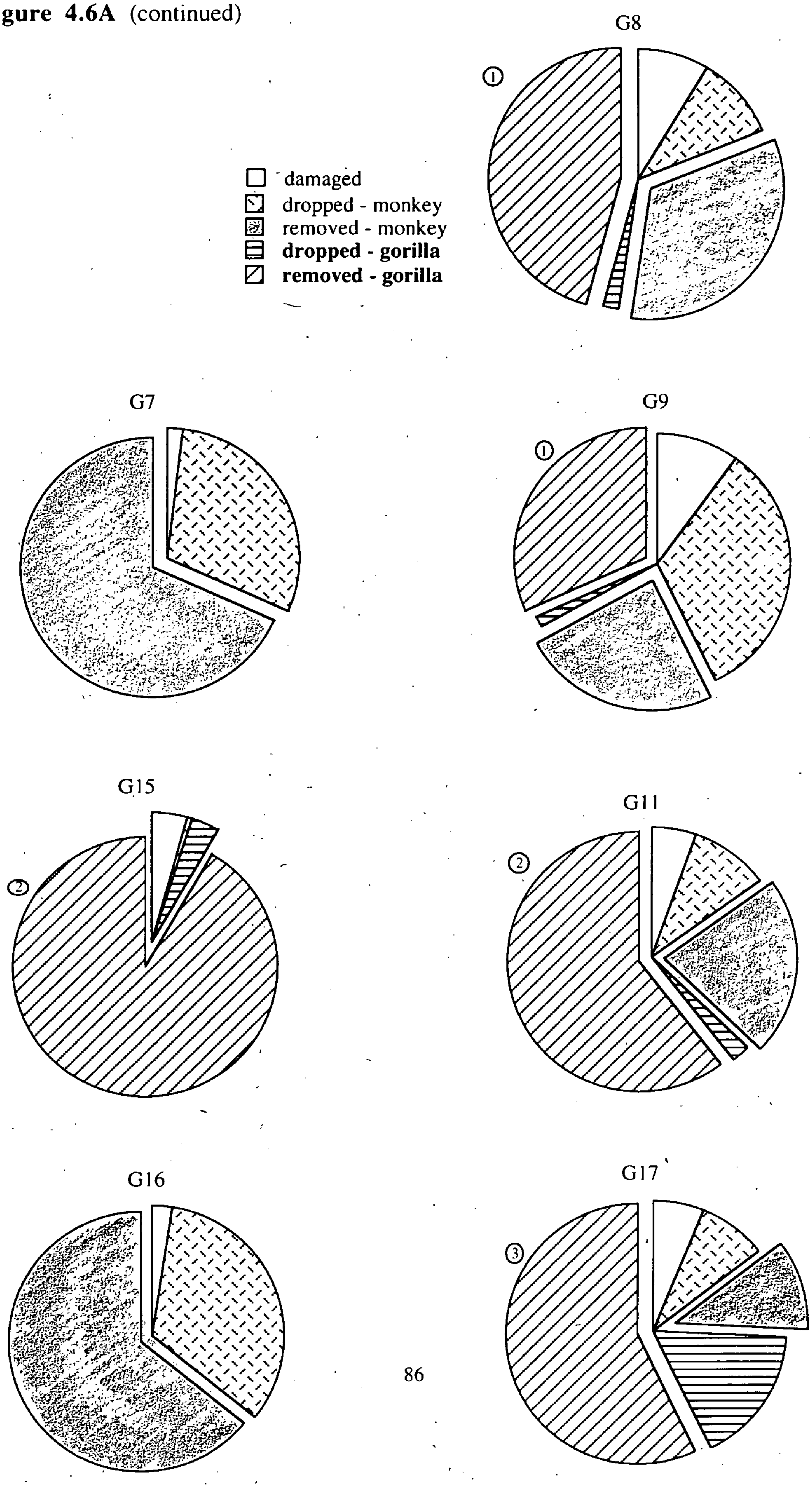


Figure 4.6A (continued)



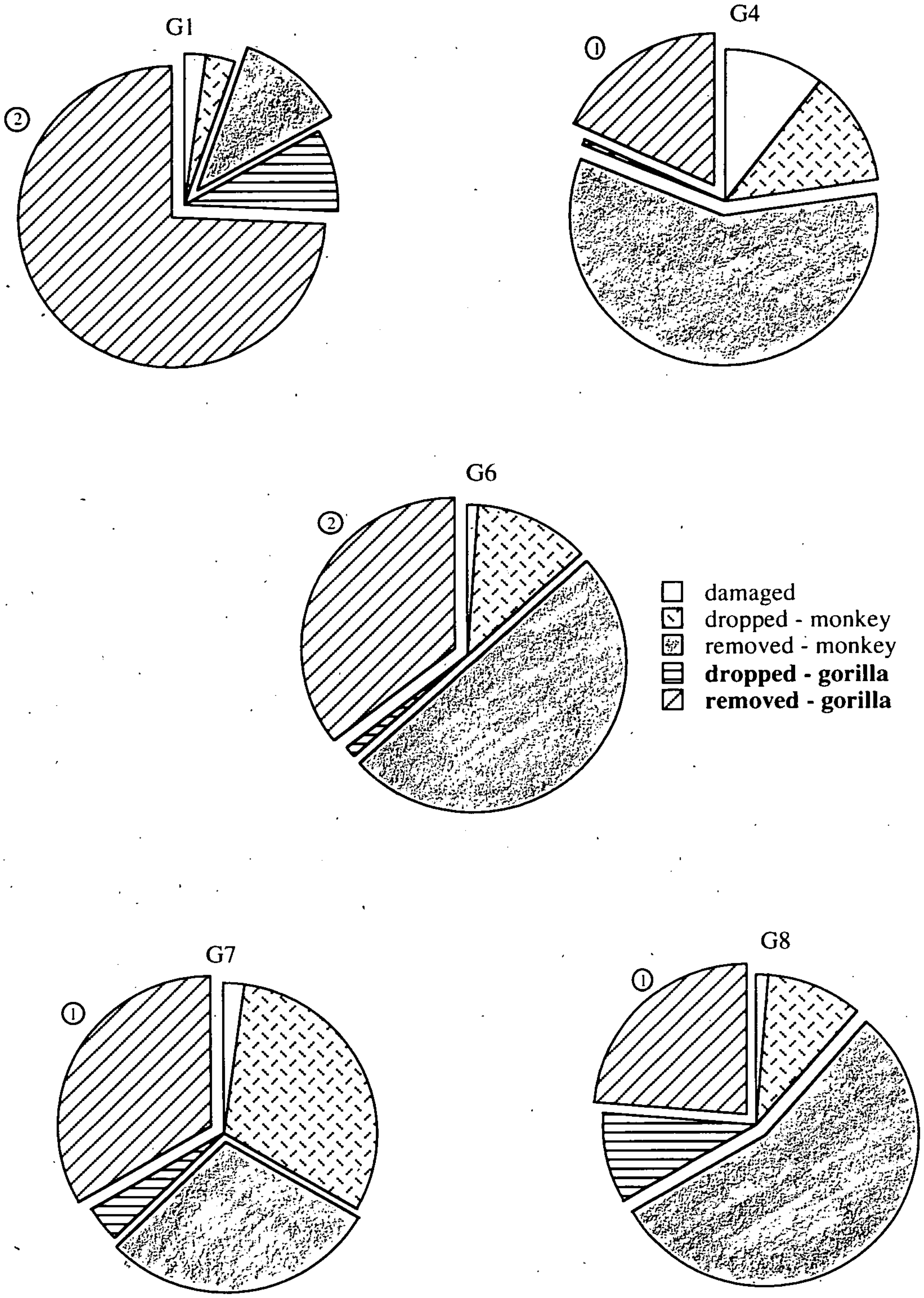
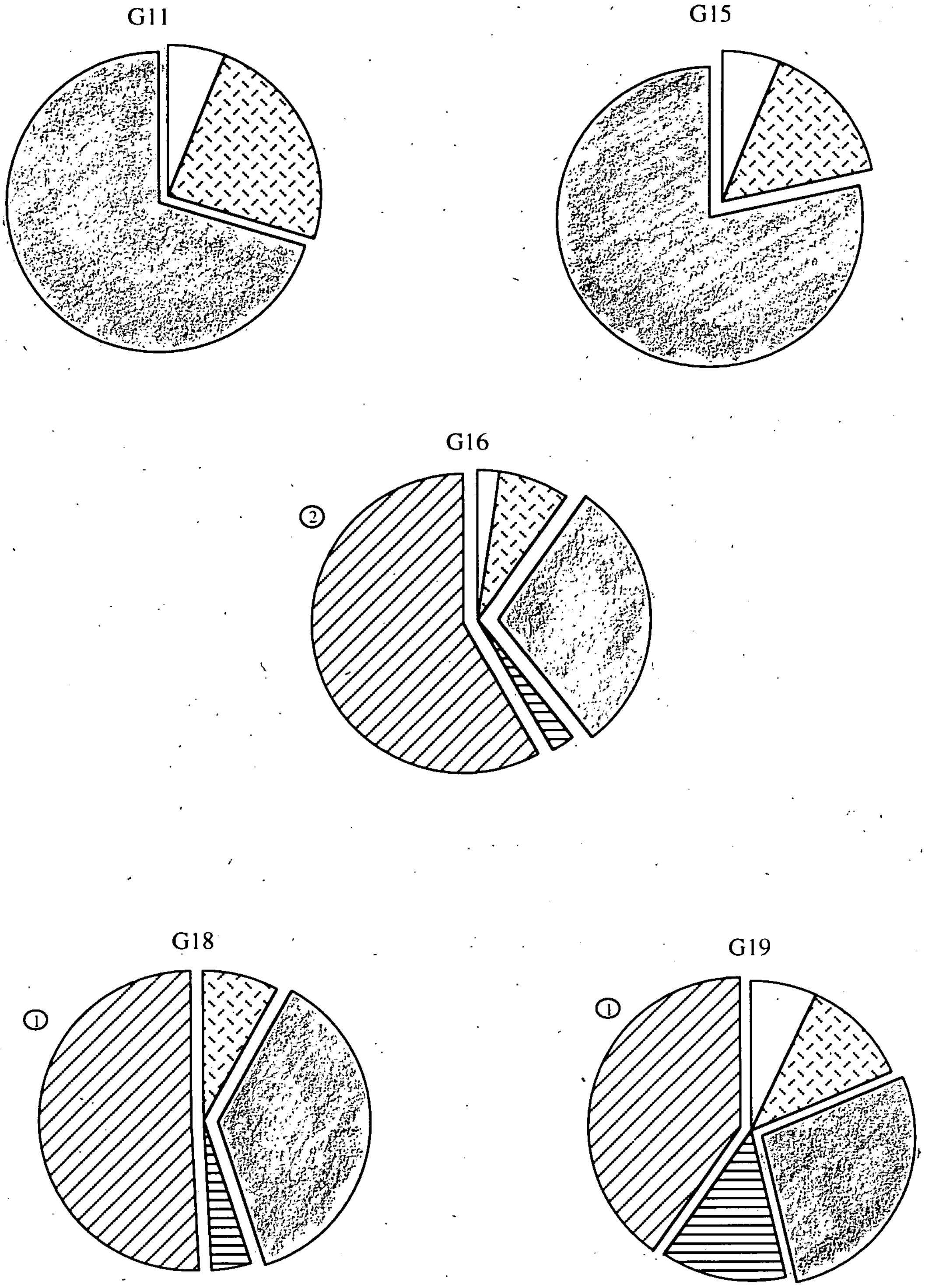


Figure 4.6B The fate of seeds from 10 *Ganophyllum* trees in 1993. Number of gorilla visits circled. (Continued overleaf).

Figure 4.6B (continued)



the 'dropped' category for gorillas were intact fruit that had been rejected (immature) or knocked down (ripe).

The fruit was slightly later to ripen than usual in 1992, but the season was, at 3 weeks (the length of time ripe fruit was on the focal trees), typically brief. While fruit was still immature, a group of gorillas spent 2 days moving rapidly through the area, apparently to check on the state of ripening of the fruit, visiting most of the trees but not feeding on the fruit. They left the area, returning ten days later to feed extensively on the ripened fruit.

Gorillas belonging to two groups were known to have fed in 11 out of the 13 focal trees in 1992, and 15 out of 20 fruiting trees (75%) checked in the area. Figure 4.6A shows the treatment of seeds at all the focal trees. For the trees they visited, gorillas removed more seeds than monkeys, which were the only other recorded disperser, and the difference was considerable in all but one instance (tree #G9). Including all 13 focal trees, gorillas removed significantly more seeds than monkeys (Wilcoxon's sign test, T=15, P<0.025, n=13, 1-tailed). In 1992, 76% of the *Ganophyllum* crop was dispersed, gorillas removing a mean of 54.7% (SD=31.7, r=0-92, n=13) and monkeys 22.4% (SD=21.8, r=0-68, n=13). The proportion of seeds that were dropped (wasted) by monkeys was considerably larger than it was for gorillas. The degree of variation in crop removal between trees is also evident from Figure 4.6A. The two trees with no recorded gorilla visit were within 100m of other fruiting conspecifics, and one (#G7) was less than 25m from tree #G6. Although #G7 was a small tree, it did not have the smallest crop by any means (see Appendix B). Overall, in 1992 gorillas removed more than twice as many seeds from focal trees, and wasted less than half as many as monkeys (Figure 4.5A).

The picture in 1993 was somewhat different, with monkeys and gorillas accounting for approximately equal proportions of seeds removed from the trees sampled (Figure 4.5B). The difference was not significant (Wilcoxon's sign test, T=25, P>0.5, n=10). The mean value for the proportion removed by gorillas was 33.4% (SD=23.9, r=0-74) and by monkeys 44.8% (SD=21.1, r=12-78). In all, 82% of the *Ganophyllum* crop on the focal trees was dispersed in 1993.

Ripe fruit lasted no longer than a fortnight on the focal trees. Gorillas were known to have visited 8 of 10 trees monitored, and removed more seeds than monkeys from 5 of them (Figure 4.6B). Only one group of gorillas was apparently active in the area during this season. They visited 14 out of 28 trees (50%) that were checked. The trees not visited by gorillas in 1993 were not the same as those they ignored in 1992. Trees #G4 and #G7 received only one very brief visit each, and had small crops; one of the trees they did not visit, #G15, had the smallest crop, and the other they 'missed', #G11, was adjacent to #G15, and had a relatively small crop.

The ranging map shown in Figure 4.7 indicates that gorillas were moving from tree to tree, undertaking 'goal-directed travel' and feeding in several trees each day. They also

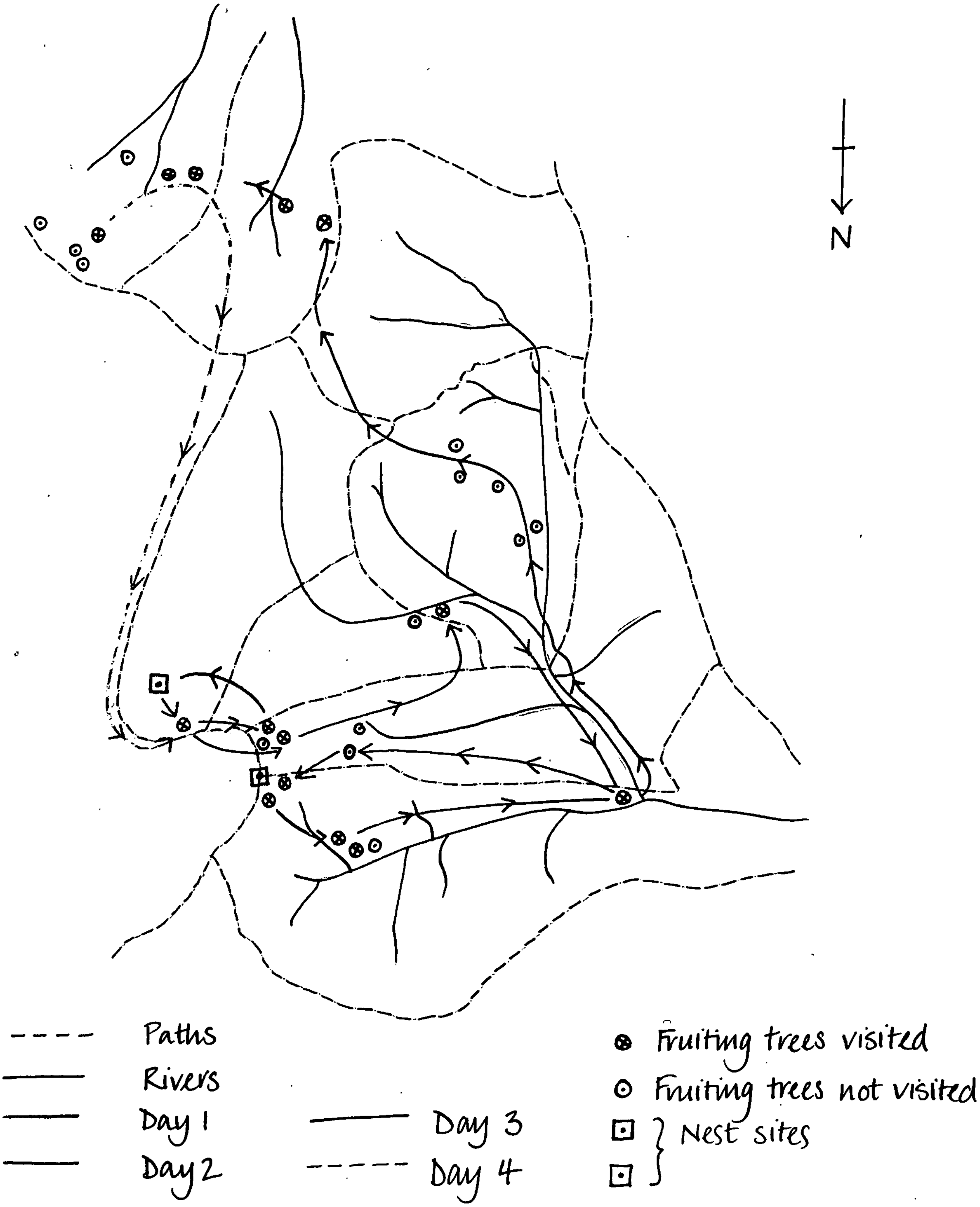


Figure 4.7 Map showing the ranging of a gorilla group during the *Ganophyllum* fruiting season of 1993. (Scale: 1:10000 approx.).

travelled under some trees even if they did not feed in them as a group. Canopy damage sustained by *Ganophyllum* trees in both seasons was slight, with some terminal twigs broken and dropped.

Other consumers

There was no evidence that chimpanzees, the only other consumer to swallow seeds in any quantity, visited any trees we checked in either 1992 or 1993, and there was very little indication generally of their presence in the study area in either season. No *Ganophyllum* seeds were found in chimpanzee dung collected during the fruiting season in 1992 but there were seeds in dung collected during fruiting in 1993. In 1993, 67% of the 24 chimpanzee dung samples contained seeds, but the median number of seeds per sample was 19 (range 1-105), considerably less than gorillas (Figure 4.4). It was predominantly *Cercocebus albigena* and associated *Cercopithecus pogonias* that fed on the fruit crops. They started eating the fruit before gorillas, but made few or no visits after the apes had fed, presumably as a result of the quantity the apes removed. Monkeys either dropped seeds under the parent (or conspecific) or scattered them in the vicinity of the fruiting tree. Monkeys were repeatedly observed to process fruit that they had stored in cheekpouches whilst in a large canopy tree such as *Irvingia gabonensis* less than 100m, and often half that distance, from the parent *Ganophyllum* tree. Squirrels accounted for a small quantity of pre-dispersal seed predation. Duikers may have eaten some fruit, for their prints were sometimes seen under the trees, but the quantity of fruit remaining on the ground after a feeding bout suggested that the amount was negligible.

Deposition (Table 4.3, Figures 4.3 and 4.4)

The number of seeds that were found in gorilla dung during each week of the *Ganophyllum* fruiting seasons in 1992 and 1993 is shown in Table 4.3. Gorillas found ripe *Ganophyllum* fruit to eat for about 5 weeks each year. A total of 49 dung samples containing 2676 seeds were collected in 1992, with the median number of seeds per sample being 44 for all samples (range 2-221). Only two nest sites were marked in 1992, with one of them having many more seeds (2073 in 13 dung piles) than the other (495 in 14 piles). In 1993, 62 dung samples with 4032 seeds were collected, with 49 seeds per dung sample the median value (range 1-417). Four nest sites were located and marked, containing from 580-1110 seeds. Details of these nest sites are given in Chapter 5. The modal value for the number of other large (≥1cm) seeded species found in the dung samples is also given in Table 4.3. At the beginning and end of the fruiting season, this value was 2-4 but during the middle weeks it dropped to 1 or zero, indicating how *Ganophyllum* dominated the diet at this time.

Figure 4.3 shows that up to 80% of collected dung samples contained *Ganophyllum* seeds, the pattern following the sharp peaked production of ripe fruit shown by Figure 4.2. The median number of seeds of *Ganophyllum* in collected dung samples is shown

	Dung collected and sieved					Dung marked in situ					
week	no. of dung samples with seeds (N)	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp	no. of dung samples with seeds	no. of nest sites	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp
1992											
18/1-24/1	20	1376	59	2-149	3	2		88	44	29-59	0 & 3
25/1-31/1	15	496	23	3-104	0	16	1	2147	115	14-391	1
1/2-8/2	12	797	44	5-221	1	17	1	613	29	8-143	0
9/2-15/2	0					0					
16/2-22/2	2	7	4	1-6	3	0					
TOTAL	49	2676	44			35		2848			
1993											
30/12-5/1	3	21	6	3-12	2	0					
6-12/1	35	2063	32	1-201	1	35	3	2857	66	9-296	0
13-19/1	17	1564	65	16-417	1	19	1	1515	73	9-274	0
20-28/1	6	351	49	3-169	1	0					
29/1-4/2	6	33	3.5	1-12	4	0					
TOTAL	67	4032	49			54		4372			

Table 4.3 Analysis of gorilla dung samples containing *Ganophyllum giganteum* seeds

per month in Figure 4.4, with over 40 seeds per dung pile a typical figure in the month of highest abundance. Although from Figure 4.3 it would seem that *Cola* overlaps with *Ganophyllum*, in that a similar proportion of dung samples contained seeds, this does not reflect their relative importance, since very few *Cola* seeds appeared in dung until March and April (Figure 4.4).

The quantity of seeds dispersed by a gorilla during the fruiting season can be estimated by using a rough calculation based on the deposition data. Each gorilla, which deposits a dung pile probably 3-5 times a day (a conservative estimate, see Tutin *et al* 1991a), dispersed between 2700 and 4550 *Ganophyllum* seeds in 1992 and between 3400 and 5700 seeds in 1993. These estimates are based on the median number of seeds per dung sample. If the mean number of seeds is used, the figures were 3700 - 6200 in 1992 and 5150 - 8600 in 1993. This figure is equivalent to the number of seeds dispersed per km^2, because gorillas are estimated to occur at densities of one individual per km^2 in the study area (see Chapter 2).

Other fruit foods

Gorillas fed extensively on the winged seeds of padouk (*Pterocarpus soyauxii* Papilionaceae) between feeding bouts on *Ganophyllum*. From the faecal analysis, the principal other large seeded species eaten during the fruiting season was *Parkia bicolor* (Mimosaceae), although *Heisteria parvifolia* Olacaceae, *Cola lizae*, *Enantia chlorantha* (Annonaceae), *Trichoscypha acuminata* (Anacardiaceae), *Dacryodes normandii* (Burseraceae) and *Santiria trimera* (Burseraceae) were recorded. None of these was eaten in any quantity.

4.3.2 *Cola lizae*

Dimensions and fruit crops (Table 4.1)

Cola trees had the smallest crowns of the four species studied, with a typical fruit fall area of 75m^2 (range 30-189m^2; see Table 4.1). As a consequence, it was possible to sample a higher proportion of the fruitfall area (28% on average) using the cleared strips. Seed production varied enormously, from an estimated 340 to 21500 seeds, with typical values around 3000 to 5000 (Table 4.1). The groups of trees treated together as a single 'patch' did not have the largest crops. In fact the largest crop was from a single individual, tree #C1, that is consistently fecund (C. Tutin, pers. comm.), whereas a 'patch' of four trees within 50m of it produced a little over half as many seeds (see Appendix B). Crop sizes did not correlate with dbh, crown volume or surface area (all $P>0.1$). During the main months of *Cola* availability, it was ranked second among 15 and 19 species of fruit foods respectively (Table 4.2).

The proportion of trees above 15cm dbh that bore fruit in 1992 varied from 12-46% among 6 linear transects, with an overall mean of 24.3%. A summary of the results from

Table 4.4 Summary of data on fruiting *Cola*trees on 6 linear transects

Name of transect (location)		Azobe I	Azobe II	PCR I	PCR II	PdF	Nicitans
Topography		ridge	ridge	slope	slope	streamside	ridge
DBH of fruiting trees ≥15cm*	mean	41.3	38	42.3	36.6	44.1	30.9
	SD	8.7	8.7	12.6	17.7	13.2	6.7
	range	30-52	31-53	19-60	22-65	25-80	20-43
	median	42	35	45	33	43	31.0
	n	7	5	10	5.0	14	22
DBH of all trees ≥15cm	mean	29.9	30.4	28.7	25.5	35.3	27.7
	SD	9.7	13.8	13.5	9.6	15.3	7
	range	16-52	15-90	15-60	15-65	17-84	15-44
	median	29.6	28.3	23.9	23.6	34	26.9
	n	47	41	40	37	41	48
% of trees ≥15cm DBH with fruit		15	12	25	14	34	46
number of non-fruiting conspecifics between fruiting individuals	mean	4	8.25	2	0.56	1.23	1.05
	SD	4.52	6.4	1.4	0.73	1.36	1.6
	range	0-11	3-17	0-3	0-2	0-5	0-5
	median	2.5	6.5	2.5	0	1	0
	n	6	4	4	9	13	21
no. of trees fed in by gorillas		1	0	3	0	3	9
		mean	SD	range	median	n	
DBH of trees fed in by gorillas		32.2	7.1	22-48	32	24	

the transects is shown in Table 4.4. As an indication of the distribution of fruiting trees along these linear transects, the number of trees ≥15cm dbh without fruit between fruiting trees is given. For the transect with the fewest fruiting trees, the median number of non-fruiting conspecifics between fruiting trees was 6.5, but for the other transects the figure was 0-2.5, indicating that fruiting trees tended to be clumped in space, something that was evident from personal observation. Although trees ≥15cm dbh are thought to be able to produce fruit (see Chapter 3.2.2), the average diameters of trees with fruit were much higher than those without. Diameters of all trees ≥15cm dbh were on average 25-35cm but those with fruit had diameters that averaged 31-44cm (Table 4.1).

Seed removal (Figure 4.8)

Cola has a long period of ripe fruit availability (*circa* 11 weeks), as shown in Figure 4.2. The fruit ripened sequentially and monkeys were able to select the small numbers of ripe fruit initially available as well as taking immature fruit, before there was ripe fruit in sufficient abundance to attract groups of gorillas. The immature fruit remains were counted along with the ripe remains. The viability of immature seeds was tested by putting 120 in nursery conditions (see Chapter 5.2), where none germinated. Removal of the seed crops in 1992 from the 19 patches as a whole is shown in Figure 4.8A. Seed removal from individual trees and patches is shown in Figure 4.8B. There was a major failure of fruit set in the following season that resulted in practically no *Cola* fruit in the study area in 1993. Of the little there was, most was eaten unripe so there was effectively no ripe fruit for gorillas.

The definitions for the categories of seed fate shown in Figure 4.8, where they differ from those stated above are as follows:

'spat'	- individual cleaned seeds that were dropped under the parent or conspecific canopy after processing;
'wasted'	- seeds that were dropped under the canopy in whole or part-eaten fruit. Those in broken fruit may germinate, but their chances of success are limited due to fungal attack on the pericarp and their close proximity in the fruit;
'damaged'	- weevils were responsible for some seed predation. The fruit that were affected rotted quickly and were discarded by consumers, so even if only one or two seeds in a fruit were directly affected by weevils, the others were wasted.
'handled'	- includes all the above, used for immature fruit category.

'RS' - ripe seeds; 'IMM' - immature seeds

As with the results for *Ganophyllum*, the segment corresponding to the proportion of seeds removed from the parent is separated from the rest of the pie chart. An asterisk denotes trees or patches that were visited by gorillas. The breakdown of the immature category (a result of monkey feeding) is shown in Appendix C, along with the values for all the other categories.

Gorillas only fed in 6 of the 19 patches (27% of trees, 32% of patches). Overall, gorillas did not remove a large proportion of ripe seeds from the available crop we monitored, and significantly less than monkeys (Figure 4.8A; Wilcoxon's sign test, T=18, P<0.002, n=19). However, for the 6 patches visited by gorillas, no significant difference was apparent between the proportions of ripe seeds removed by gorillas and monkeys (Wilcoxon's sign test, T=6, P>0.5, n=6). The mean proportion removed from individual trees or patches by gorillas was 24.6% (SD=19.3, range=10.1-62.7%, n=6)

Figure 4.8A. The fate of seeds from the estimated crops on a sample of *Cola lizae* 'patches' in 1992 (n=19).

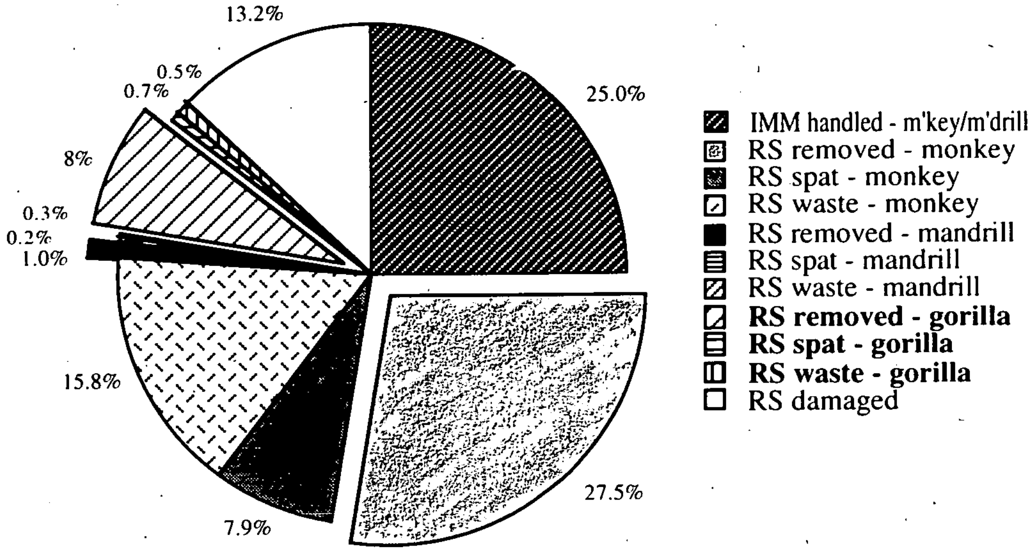


Figure 4.8B The fate of seeds from 19 'patches' of *Cola* fruit in 1992. (Continued overleaf).

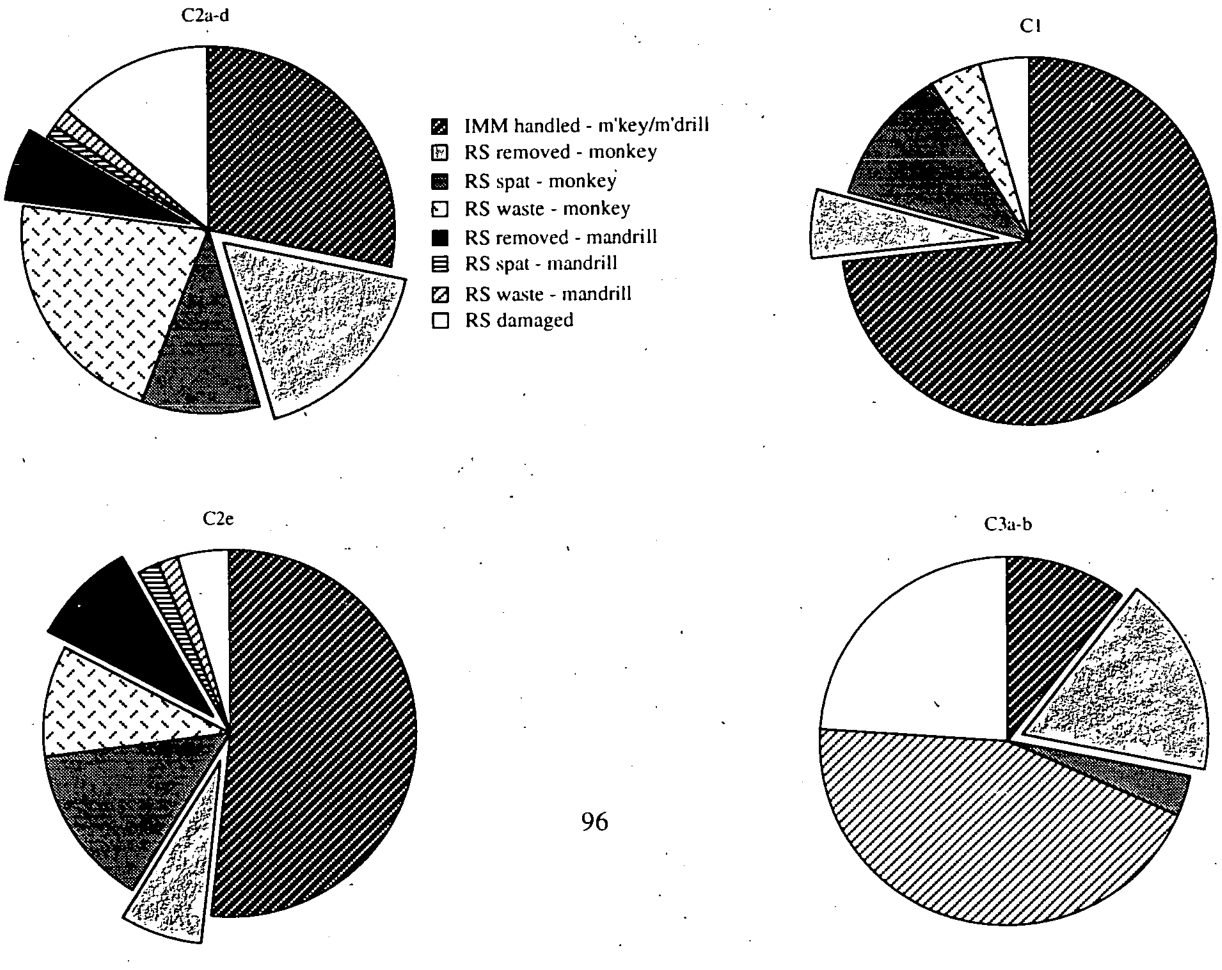


Figure 4.8B (contimued)

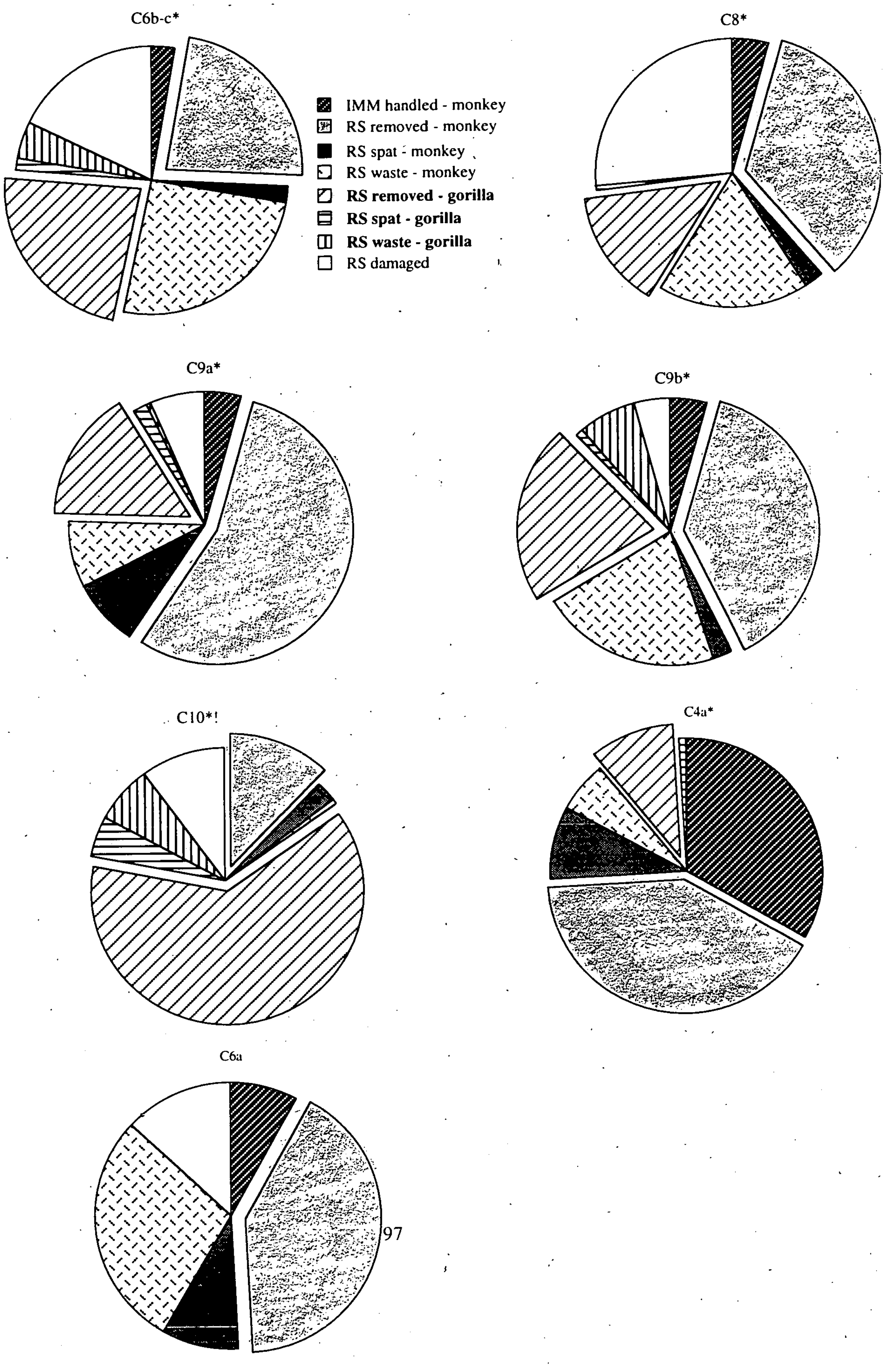
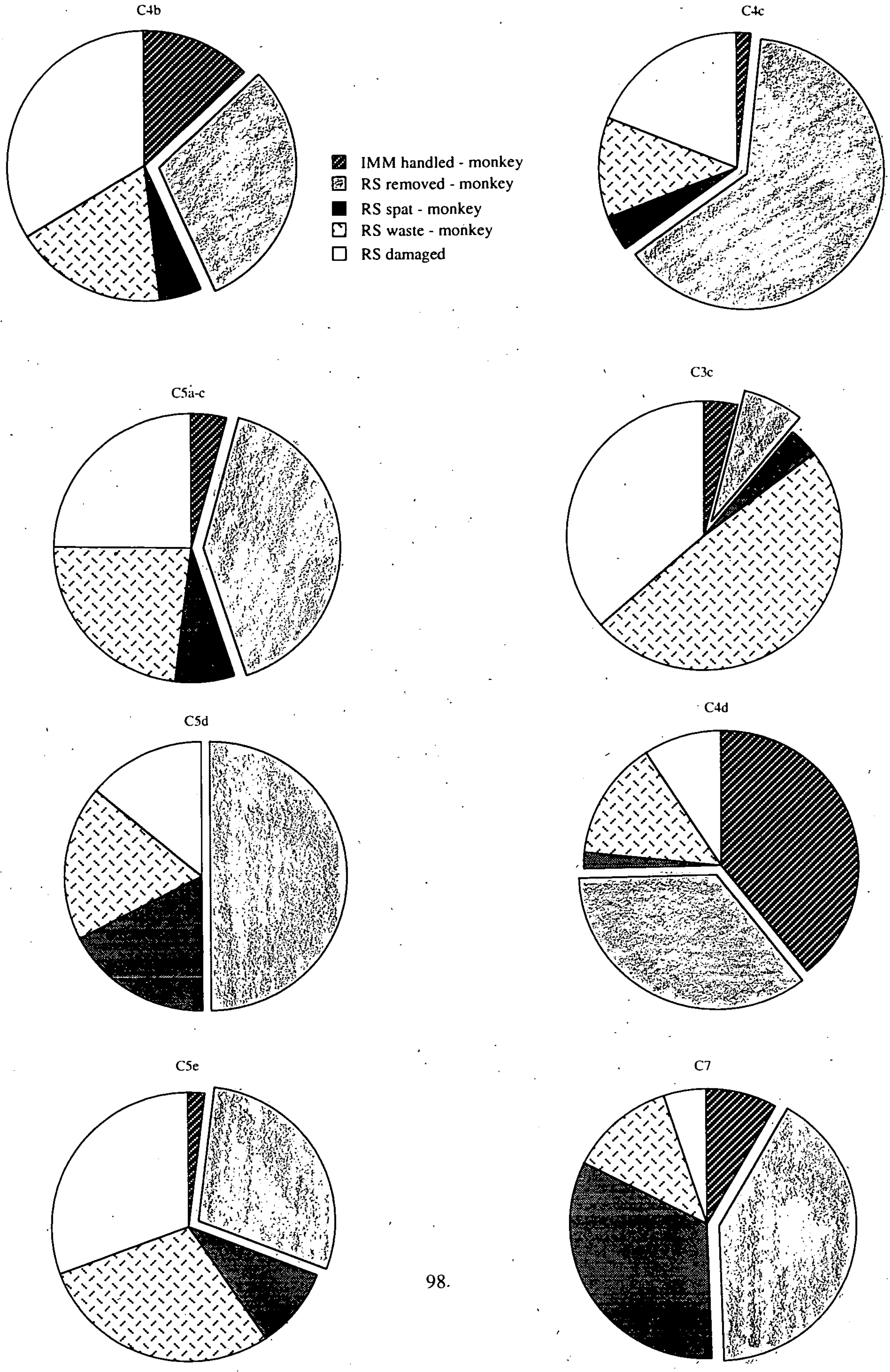


Figure 4.8B (continued)



and that by monkeys was 31.9% (SD=15.8%, range=6-63.2%, n=19). In all, only 35% of the sampled crop was estimated to have been dispersed, and much of it was spat or wasted by monkeys (see below). One large individual, tree #C10, had most of its seed crop removed by gorillas (Figure 4.8B). Counts under this tree were made only after the first gorilla visit, so only the ripe fruit crop is considered. However, there were very few older remains indicating earlier feeding, so the counts were broadly representative of actual events.

Gorillas did not use the area containing the focal trees very much, because they were using areas further west. There was evidence that they fed extensively on *Cola* fruit in an area where a much higher percentage of *Cola* trees had fruit than elsewhere, according to transect data (see Table 4.4, Nictitans transect). The diameter of trees with fruit in this area was smaller than elsewhere, perhaps contributing to easier access for gorillas. The higher proportion of trees in fruit effectively provided a larger patch of food (see section 4.2.1). *Cola* canopies are generally too small to accommodate several gorillas at the same time, which possibly explains the use of a patch of fruiting trees in close proximity.

Other consumers

The seeds which arboreal monkeys do not drop under the parent are scatter dispersed, often not far from the parent. They are also likely to be dropped close to or underneath a conspecific, given the abundance of *Cola* trees. There was a great deal of waste as a result of monkey feeding, both from the loss of inviable immature seeds and the dropping of seeds in intact or partly-eaten fruit. The proportion of a crop wasted was frequently 25% or more, with a further proportion dropped as cleaned seeds under the crown (Figure 4.8B). Most trees had less than half their seed crop removed, but monkeys usually accounted for most of this.

The loss of immature seeds could be considerable, especially for those trees fed in by mandrills. Mandrills travelled through the study area in large numbers (the group size was estimated at more than 450 individuals) before *Cola* fruits were ripe, and contributed to the large proportions of wasted seeds from trees #C1, and #C2 (see Appendix C). Weevil larvae ate a considerable proportion of the seed crops of some trees (or wasted others by rendering the fruit unappetising for other consumers). Some trees seemed to suffer greater infestations of weevils than others, with 25-30% of the crop in some cases affected by these predators. Chimpanzees were never observed to eat *Cola* fruit during the study, although the skins surrounding the mesocarp were found in their dung (see below), and clumps of wadged seeds were found on occasion.

Deposition (Table 4.5, Figures 4.3 and 4.4)

The results of the seed counts from dung samples collected for analysis and left *in situ* for monitoring are listed in Table 4.5. The data are sorted into 2-week intervals, in order to illustrate the development of the dominance of *Cola* in the diet as the fruit crops

	Dung collected and sieved					Dung marked in situ					
2- or 3-week period	no. of dung samples with seeds	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp	no. of dung samples with seeds	no. of nest sites	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp
1992											
2-24/1	20	52	2	1-8	3						
25/1-20/2	8	12	1	1-4	1						
21/2-8/3	16	94	3	1-26	2						
9-23/3	34	274	4	1-59	2						
24/3-14/4	45	2085	36	7-185	1	64	4	2199	21	1-113	
15/4-9/5	33	1387	29	1-137	1						
TOTAL	156	3904	14			64		2199			
1993											
12/1-4/2	6 (plus 3 samples with skins)	6	1	1							

Table 4.5 Analysis of gorilla dung samples containing seeds of *Cola lizae*

ripened. A total of 156 dung samples were collected, containing 3904 seeds, with an overall median of 14 seeds per sample (mean=27.7, SD=31.6, range=1-185). The median during the peak period of consumption was 36 seeds per sample. The availability of ripe fruit finishes abruptly, as it is all eaten quickly once it is ripe, or in some years is replaced in the diet by the ripening of another favoured food, *Dialium*. This pattern is clearly seen in the data presented in Figures 4.3 and 4.4. The peak of *Cola* feeding is in April, when in 1992, 100% of dung samples collected contained *Cola* seeds and the median number of seeds per sample was over 36. The graphs clearly show the overlapping of *Cola* with the start of *Dialium* fruit availability.

Those dung samples that had large numbers of *Cola* seeds contained very little matrix. The proportion of the wet weight of dung accounted for by *Cola* seeds was over 70%, even close to 100% in some cases. The occurrence of a very few *Cola* seeds in dung early in the season might have been a result of precocious ripening of some fruits (or trees), or feeding by gorillas on fruit that was not quite ripe. All 4 nest sites that were monitored were first marked in the 'peak' fortnight of *Cola* consumption. In 1993, only 6 dung samples had *Cola* seeds in them, all in January and early February, suggesting that they were from immature fruit. Otherwise, no ripe fruit was eaten, for none was available. As already stated, chimpanzees very rarely swallow *Cola* seeds, as they tend to wadge them using their lower lip. In 1992, 7 out of 19 chimpanzee dung samples (37%) had remains of *Cola* fruit (the thin skin covering the mesocarp) in them, although this figure was 80% in 1991 (SEGC, unpub. data).

Using the deposition data, each gorilla dispersed an estimated 4600 to 7600 seeds during the *Cola* fruiting season. This is calculated using the median value for each 2 or 3-week interval. If the mean value for the whole period is used, then the figure was 10500 to 17500 seeds per gorilla, akin to that calculated by Tutin *et al* (1991a).

Other fruit foods

An important aspect of the 1992 season was that a relatively uncommon mast-fruiting species, *Celtis tessmannii* (Ulmaceae), produced fruit at the same time as *Cola*. The fruit of *Celtis* is much favoured by gorillas, and it was last known to fruit substantially in 1984. The period of fruit availability was shorter, so *Cola* fruits were still available after *Celtis* crops were exhausted. Nonetheless, during a part of the *Cola* season, gorilla movements and feeding were to some extent influenced by the location of *Celtis* trees. This may have affected the removal of *Cola* seeds from the available crops. *Celtis* seeds were the main other large seed found in gorilla dung during the *Cola* season. When gorillas first started eating *Cola*, *Ganophyllum* seeds were also found in the dung. Towards the end of the season, *Dialium* seeds became apparent. Other large-seeded species that were found during faecal analysis in the main *Cola* season included *Uvariastrum pierreanum* (Annonaceae) and *Parkia bicolor*.

4.3.3 *Dialium*

Dimensions and fruit crops (Table 4.1)

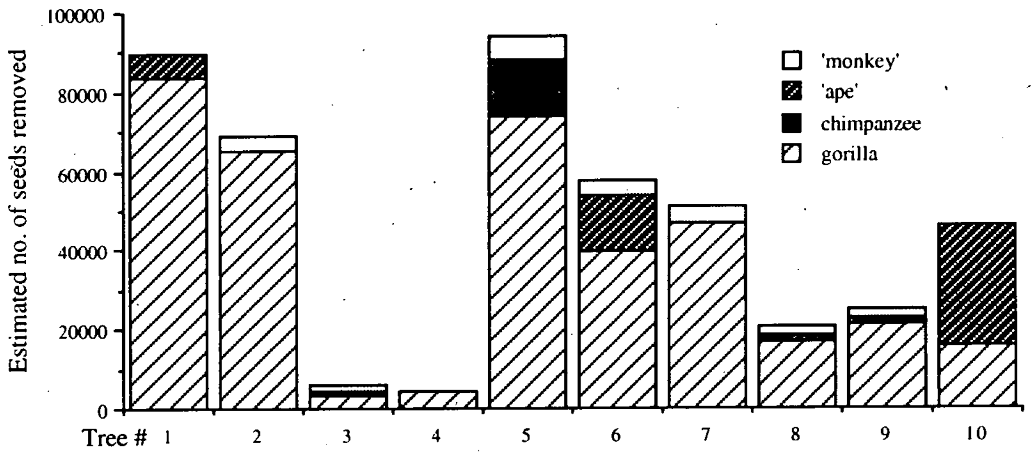
The *Dialium* trees sampled were on the whole slightly smaller than *Ganophyllum* trees, with fruitfall areas of 107-290m², the median being 192m² (see Table 4.1). The fruitfall strips sampled about 8% of the area. The difficulties associated with estimating the crop size of *Dialium* trees have been discussed above (section 4.2.1). Average fruit crops consisted of about 50000 seeds in 1992, with some trees producing nearly twice this amount. Two trees were estimated to have poor crops, although one of these low estimates (tree #D4) was in part due to the fact that some of the crop was still in place uneaten at the end of the period of study, so was not counted. The majority of trees in the study area produced fruit in 1992, but none did in 1993 (pers. obs.). Crop size was not correlated with dbh, crown surface area or volume (all $P>0.1$). Most of the focal trees were within 50m of a fruiting conspecific. Also within 50m of focal trees were 1-14 (median=2) fruiting individuals of *Diospyros dendo* (Ebenaceae) and 1-11 (median=2) fruiting *D. polystemon* trees, which also provided food for gorillas during the *Dialium* season. *Dialium* was ranked fifth in availability of 19 and 11 fruit foods in the months in which it was available (Table 4.2).

Seed removal (Figure 4.9)

Figure 4.9 shows the quantites of ripe seeds estimated to have been removed by the different primate consumers from each of the focal trees. Where it was not possible to distinguish between chimpanzee or gorilla feeding remains, they were classed as 'ape' feeding remains. Intact fruit (those wasted or damaged by insects) were not represented as a category because they were not recorded on a systematic basis. Despite the earlier cautionary statements, and the suspicion that the counts for monkeys were uncertain, gorillas were probably the main consumers for all trees monitored. The distinct evidence of a visit by gorillas, principally the quantity of broken and fallen material, dung and urine, and relatively few observations of monkey feeding, indicated that gorillas did indeed remove the bulk of the *Dialium* crops in 1992. This was corroborated by occasional observation of extensive gorilla feeding bouts in some trees which were followed by immediate and therefore more precise counts, as well as the results from the pilot study of frugivory (Rogers & Parnell 1991).

Gorillas fed in all ten focal trees, even those with smaller crops. Of 37 known fruiting trees in the area, gorillas fed in 26 (70%) of them. They made 2 or 3 visits to most trees, but only visited the trees with the smallest crops once (Figure 4.9). Gorillas did not seem to favour trees with more neighbour *Diospyros* trees in fruit (no correlation between the number of visits and the number of neighbour *Diospyros* trees). Chimpanzees were only confirmed to have visited 4 of the focal trees, but they may have

Figure 4.9 The fate of seeds from 10 *Dialium lopense* trees in 1992, and the number of confirmed visits by gorillas and chimpanzees. When identification was uncertain, the category 'ape' was used.



No. of visits		1	2	3	4	5	6	7	8	9	10
	gorilla	3	2	1	1	2	2	2	2	3	1
	chimp	0	0	1	0	1	0	0	1	2	0
	'ape'	1	0	0	0	0	0	2	0	0	1

Table 4.6 Analysis of gorilla dung samples containing seeds of *Dialium lopense*

2-week period	no. of dung samples with seeds	no. of seeds	median no. of seeds per sample	range	proportion as hard seeds (median)	proportion as soft seeds (median)	mode no. of other large-seeded spp	no. of nest sites
	Dung collected and sieved							
1992								
16-31/3	15	241	11	1-61	0	1	2	
1-14/4	19	591	23	1-160	0.573	0.427	1	
15-27/4	25	1563	15	1-439	0.906	0.094	1	
28/4-10/5	9	247	15	6-96	0.919	0.081	1	
11-24/5	13	342	24	1-92	1	0	2	
25/5-8/6	43	7371	51	1-1235	0.917	0.083	2	
9/6-21/6	20	717	21.5	1-189	0.882	0.118	1	
22/6-6/7	14	392	12.5	1-191	0.7	0.3	2	
TOTAL	158	11464	22					
	Dung marked in situ							
28/4-10/5	8	591	68	22-110	0.95	0.05	0	1
11-24/5	1	117			1	0	1	
TOTAL	9	708						
1993	Dung collected and sieved							
25-26/2	12	296	3	1-128	0	1	1	
16-17/3	6	7	1	1-2	0.25	0.75	1	
TOTAL	18	303	2					

visited 7 of them. Based on the estimates from feeding remains at the trees they visited, gorillas removed more than either chimpanzees (Wilcoxon's sign test, T=0, P<0.001, n=7) or monkeys (T=0, P<0.001, n=8). No difference was apparent in the amount removed by chimpanzees and monkeys (T=6, P>0.5, n=7). Estimates for the average proportion of the focal crops that were removed by the different consumers were 78% (±20%, n=10) for gorillas, 12% (±6%, n=4) for chimpanzees and 7% (±7%, n=10) for monkeys.

On one occasion, a group of gorillas comprising 5 adults and 4 infants was observed in the morning feeding in a focal tree. Although observed for only 30 minutes, they had been there for somewhat longer, probably over 2 hours. A count immediately after they left suggested that they had eaten over 43000 fruit in that one feeding bout. Other feeding bouts, estimated from observations of feeding rates and the time spent feeding, have been suggested to account for 10000 to 17000 fruits (Rogers & Parnell 1991). It was observed that the silverback of a group usually spent the longest time feeding, presumably because his bulk required the most energy.

Damage inflicted on the trees was severe, and in some cases up to 40% of a tree's canopy suffered broken branches. Rogers and Parnell (1991) found that the degree of damage was directly related to the number of visits made by gorillas. A number of trees some kilometers to the west of the study area bore fruit in 1993 but the entire crops were removed immature by gorillas, chimpanzees and monkeys in February and March.

A sample of remains (panicles broken and dropped) were examined to estimate the proportion of fruit left intact. This indicated that feeding was very efficient. Of 20 panicles with 634 fruit sampled early in the season, a median value of 0% of the fruit on each panicle were intact, and 5% were damaged by insects. At the end of the season 26 panicles with 485 fruit were examined. The proportion wasted (intact) was the same, but the proportion suffering invertebrate damage had risen to 35% (the mean value; SD=21%). In a previous study, the median proportion wasted was 1.8% and that damaged 0.7% (n=153 panicles; Rogers & Parnell 1991).

Other consumers

Chimpanzees also favour *Dialium* fruit, although they visited fewer of the focal trees than gorillas. Travelling in smaller groups, and with longer day ranges and larger home ranges, they left less clear evidence of feeding so were likely to have removed more seeds than were recorded (see below for data on seed deposition). The three *Cercopithecus* species of monkey that eat *Dialium* fruit feed on the mesocarp and swallow or discard the seed. *Colobus satanas*, *Mandillus sphinx* and *Cercocebus albigena* eat the seeds and discard the mesocarp, so they do not act as dispersers in any way. *Cercocebus albigena* may destroy large numbers of seeds. Using averaged observational data, a group of them feeding for a typical time at an average rate can remove over 4000 seeds in one visit (R. Ham, unpub. data). Parrots have been observed to predate the seeds, but this is not thought to account for many (R. Parnell, unpub. data). The small fraction of elephant dung found to contain *Dialium* seeds by White (1992) is negligible in comparison to the quantities consumed by the apes. Considering the small amount of intact fruit that reaches the forest floor, it can hardly provide much food for elephants, and may be incidentally ingested along with foliage eaten from freshly-dropped branches.

Deposition (Table 4.6, Figures 4.3 and 4.4)

Table 4.6 lists the results from faecal analysis and data from the one nest site that was located and marked for monitoring. In all, 158 dung samples were sieved, containing 11464 *Dialium* seeds. Dung piles may evidently contain a large number of seeds (a maximum of 1235 in a sample during this study), but even a lot of seeds do not make up a large proportion (rarely 50%) of the weight of a dung sample. The ratios of soft seeds to hard seeds reflect the ripening process, with most seeds in dung at the start of the season in the soft (immature) state.

Coprophagy is commonplace during the *Dialium* fruiting season. During the fruiting season of 1991, 46% of nest sites, and 53% of the dung at these sites were coprophaged (Rogers & Parnell 1991). Split hard seeds, crunched soft seeds, and rolled testas from soft seeds were all found in small quantities in dung samples, evidence of some seed predation. These categories were found in 2%, 8% and 34% of dung samples respectively. The percentage of dung samples each month that contained *Dialium* seeds is shown in Figure 4.3. Although fruit on the focal trees generally lasted 7 weeks, gorillas ate *Dialium* fruit over a period of 16 weeks. The peak in consumption was in May. This is clarified by the median number of seeds per sample (Figure 4.4). During the fruiting season, each gorilla was estimated to disperse between 7300 and 12100 seeds, using the median values. Using mean values, the figures were 16700 to 28000 seeds per gorilla. The latter figure is still likely to be an underestimate, because the figure derived from a precise count after a single observed feeding bout is 6200 seeds per gorilla, and each gorilla is likely to have many such bouts during the fruiting season.

The scant amount of immature fruit eaten in 1993 is also represented in Table 4.6. Although nearly 40% of dung samples contained seeds (Figure 4.3), there were very few seeds in each sample (Figure 4.4). In this year, 67% of dung samples contained crunched (soft) seeds, and rolled testas were found in 25% of samples.

Chimpanzees also dispersed considerable quantities of seeds. In April, May and June of 1992, the proportion of dung samples with *Dialium* seeds was 60%, 92% and 94% respectively (n=10, 26 and 31), which is higher than that quoted for gorillas. The median number of seeds per sample was also higher than for gorillas, being 19, 146 and 114 in the respective months.

Other fruit foods

The other large-seeded species to appear in the dung during *Dialium* season were *Cola* (at the beginning), some *Celtis tessmannii*, *Diospyros dendo* and *D. polystemon*.

4.3.4 *Uapaca*

Dimensions and fruit crops (Table 4.1)

Uapaca trees, growing mostly at the forest edge, show a large range of crown sizes, although almost all approximate to a hemisphere in shape (see Table 4.1). Some of the large spreading crowns have diameters of up to 24m. The fruitfall areas of those trees sampled in 1992 averaged 190m^2 and for those used in 1993, 130m^2. The fruitfall strips sampled on average 9% of the fruitfall area. The median seed crops estimated for the two seasons studied were 70000 in 1992 and 41000 in 1993. The variation was larger among the trees sampled in 1992, with one large tree estimated to have produced over 80000 seeds, and the smallest crop estimated at 5600 seeds. In 1993 the range of estimated crops was 9200 - 55000 seeds. There was a significant correlation between crown surface area and crop size, both in 1992 (Spearman rank order correlation, $r_S=0.86$, $P<0.05$, $n=7$) and in 1993 ($r_S=0.8$, $P<0.01$, $n=12$), but not between crown volume or dbh and crop size (all $P>0.1$) (Appendix B).

The median distance between fruiting trees along four forest edge transects measuring 550m, 720m, 550m and 500m in length was 13m, 20m, 22m, and 43m respectively, and ranged from 0m (where the canopies were in contact) to 167m. On these transects, an average of 38% of trees fruited in 1992, and 35% in 1993 (Appendix B). If there are approximately even numbers of males and females, then these figures represent quite a high proportion of the potential number of fruit-bearing trees. The minimum diameter of reproductively mature trees was unclear from the measurements, but the smallest tree >10cm dbh with fruit measured 30cm dbh, and was also the smallest tree on the transects.

The fruiting period of *Uapaca* usually lasts for 3 months, with a 'peak' around November, although in 1993 fruit was available for much of the year (Figure 4.2, and see Chapter 2.3). In terms of fruit availability in the three peak months in 1992, *Uapaca* ranked second in two and fourth in one of them, out of 15, 19 and 16 available fruit species, but in the same months in 1993 poor fruit production by the trees in the central study zone meant it was ranked eighth and thirteenth out of 10, 16 and 17 available species (Table 4.2).

Seed removal (Figures 4.10 and 4.11)

The fate of seeds from the focal trees in the two seasons, summed for all individuals, is shown in Figure 4.10A (1992) and B (1993). The different seed fates, where they differed from those for other species, were defined as follows:

'dropped'	- fruit that were dropped intact under the tree; some of these (ripe ones) would be removed by terrestrial consumers and others would germinate *in situ*; the immature ones would probably be inviable or unlikely to be removed;
'wasted'	- seeds that were sucked and spat out under the tree; these were not likely to be removed, were often squashed into the soft ground, but may germinate;

Although 'monkey' is used as a category for arboreal consumers other than apes, some of the fruit remains (such as seeds) may have been left by animals other than primates (such as birds). The removal of seeds by particular non-primate frugivores (e.g. birds, elephants, civets) was not assessed (see Chapter 3.2.4). The contributions made by different consumers to the category of dropped immature fruit (effectively wasted seed) is given in Appendix C, which contains all the values for the different categories.

Uapaca fruit can take a long time to ripen. In 1992, a number of trees that were selected had fruit that did not ripen when expected, and were not fed in by any primates to any extent during the time they were monitored. Gorillas did not use this part of the study area during the *Uapaca* fruit season of 1992, so fruitfall data came from only 7 trees, 4 of which were known to have been visited by gorillas and one by chimpanzees. Of the 12 'patches' (14 trees) monitored in 1993, 9 of them (75%) received confirmed gorilla visits. The estimated proportion of the crop that was removed from the crown directly was 36% in 1992 and 34% in 1993.

Figure 4.11A shows the seed fate from the individual focal trees in 1992. Two of the three trees in the forest interior (#U8 & 9) were fed in by gorillas, but only briefly, in passing. Where a gorilla group did feed in a tree (e.g. #U51), they removed a greater proportion of seeds than other consumers. The mean percentage of the seed crop removed by gorillas was 7% (±10.8%, n=7) for all trees, and 12.3% (±12.2%, n=4) for the trees they fed in. The value for monkeys (all trees were fed in) was 35% (±16.1%, n=7). Gorillas did however create considerable 'knockdown'. Ripe fruit falls easily as primates move about the crown, and rejected immature fruit was dropped on broken branches. For many trees, the majority of the seed crop ended up under the parent crown. Dropped ripe fruit may be dispersed by elephants and duikers. Carpets of seedlings may subsequently emerge from fallen fruit and seeds, but they are unlikely to survive long (see Chapter 5).

The data for 1993 are shown in Figure 4.11B, and reinforce the point that, when a gorilla group did feed in an *Uapaca* tree (e.g. #U5), they swallowed and therefore dispersed a considerable proportion of the seed crop, more so than other consumers. This can also be said for chimpanzees for some trees (e.g. #U7). The mean percentage of the total seed crop removed by gorillas for the sample of 12 patches was 11.8%

Figure 4.10 The fate of seeds from the estimated crops on a sample of *Uapaca guineensis* trees. A: 1992 (n=7); B: 1993 (n=12 'patches').

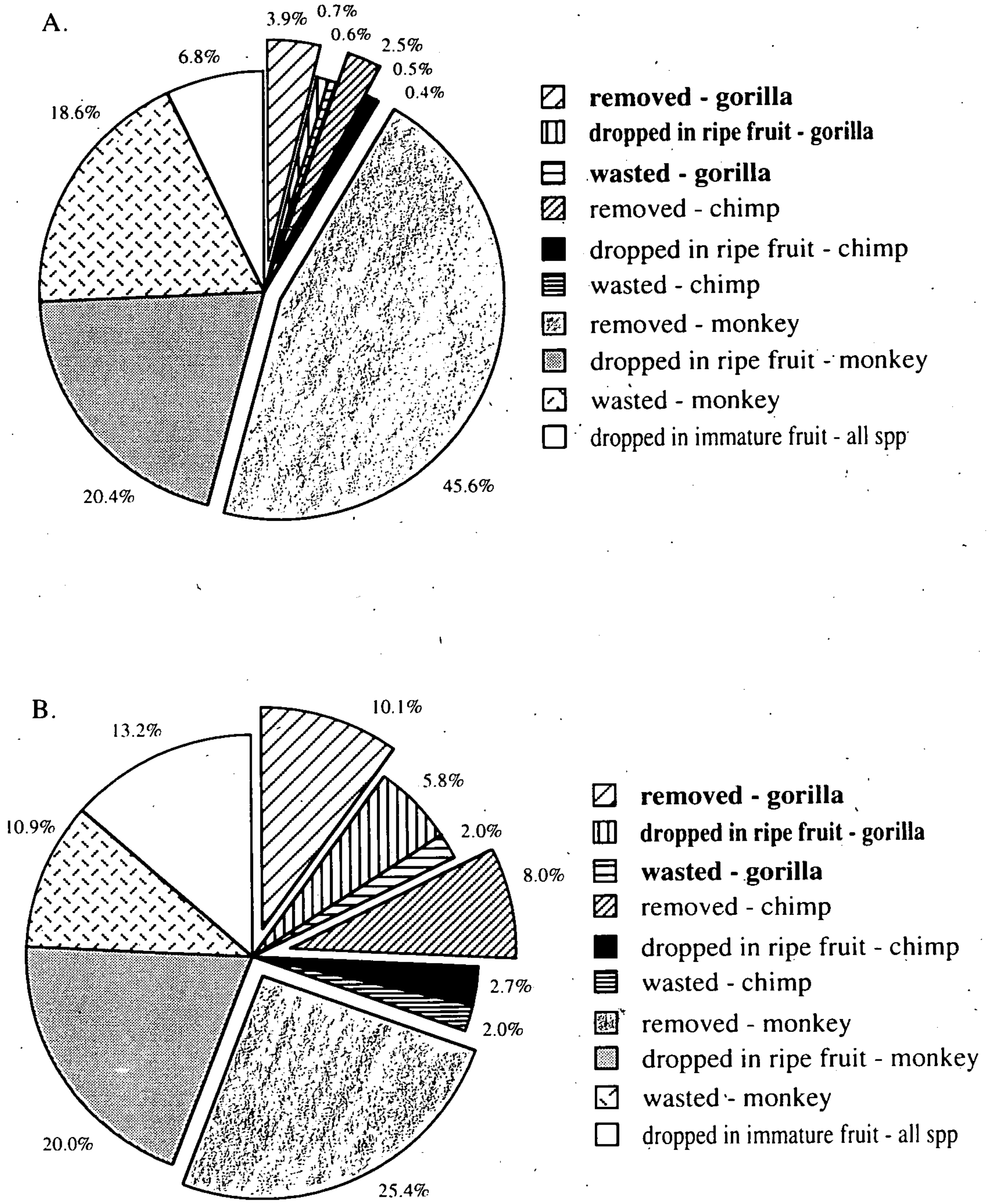
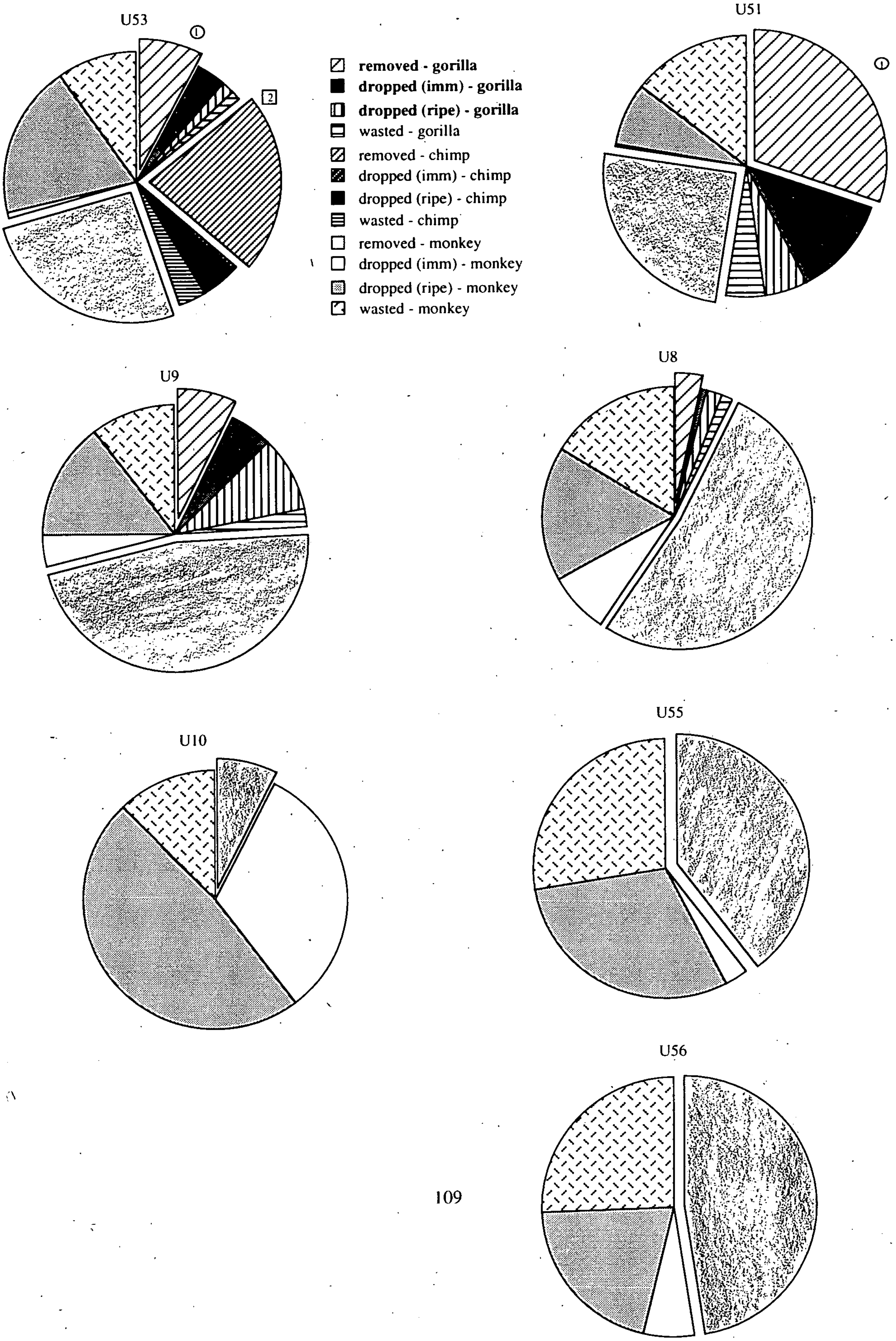


Figure 4.11A The fate of seeds from 7 *Uapaca guineensis* trees in 1992. No. of gorilla visits circled; no. of chimpanzee visits shown in squares.



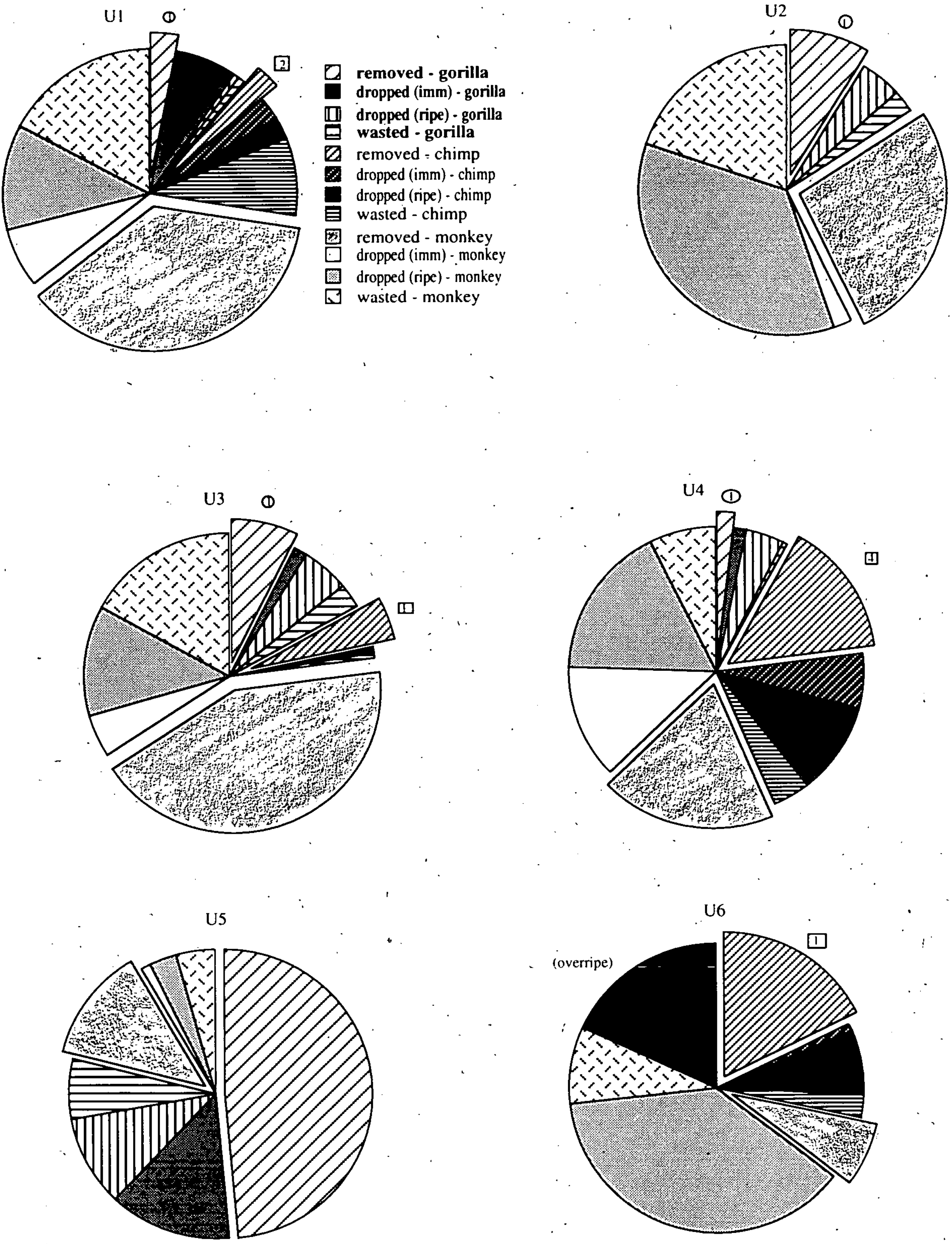
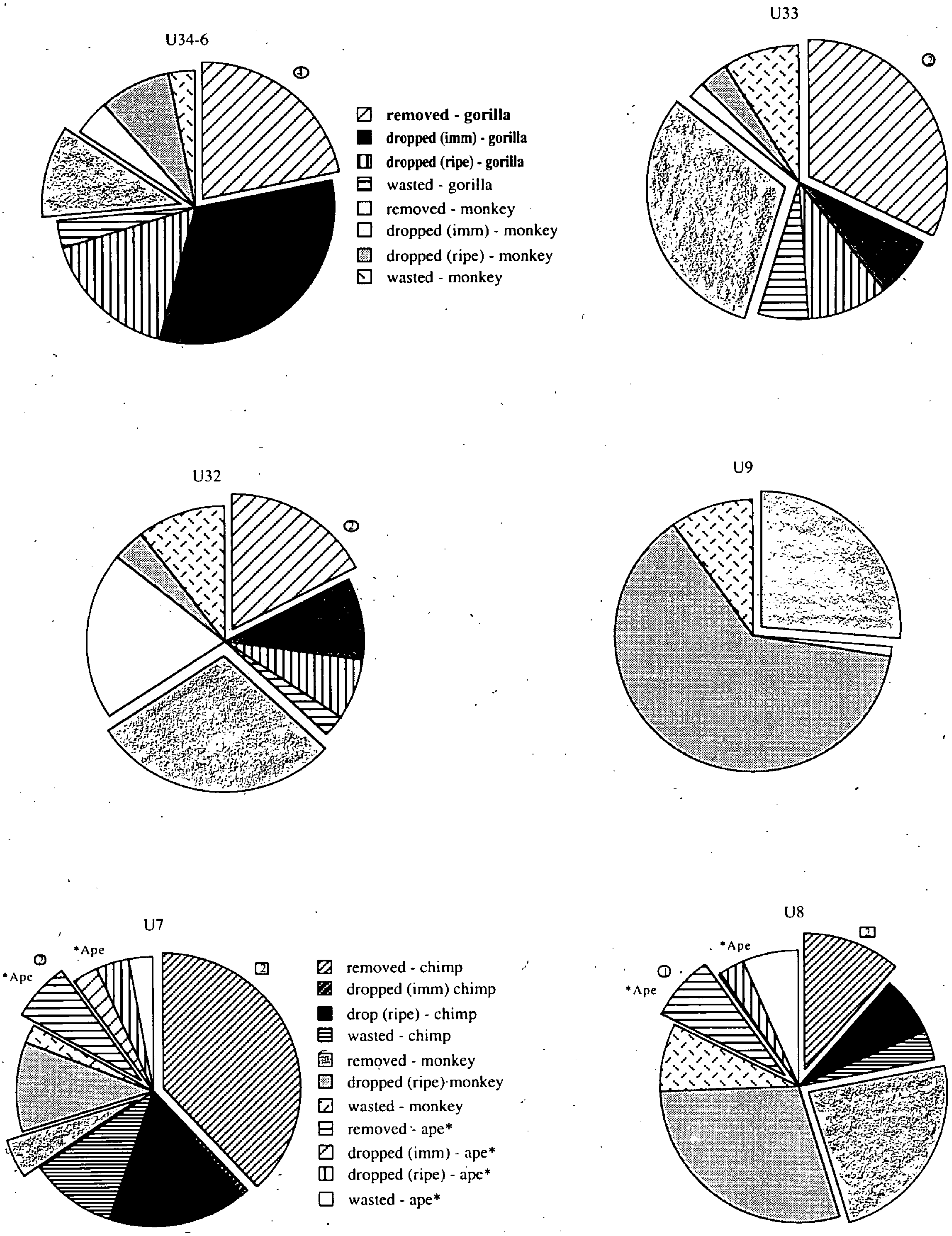


Figure 4.11B The fate of seeds from 12 *Uapaca guineensis* patches in 1993. No. of gorilla visits circled; no. of chimpanzee visits shown in squares. (Continued overleaf).

Figure 4.11B (continued)



(±15.6%, range=0-48.6%) and for the 8 patches they fed in the figure was 17.7% (±16.2%, range=1.7-48.6%); for the 4 patches fed in by a gorilla group (excluding lone male data), the mean percentage removed was 30.1% (±13.8%, range=17.6-48.6%). Overall, monkeys removed an average of 22.1% (±11.4%, n=12, range=4.8-42.9%) and chimpanzees 9% (±12.2%, n=12, range=0-38%) (see Appendix C). There were mandrills involved in the removal of some seeds from certain trees (#U2 & 3); for clarity, their contribution has been lumped with other monkeys, but is quoted separately in Appendix C. The proportions removed by gorillas from trees #U2, U3 & U4 were entirely the result of feeding by a solitary silverback.

Overall, there were no significant differences in the percentage of the seed crop of the sample of trees removed by gorillas and chimps (Wilcoxon's sign test, T=29, P>0.05, n=12), gorillas and monkeys (T=17, P>0.5, n=12) nor chimpanzees and monkeys (T=14, P>0.05, n=12). For most trees, a majority of the crop was dropped under the crown. Tree #U6 was situated alone at the edge of a marsh in the savanna, some 15m from the nearest continuous tree cover, which was *Raphia* palm. This tree received only a single visit by chimpanzees, so most fruit fell intact, and ripe, under the crown. Elephants removed a lot of these (pers. obs.). Storms resulted in considerable quantities of 'dropped' seeds recorded at some trees. The large amount of 'dropped' fruit attributed to gorillas for the patch #U34-6 was in part due to severe storms with high winds the evening before they fed extensively in the patch of trees.

The principal group of gorillas in the study area shifted from their normal home range to a previously unused area in October 1992, feeding extensively on trees in gallery forest some kilometers north of the central study zone. For that season, many trees in that particular area had most of their crops removed by gorillas (pers. obs.), and a majority of fruiting trees were fed on. Observation suggested that gorillas tended to feed only in those trees that were scored above 2 using the phenology scoring system, but no quantitative data exist for this. With the disappearance of that particular group after the death of its silverback in April 1993, our data on fruit removal by gorillas for that year came from trees and a new group of gorillas several kilometers to the west of the main study area.

Sometimes gorillas did eat considerable amounts of entire fruit, in which case there would be no remains to count. This was not a general feature of their feeding behaviour however. On one occasion, when a group of five gorillas were known to feed for 85 minutes in a non-focal tree, practically no remains were found underneath. The circumstances might have dictated a very rapid consumption: the tree was in a very narrow stretch of gallery forest and the gorillas probably knew they were under observation.

Damage to *Uapaca* trees was sometimes severe, especially if gorillas made feeding nests. The degree to which a crown suffered broken branches seemed to depend on the number of gorillas in the group, the length of time they spent feeding, the construction of feeding mats, and the number of times they came to feed in the tree. At the end of the fruit season, some trees looked extremely battered.

Other consumers

Chimpanzees eat a lot of *Uapaca* fruit (see below), and may remove as many as gorillas (Figure 4.11B). Monkeys only scatter-dispersed the seeds from fruit they removed in their cheekpouches by spitting them out as they processed the fruit. Mandrills both swallowed and spat out seeds. Apes and elephants swallowed seeds. As reported above, a large proportion of the seed crop ended up under the crown. Fallen or dropped fruit often accounted for more than 25% of the seed crop. Of these, many were removed by secondary dispersers, particularly elephants. A wide range of animals fed on *Uapaca* fruits (see Chapter 3.2.4). Although quantitative data on removal do not exist for them all, anecdotal evidence suggests that birds disperse relatively few, and most of those are removed by large blue touracos (*Corythaeola cristata*). Civets tend to deposit seeds in middens, often on rocks or roads in open savanna, making them poor dispersers.

Deposition (Table 4.7, Figure 4.3 and 4.4)

Due to the long fruiting period, the data on seed deposition are presented in Table 4.7 in 3-week intervals for each of the two seasons. A total of 153 dung samples, containing 5790 seeds, were collected during the 1992 season. In 1993 the figures were 220 and 9679 respectively. There were some *Uapaca* seeds in dung that was collected in what could not be regarded as the usual fruiting season, but the numbers were extremely small. *Uapaca* evidently dominates the diet when available, because no, or only one, other large-seeded species appeared in the dung at the peak times of consumption, and only in limited numbers. During the peak months of consumption, the proportion of dung samples with *Uapaca* seeds was as high as 97% (Figure 4.3), with a median value of 40 seeds per sample (Figure 4.4). This was the case even when overall *Uapaca* availability was low (Figure 4.2).

A wide range of seed numbers occurred in the samples, up to a maximum of 1196 seeds. One of the nest sites was particularly rich in seeds, containing nearly twice the number of *Ganophyllum* seeds and eight times the number of *Cola* seeds usually found at nest sites. Five nest sites were located and marked for monitoring in 1992, and six sites were found in 1993. An estimated 6800 - 11300 seeds (using median values) were dispersed by gorillas in 1992 (or 16700 to 27800 using mean value) and 9100 - 15100 in 1993 (or 19400 to 32300 using mean values).

Seeds were found in large numbers in chimpanzee dung as well. In November and December 1992, 50% and 73% of dung samples contained *Uapaca* seeds, with a median of 26 and 21 seeds per sample respectively. During the 4 months of September to December 1993, 46%, 50%, 67% and 45% of samples for each month contained seeds, and median numbers per sample were 48, 16, 21 and 21 respectively.

	Dung collected and sieved					Dung marked in situ					
3-week period	no. of dung samples with seeds	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp	no. of dung samples with seeds	no. of nest sites	no. of seeds	median no. of seeds per sample	range	mode no. of other large-seeded spp
1992											
25/6-10/7*	11	44	2	1-15	2						
6-27/10	32	1211	14	1-185	1	2		12	6	5-7	0
28/10-17/11	14	189	5	1-74	0	27	3	1089	17	1-198	1
18/11-8/12	39	1198	18.5	1-158	0	7	1	253	39	14-60	0
9/12-29/12	37	2779	15	2-971	0	7	1	3192	392	129-1196	0
30/12-12/1/93	14	92	3.5	1-18	3						
13/1-4/2	6	277	50	7-101	4						
TOTAL	153	5790				43		4546			
1993											
Apr/May/June*	16	71	2	1-21	1						
July*	15	273	11	4-60	0						
4-25/8*	24	215	7.5	1-24	1						
26/8-15/9*	14	119	5	1-45	0	2		130	65	20-110	0
16/9-6/10	22	591	21	1-95	0	41	4	1416	17	3-127	0
7-27/10	48	3057	47.5	1-490	1	12	2	432	34	7-88	1
28/10-17/11	53	4833	46	1-655	2						
18/11-8/12	10	114	3.5	1-39	1						
9-29/12	18	406	13.5	5-79	1						
TOTAL	220	9679	18			55		1978			

*not the usual fruiting season

Table 4.7 Analysis of gorilla dung samples containing seeds of *Uapaca guineensis*

Other fruit foods

Apart from some *Vitex doniana* (Verbenaceae) at the beginning of the season in 1992, and a considerable quantity of *Gambeya africana* (Sapotaceae) in 1993, dung samples contained few other large seeds during the *Uapaca* seasons (see Table 4.6). Small-seeded species were eaten however, and gorillas also fed extensively on *Pentadesma butyracea* (Guttiferae) and *Irvingia gabonensis* (Irvingiaceae). The seeds of both these favoured foods are discarded due to their size.

4.4 DISCUSSION

4.4.1 Methodological problems

The estimation of the size of a tree's fruit crop, and therefore the number of seeds produced, is a persistent problem for fieldworkers. The merits of several methods for estimating fruit abundance have been discussed by Chapman *et al* (1994). They suggested that observational scoring on a phenology circuit of some kind is reliable, repeatable and gives a good indication of relative and total fruit availability, is efficient in terms of the field effort required, but does not attempt to quantify individual crops. The diameter of a tree was the measure they found most accurately reflected crop size, but in this study no consistent correlations were found between dbh, crown surface area or volume, and crop size, although dbh of *Ganophyllum* trees did correlate with crop size in 1992 (section 4.3.1), and *Uapaca* crown surface area correlated with crop size (section 4.3.4). As the fruit of three of the four study species is borne on the upper, outer surface of the canopy, the crown surface area is perhaps a more useful measure of potential crop size.

The lack of correlation between crown volume or surface area and crop size in this study was probably due in part to the myriad of biotic and abiotic factors affecting the final size of a crop of ripe fruit (and individual fecundity), as well as the difficulty of simplifying the architecture of tree canopies. *Uapaca* canopies had the most easily simplified shape, which may explain the correlation with crop size. A large tree inevitably has the structure and therefore the potential to produce more fruit than a smaller tree, assuming their fecundities to be the same. The historical crop size might be a better correlate. The estimate obtained from trying to count fruit crops directly turned out to be wildly inaccurate and highly variable between observers. A figure based on the fruit counts from fruitfall strips indicated that we were massively undercounting fruitcrops.

Using fruitfall to estimate a fruit crop, whether by traps or strips on the ground, is dependent on what reaches the ground. This will be determined by the structure of the fruit and how it is borne on the tree, as well as the treatment it gets from consumers. If every fruit that is fed upon results in a distinct piece of evidence under the canopy, then it makes crop estimates more secure, but there may be no such evidence. Some fruit may be removed entire from the canopy, feeding remains may stay attached to the tree, or animals might feed on the evidence below before it has been counted. Traps generally sample a small proportion of the fruitfall area and can give unreliable estimates (Chapman *et al* 1994).

Ganophyllum was perhaps the most straightforward of the four species in this respect. Skins were dropped under the parent tree by all consumers, even by monkeys that cheekpouched fruit for later processing. No animals seemed to remove skins from the forest floor, and very few intact fruit were thought to be removed (pers. obs.), perhaps because the skin 'burns' (human) mouths (C. Tutin, pers. comm.). The pods of *Cola* were usually dropped under the canopy, although on occasion monkeys were seen removing intact fruit to process elsewhere. The main problems were encountered with *Dialium*, as explained in section 4.2.2. Monkeys tended to leave the distinct part of their feeding remains attached to the canopy, only dropping fragments of capsules. Broken panicles were also missed if they were snagged in the canopy. For situations such as this, then information from observation becomes important in order to assess at least the relative removal of the crop by different consumers. Counting fallen feeding remains under *Uapaca* trees was complicated if elephants got under the tree after a primate feeding bout before researchers did. Fortunately this did not happen very often, but removal of some intact fruit from the canopy by gorillas probably occurred, resulting in the underestimation of their contribution to seed removal.

In spite of the vagaries of trying to quantify the actual crop size of a tree, the objective of this study was to assess whether gorillas removed more seeds than other consumers, so the interest was in relative amounts rather than actual numbers. There can be pitfalls that come with a passion for quantification. Ecologically, what matters to a gorilla is whether there is sufficient fruit to fill its belly; what 'matters' to a tree is how it is most likely to have its seeds deposited to favourable sites in large numbers. In this respect, none of the issues outlined above seriously marred the overall aims of this part of the study (i.e the relative amounts of seeds removed), even if they did affect the accuracy of the estimates of seed crops.

4.4.2 The removal of ripe seeds from the parent tree by gorillas

As stated in Chapter 1, reliable visitation and the removal of many seeds by a consumer are two criteria that are thought to contribute to high quality dispersal. From a tree's point of view, both can be an aggregate result of more than one species of consumer if the consequences of their visits are the same in terms of post-removal effects. Visitation (and consequent removal of seeds) may be reliable on a time-scale that is more relevant to the fruiting tree, such as the tree's productive lifetime, than on one that is represented by a brief period of study.

Are gorillas reliable visitors to these tree species?

The reliability of visitation by gorillas varied for each of the four species studied but all four dominated the diet of gorillas when available, so at a species level seed removal was reliable. Selection acts at the level of the individual however. The removal of seeds from a particular individual is thought to be influenced in part by the distribution and abundance of fruiting conspecifics as well as other species (the 'fruiting environment', see Chapter 1), the relative crop sizes of the trees, and competition. During this study, some of these elements were apparent.

A higher proportion of *Ganophyllum* trees were fed in by gorillas in 1992 than in 1993. This was possibly a result of intra-specific competition. *Ganophyllum* is not an abundant tree but can be locally common (see Chapter 3.2.1). Two groups of gorillas were active in the area of focal trees in 1992, but tended to maintain some degree of separation, in that the presence of each group somewhat restricted the access of the other to particular areas. This was by non-aggressive means of mutual avoidance. As a result of more gorillas in the area, and thus a more limited choice of fruiting trees for each group, more individual trees were visited (section 4.3.1). In 1993, only one gorilla group was present, and they ranged more extensively, feeding in fewer trees, possibly because they could be more selective and concentrate on large crops given the absence of inter-group competition. The trees ignored by gorillas in 1993 included those with the smallest crops. Monkeys took a larger proportion of the available fruit in 1993, due possibly to the reduction in competition with gorillas. All the focal *Dialium* trees, and a large proportion of others, were fed in by gorillas, with some also attracting chimpanzees (section 4.3.3). *Dialium*, like *Ganophyllum*, is not abundant but can be locally common.

For the hugely abundant *Cola*, however, gorillas may not visit some individuals at all, nor even visit a majority of fruiting trees in their home range in years of fruit abundance. Even if a small proportion of adult trees bear fruit, they remain in such abundance that the number of trees visited in a particular area depends very much on the gorillas' ranging behaviour. Gorillas visited a minority of *Cola* trees (patches) during this study (section 4.3.2). An area used by a group of gorillas in one season may not be used in the following year. *Cola* does however have a prolonged period of fruit availability, which increases the chances of attracting gorillas at some stage during the season. The poor fruit crops of *Cola* and *Dialium* in 1993 showed that it is disastrous for a tree to bear fruit when only a small minority do so, as all the seeds are destroyed or wasted.

Uapaca is also abundant in the habitat in which it occurs. Visitation to a particular tree again depends very much on the gorillas' ranging behaviour. In one small forest gallery favoured by a gorilla group in 1992, at least 8 nest sites were found in the immediate vicinity of a patch of trees, and observation suggested that they visited a majority of the trees in that area. Trees in other areas were not visited by gorilla groups at all. The seeds of those trees would have been scatter-dispersed by monkeys and birds, or dropped and removed by elephants, but more wastage might be expected (section 4.3.4, Figure 4.11).

There was some indication that gorillas preferred to feed in trees with larger crops, even though focal trees were chosen in part on the basis of large crop size. Mannasse and Howe (1983) suggested that trees with intermediate crops are likely to have a greater proportion of seeds removed by birds or monkeys, due to satiation at trees with large crops, but it is unlikely that a group of gorillas is satiated by anything but very large crops. In such cases they may make two or more consecutive visits to the trees. As mentioned above, when in 1993 gorillas had more choice due to there being only one group in the area, the *Ganophyllum* trees they did not feed in included those with the smaller crops (Appendix C). Gorillas fed in an area of *Cola* trees that was in effect a larger food patch, since a higher proportion of the trees there had fruit than was sampled elsewhere (Table 4.4). In this case it seemed that gorillas selected a patch with many fruit rather than individual crops. Other large-bodied frugivores have been shown to select for patch size. Orang-utans apparently do so in Kalimantan (Leighton 1993), and tapirs feeding on *Mauritia flexuosa* (Palmae) fruit in Amazonian forest in Brazil tend to seek out dense patches of this species (Bodmer 1990).

Gorillas made more visits to the *Dialium* trees that were estimated to have larger crops (Figure 4.9), although the estimation itself was skewed upward by repeated gorilla visits and the quantity of remains they left. Assessment by eye of a range of *Uapaca* trees, scoring each using the system described in section 4.2.1, suggested that gorillas tended to feed in trees that had crops scored above 2, out of a possible 4 (pers. obs.). In the extensive system of gallery forest they used in 1992, they seemed to ignore trees with smaller crops and travel to more loaded trees (pers. obs.).

The selection of trees with large crops will tend to provide not only sufficient food to minimise feeding competition, but also a more economical harvest of a quantity of fruit. The energy costs of travel and climbing a tree will be more easily offset if a gorilla can feed for longer in that particular crown. A tree crown has to be large enough to provide sufficient feeding space for several individual gorillas, otherwise competition and exclusion may occur. Most *Ganophyllum, Dialium* and *Uapaca* trees seem to be able to provide this, but individual *Cola* canopies are generally too small to host more than one adult gorilla, which might explain the selection by gorillas of a dense patch of fruiting trees in close proximity.

The fruiting environment might influence whether a tree is fed in by a consumer or not, and possibly the proportion of its crop that is taken (Loiselle & Blake 1993). A tree may be disregarded, or only briefly fed in, if there is a nearby one with a much larger crop (Mannasse & Howe 1983). The overall abundance of fruiting trees will also play a part. Individuals with smaller crops of a rare species are more likely to be visited than those of a common species. This was the case for two focal *Dialium* trees. Gorillas fed in tree #D5, which had a large crop, on 3 occasions, whereas they only fed once, for a limited bout, in the neighbouring tree #D3, which was only 30m away but had a poor crop. Although the number of fruiting conspecifics within 50m of a focal tree was recorded, gorillas seem to have a very detailed knowledge not only of the fruiting patterns of particular species, but also the location of individual trees and even their history of fruit production. Consequently the 50m 'neighbourhood' of a fruiting tree may be of little relevance to gorillas feeding in a tree, for a nearby fruiting conspecific with a relatively small fruit crop may be disregarded if gorillas know that a larger food patch exists elsewhere.

Howe (1990) suggested that the high energy requirements of large mammals might mean that they are only attracted by a fruiting species in years of high productivity. This probably depends on the importance of that species in the diet and the availability of alternative food sources. Gorillas at Lopé do exhibit dietry flexibility and in years or seasons of low fruit production eat immature fruit and/or seeds, or feed on other (non-fruit) foods (Rogers *et al* 1988 & 1994, Tutin & Fernandez 1993b). The four species that comprised this study dominated the diet when they were available, but other species were also eaten to some extent during the same period. If fruit crops of one species are poor, then gorillas are more likely to concentrate on other species. During the *Cola* fruiting season, a highly favoured food that fruits only rarely (*Celtis tessmannii*) bore fruit that influenced the gorillas' foraging patterns. Gorillas may have fed in more *Cola* trees had *Celtis* fruit not been available. Unfortunately the lack of *Cola* fruit in the following year prevented this from being tested. Nonetheless *Cola* remained prominent in the diet, probably due in part to its abundance. Towards the end of the *Cola* season, when the availability of ripe fruit declined, gorillas began to eat *Dialium*. *Dialium* appears to attract reliable visitation by gorillas, but for *Uapaca* trees it is not so certain. The distribution and abundance of *Uapaca* trees meant that, despite a prolonged fruiting season, gorillas were only reliable visitors to certain trees in a particular area.

Do gorillas remove a large part of a tree's crop?

For those *Ganophyllum* trees visited, the data suggest that the answer is 'yes'. That is also the case for *Dialium*. To extrapolate with some caution, it might be that gorillas remove a large proportion of the seeds produced by a population of these two species in most, if not all, seasons. The answer for the other two species is more equivocal. For a *Cola* tree, it may be the case that gorillas remove a large proportion of the crop, but it is by no means the rule. The likelihood of removal by gorillas probably increases if the tree is located among a group of fruiting trees that together provide a larger food 'patch'. This might select for synchronous fruiting of *Cola*. For the sample of trees monitored in 1992, when a small proportion of trees in the area bore fruit, monkeys removed more of the crop than gorillas did, and a majority of the seeds (intact or damaged) ended up under the parent crowns. This probably reflects the picture for a larger population of trees.

The *Uapaca* trees in the sample that were visited by a group of gorillas tended to have a considerable proportion of seeds removed, but it was never the majority of the crop. It was often more than was removed by alternative arboreal consumers however (see below) but there was also considerable knockdown of intact fruit (Section 4.3.4, Figure 4.11). Most trees of the four species were only visited once, the amount remaining after a single serious feeding bout presumably insufficient for a second bout. Only trees with large crops were visited more than once, or if the first visit was brief, as happened with *Dialium*. Trees of species with sequential ripening, such as *Uapaca*, were more likely to be visited more than once, but this was influenced by the abundance of trees with good fruit crops. Gorillas returned to certain trees if they still had good crops of ripe fruit on, but otherwise found other trees to feed in. Jordano (1992) suggested that sporadic visits by large frugivores can have a bigger effect on crop removal than consistent visitation by small ones. Gorillas are big as well as consistent for these species, so may well account for considerable crop removal for those trees they visit, even if they make only one or two visits.

One consequence of attracting gorillas as dispersers is the potential damage that may be sustained by the tree (Chapter 2). Canopies of *Dialium* and *Uapaca* in particular are frequently damaged by these heavy animals that cannot move out to the canopy's edge. A group of feeding gorillas, or a solitary adult male, can inflict considerable structural damage by breaking branches both to bring fruit at the ends of branches within reach and to construct feeding mats. This is potentially a considerable cost for the tree. It loses photosynthetic capability as a result of leaf loss, becomes vulnerable to pathogenic infection through wounds, and has to divert resources to repair its structure and foliage which might otherwise have been used to increase leaf area or for reproductive allocation. The degree to which gorillas will damage a tree depends in part on the architecture and structural strength of the species, as well as the number of gorillas that feed in the canopy at the same time. It may be that *Ganophyllum* branches are more pliable, so do not break when they are bent towards a gorilla, or its architecture allows fruit to be harvested from above or below a secure branch. The 'pruning' effect of gorilla damage may result in a more branched structure, which would increase the number of potential inflorescences. To the naked eye, *Dialium* canopies do seem more densely branched than the similar-sized *Ganophyllum* trees.

4.4.3 What are the alternatives to seed removal by gorillas?

Even if gorillas do not remove the majority of a crop of seeds, they may still remove more than other consumers, or be less wasteful in their treatment of seeds. For the species in this study, at the size scale of the fruits as well as their structure, birds are unlikely to make anything but a small contribution to crop removal, even for the more generalist *Uapaca*. Smaller primates are more likely to be "pulp predators" (fruit thieves), spitting seeds under the canopy (Terborgh 1983). The cheekpouches of the Cercopithecine monkeys enable them to carry out scatter-dispersal, but they are still generally restricted to pre-ingestion processing of the four study species of fruit to avoid unwanted ballast in the gut.

The data for *Ganophyllum* suggest that gorillas did remove more seeds than the other consumers, monkeys, for the trees they visited. This was the case in all trees visited in 1992, and all but 3 trees in 1993, and was the pattern observed for clusters of other *Ganophyllum* trees in other parts of the study area (pers. obs.). Monkeys certainly wasted a larger proportion of the seed they handled than did gorillas, so a tree that was not visited by gorillas was likely to have more of its crop dropped under the canopy (Figures 4.6). Those seeds that *were* removed by monkeys were spat out usually under intact forest canopy in the vicinity (less than 100m) of the parent. In this case they were scatter dispersed by legitimate but wasteful dispersers.

Ganophyllum was ranked 47th among food species of *Cercocebus albigena* in terms of the time spent feeding by a group by Ham (1994), but this figure is probably misleading because of the very short fruiting season. Observation suggested that these monkeys spent a lot of time feeding on *Ganophyllum* when it was in fruit. Their visits usually preceded those of gorillas, and no (or very few) visits were made after gorillas had fed extensively in a tree. Invertebrates fed on some developing seeds and accounted for what was usually a small proportion of seeds. Chimpanzees swallow and disperse *Ganophyllum* seeds, but as no evidence of visits to any focal trees was found, and seeds were found in only limited numbers in chimpanzee dung, they could not be regarded as reliable visitors, nor did they appear to remove many seeds. It is possible that at this time they feed on another, preferred, fruit that gorillas do not eat, or their more fluid social structure enables them to forage alone or in small groups further afield where other foods are available (Tutin *et al* 1991b).

Cola trees provide monkeys not only with fruit that they eat immature as well as ripe, but also ants, on which they feed extensively (Ham 1994). *Cola* was ranked by Ham as the most important fruit pulp food for *C. albigena*, but data from this study suggest that they waste a lot of seeds by eating fruit immature (Figure 4.8). They may do this as a means of competition avoidance because it is such an important food for gorillas (Ham 1994), although the abundance of the tree suggests that such competition is unlikely to be intense every season. In 1992 gorillas were perhaps distracted from *Cola* by the fruiting of *Celtis*, and towards the end of the season switched to *Dialium*. A large group of mandrills wasted a lot of *Cola* seeds by eating fruit whilst it was immature. Although they only fed in 3 focal patches, they wasted nearly a quarter of each crop in the one visit they made. They were observed to feed predominantly in *Cola* trees as they moved through the study area. A large proportion of seeds that were handled by monkeys were dropped under the canopy, either individually or in broken or intact fruit. Nonetheless the proportion of a tree's crop removed by monkeys was in the order of 25-50%. Most of these would have been dropped under or close to conspecifics, because a *Cola* tree is never far away in the study area.

Only gorillas and chimpanzees disperse *Dialium* seeds in any quantity; the contribution of *Cercopithecus* monkeys is probably relatively minor (C.Tutin, pers. com.). Visits by chimpanzees could only be confirmed at 4 of the 10 focal trees (Figure 4.9), and they did not seem to remove anything like the quantity removed by gorillas, even taking into account the difficulties of assigning absolute quantites to chimpanzees and monkeys. Seeds appeared in greater numbers in chimpanzee dung, but this might be explained partly by the smaller quantity of non-fruit plant parts eaten by chimpanzees; gorillas eat a much larger amount of fibre. Both apes also act as seed predators of this species, either splitting seeds in the tree or, in the case of gorillas, by eating seeds from their dung. *Dialium* seeds are a preferred food of*C. albigena* (Ham 1994), perhaps due to the high concentrations of protein. A group of monkeys can destroy a considerable number of *Dialium* seeds, but the preingestion processing is time-consuming, so they are unlikely to affect a large proportion of a tree crop.

The more generalist strategy exhibited by *Uapaca* means that seeds are removed by a number of consumers, and this sets *Uapaca* apart from the other species in terms of dispersal. The initial fate of many seeds is to end up under the parent canopy, often in intact fruit. Monkeys only scatter-disperse the seeds they remove, blue plantain eaters probably regurgitate or defaecate some of the seeds they ingest away from the canopy and civets swallow seeds. The ripe fruit fall easily from the canopy and provide food for elephants, which in turn disperse the seeds in considerable numbers over a wide area, although White (1992) recorded seeds in only 5% of dung piles in the 5 months they were apparent. Elephants go to trees of some species (such as *Celtis tessmannii* and *Gambeya africana*) that have just been fed in by apes to feed on the fruit that has been knocked down, probably using smell and possibly sound as their cue. Chimpanzees may remove and disperse through their dung a considerable proportion of the seed production of an *Uapaca* tree. In this study, for some trees it was over 25% of the estimated crop (Figure 4.11). This can depend in part on the location of the tree and the ranging patterns of chimpanzees that particular season.

No direct evidence of competition between gorillas and chimpanzees for any of these food species has been recorded, possibly due to different behavioural and foraging strategies, the abundance of the species, or their respective importance in the apes' diets.

4.4.4 Deposition

Nearly all the seeds of these four species that gorillas handle are ingested and deposited intact in a pile of dung some distance from the parent tree. The numbers of seeds found in dung are a clear indication of the quantity that they disperse from fruiting trees. For each of the species, seeds were found in a majority of dung samples throughout the main fruiting period (Figure 4.3 & 4.4). If gorillas usually make one visit to a particular tree but visit several trees in a day, then the seeds they remove will be deposited in clumps, but will be of mixed parentage. Gut passage times are "long and variable" and may be up to 36 hours (Milton 1984), so seeds are unlikely to be deposited close to the parent. As discussed in Chapter 2, gorillas defaecate at least 3-5 times a day, and much of their output occurs at nest sites (Schaller 1963), which become effectively seed repositories. The rough calculations suggest that each gorilla disperses thousands of seeds of these species each season. In the case of *Ganophyllum*, *Cola* and *Dialium*, the number of seeds removed in a single feeding bout, derived from the precise counts of fruitfall, suggest that these were considerable underestimates.

Apes may be far more important consumers of seeds than their densities indicate. In Kibale forest in Uganda, the number of seeds in guenon and managbey dung is only 2% that found in the average chimpanzee dung pile (Wrangham *et al* 1994). The authors state that chimpanzees, although making up only 1.4% of the population of frugivorous primates, account for 45.3% of defaecated seeds. No gorillas occur at Kibale. At Lopé mangabeys have been found to be more frugivorous than at other sites, but eat more seeds than they disperse (Ham 1994), although no quantitative data exist for seeds in monkey dung at Lopé. Based on the same criteria used by Wrangham and colleagues, gorillas are likely to be even more important than chimpanzees as seed dispersers of some species at Lopé because they are bigger, and ingest a higher quantity of seeds.

4.4.5 SUMMARY

In spite of the dangers of generalisation, especially from such small samples in only one or two seasons, it can be said that for these four species, gorillas may not be the only "legitimate" consumers but they are generally less wasteful and in some cases remove more seeds from the trees they visit than do other consumers. If legitimacy or quality is associated with seed swallowing, then the relative importance of gorillas as consumers is even greater. For *Ganophyllum*, they were the only reliable visitors to swallow seeds; for *Cola* they were the only consumer to swallow seeds, but did not account for most of the seeds removed; for *Dialium* they were the only reliable visitor and swallowed seeds in large quantity, and for *Uapaca* their services were probably akin to the other seed-swallowing ape, the chimpanzee, in that they removed a similar quantity of seeds. The greater proportion of knockdown associated with gorilla feeding on *Uapaca* provides more food for elephants and thus a likelihood of secondary dispersal.

There is probably no such thing as a "typical" year in terms of tree phenology and gorilla behaviour, for every year is different in terms of fruit production and foraging patterns. Nonetheless, by studying what happened in a more normal year, as well as one that was somewhat unusual, a good general idea of the importance of gorillas as consumers of these species has been obtained.

Gorillas might be important for these species as consumers and dispersers of their seeds, but the post-dispersal component of quality (the fate of deposited seeds) had also to be assessed because, as Janzen (1983) put it, "lots is not necessarily best". This forms the contents of the following chapter.

The main summarising points of this chapter are as follows:

1. All four species were confirmed as preferred or important foods for gorillas, dominating the diet whenever available.
2. Reliable visitation to individual trees was documented for all species: in the case of *Ganophyllum* and *Dialium*, the majority of fruiting trees were visited, but gorillas visited a minority of the abundant *Cola* and *Upaca* trees that were sampled. Visitation frequency is related to the abundance of the tree species and is affected by gorilla behaviour.
3. Gorillas were the major consumers for all of the *Dialium* and most of the *Ganophyllum* trees they visited, and for some of the *Cola* and *Uapaca* trees they fed in.
4. The treatment of seeds by gorillas was less wasteful than by other consumers in terms of the proportion dropped under the canopy, and they swallowed rather than spat out the seeds. Only chimpanzees swallowed *Uapaca* seeds in similar quantites to gorillas, and they were the only other animal to swallow *Dialium* seeds. From faecal analysis, chimpanzee dung contained more *Dialium* seeds than gorilla dung, but this was not the case for *Uapaca* seeds.
5. Gorillas caused considerable damage to many of the trees they fed in, especially *Dialium* and *Uapaca*. This is an additional energetic cost to the tree for the dispersal services provided by gorillas.
6. Each gorilla disperses thousands of each species' seeds every season, depositing them in dung piles, often located at night nest sites.

Chapter 5

STUDIES OF SEED DISPERSAL II: FROM SEED TO SEEDLING

5.1 INTRODUCTION

In the previous chapter it was shown that gorillas consume and disperse large quantities of seeds of the four study species. Gorillas often removed more than other consumers and at some trees even the majority of the crop. That makes them important consumers of these species, but it does not necessarily follow that they are important dispersers. The quality of seed dispersal depends on what happens to the seeds once they have been removed from the canopy. This 'post-dispersal' component of quality must be addressed in order to assess the contribution that gorillas make to effective seed dispersal. The only control a tree has over the fate of its seeds is by means of the characteristics of the fruit, seed and seedling. Chance plays an enormous part in determining which seeds ultimately survive to become reproducing adults. This chapter deals only with the very start of the process, but it is a vulnerable stage of a plant's life-cycle. Most mortality occurs at the seed and seedling stage, so factors influencing seedling survival inevitably determine the potential distribution of adults. A number of issues relating to the fate of dispersed seeds have been discussed in Chapter 1. The site of deposition in particular is likely to be crucial to the survival and growth of seeds and seedlings.

As described in Chapter 3, the seeds of the four study species may be dropped singly under the parent canopy or spat out singly under intact forest cover a short distance away (scatter-dispersed), or they may be swallowed and deposited in dung (clump-dispersed), often far from the parent. The quality of seed dispersal by a particular frugivore may not always be high for a particular species, but if it is consistently better than the alternatives provided by other consumers then that frugivore is probably important.

The main aim of this part of the research was to follow the fate of seeds dispersed by gorillas, especially of those deposited at nest sites. Questions guiding the study were: Does dispersal by gorillas make a difference to the plant's chances of reaching maturity? Are some places of deposition better than others for establishment and growth? By comparison with seeds that were spat out by monkeys under or away from the parent tree, it was hoped to establish whether seeds and seedlings survived or grew better if dispersed by gorillas. The underlying assumption was that if some of the seeds removed by gorillas are reliably deposited in more favourable sites than by other species, then from an ecological and evolutionary perspective, gorillas are likely to be important as dispersers. Another objective was to investigate the germination strategies of the species.

5.2 METHODS

5.2.1 Seeds dispersed by gorillas

Gorilla dung at nest sites located during the fruiting season of each species was marked and checked at intervals to monitor the survival and growth of seeds and seedlings. Upon finding a nest site, each dung pile was examined to count the total number of seeds of the study species it contained. The dung had to be broken apart in order to do this, so it was reformed as near to its previous state as possible afterwards. Seeds of other species in the dung pile were noted and the age class of the gorilla (judged from the diameter of the dung) was recorded when possible. The number of seeds in a clump was used, rather than the number per unit weight of dung, because the number in a clump (the size of the seed aggregation) is more relevant in ecological terms. Every dung pile was marked with an aluminium tent peg that had a numbered tag attached to it, made of adhesive PVC tape. Dung piles that were found on gorilla feeding trail were also included, and data were taken as described above. For the most part, these dung piles were on or close to animal paths used by the gorillas when travelling. Dung found on feeding trail far from paths was not marked, because relocation would have proved too difficult in the dense vegetation.

Features of the local environment at a nest site were recorded as follows: a measure of the canopy cover at three height classes (≤4m, 5-20m, >20m) above each dung pile was obtained using a point quadrat method (Greig-Smith 1983). Looking vertically upwards through a clinometer, cover was scored if vegetation at a particular height obstructed the narrow field of view. Cover at less than 2m was visually assessed with the naked eye. A canopy cover score was given to each clump in a nest site. 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 ≤4m, it scored 6 points, at 5-20m, 3 points, and at ≥20m, 1 point, giving a maximum of 10 points for vegetation cover at all levels. The presence of leaf litter, slope, distance to the nearest tree ≥10cm dbh, and the position of the dung pile relative to the nest construction (inside, on the rim, outside) was recorded, along with any other salient features (e.g. by a log, under a vine tower, near the savanna edge).

For each dung pile found and marked, the number of seeds it contained was counted. Dung was then monitored to follow survival and growth. Generally, dung was checked every week for 6 weeks, then every 2 weeks for 6 weeks, then monthly for 3 months and thereafter every 3 months. This schedule had to be somewhat flexible for logistical reasons. Initially the number of germinating seeds was recorded, but this was not done accurately, because the disturbance of the pile of seeds required would have damaged the emerging radicles or otherwise disrupted the pattern of survival. For the same reasons, it was not possible to count the number of ungerminated seeds. Once the seedlings started to emerge, the following data were recorded: the number surviving in the clump; the range of their heights (ground level to apical bud); the length of the longest leaf in the group; the maximum number of leaves on any one seedling in the clump; and any indication of causes of mortality (e.g. seed predation, browsing by herbivores, trampling, or attack by pathogens). Measurements were taken for the clump as a whole, using the maximum values in each category, because it was not feasible to tag, measure and monitor individual seedlings. Height, longest leaf and number of leaves were assumed to be an indication of individual performance, if not fitness. Clumps of seedlings were monitored until the end of the study in mid-November 1993. Nest sites were monitored for 92 weeks for the first *Ganophyllum* sites marked, to just 4 weeks for the last *Uapaca* sites. Surviving clumps of seedlings continue to be monitored by permanent researchers at SEGC.

5.2.2 Scattered and dropped seeds

A variety of approaches was used to investigate the fate of seeds that were dropped under the parent or conspecific canopy, or scatter dispersed by monkeys processing fruit near to a focal tree. For logistical reasons, not all techniques were used each season for all four species.

Seed quadrats

Seeds dropped onto the fruitfall strips were collected and placed in quadrats under focal trees or away from them, under intact forest canopy. Each quadrat measured 50x50cm, with seeds placed regularly at 10cm spacing, a total of 36 seeds per quadrat (for the large *Cola* seeds only 25 were placed per quadrat). Aluminium tent pegs with a PVC tag were used to mark the corners of the quadrats, which were oriented in the same direction. Quadrats were established under focal trees (avoiding the fruitfall strips), or on the forest floor under other tree canopies up to 80m distant from the parent. This was generally done towards the end of the fruiting season in order to minimise the chance of additional seeds being dropped, or falling, into the quadrat. Monkeys transport seeds in cheekpouches up to 100m from fruiting trees, spitting them out under the trees in which they stop to process the fruit. This was the treatment mimicked by placing out the marked quadrats.

Quadrats of *Ganophyllum* seeds were set out in the second season only (1993). Eight were located under parent trees and 6 were located under intact forest canopy away from the parent. The 14 quadrats contained a total of 504 seeds. Ten quadrats of *Cola* seeds were set out under 3 focal trees in 1992. Quadrats away from focal trees were planned for the following season, but due to the failure of the fruit crop this proved impossible.

Dialium seeds from washed gorilla dung (insufficient numbers were found in fruit or under parents) were stored over the dry season, then subject to 2 treatments before being set out at the start of the rainy season. It was thought that moisture uptake influenced the germination ability of *Dialium* seeds, so some were put out dry whereas others were soaked for 36 hours in rainwater. A total of 14 quadrats of each treatment were set out under 5 focal tree crowns (3 of each under 4 trees and 2 of each under 1 tree); each quadrat of dry seeds had a quadrat of soaked seeds adjacent to it. A corresponding 14 quadrats of soaked seeds were set out up to 50m away from the 5 focal trees. The total number of dry seeds put out was 504 and of soaked seeds, 1008, half under focal trees and half away.

In the case of *Uapaca* in 1992, fourteen quadrats of seeds were placed under 5 focal tree crowns, and 10 quadrats away from focal trees, a total of 864 seeds. In 1993, 10 seed quadrats were set out away from *Uapaca* trees in gallery forest at the very start of the season (September), and 11 quadrats were set out in the forest interior in October, away from focal trees. No quadrats were placed under fruiting *Uapaca* trees in 1993.

When it was realised that severe predation of *Ganophyllum* seeds was occurring in 1993 (see below), a search was made under 4 focal tree canopies 10 days after the end of the fruiting season to establish if seeds under parents were as vulnerable as those in dung piles. Twelve random quadrats of 50x50cm were thrown under the trees and, as long as they did not fall on the fruitfall strips, all germinating and ungerminated seeds in each were counted.

To test the viability of immature *Cola* seeds that had been dropped or spat out by monkeys, 150 seeds were set out in 7 quadrats in the forest, and 120 seeds were taken and placed in the nursery in camp (see below).

Labelled seedlings

As a means of following the growth and survival of seedlings originating from dropped and scatter-dispersed seeds, searches were made under focal trees for seedlings 1-4 months after fruiting. Seedlings (of that season) were individually labelled with white plastic tags, and their heights recorded. The tags had a self-locking collar and numbers were marked on in pencil. These seedlings were checked and remeasured every three or six months. If a tag was found without a seedling, it was presumed that the seedling had died. Any tag that was not found after two successive checks, was presumed to have been buried or lost after the death of the seedling. The use of labelled seedlings compensated for the high losses of seeds and early seedlings which diminished sample sizes. By labelling those seedlings that had escaped the high mortality affecting the first few weeks, the 'next stage' of early seedling survival could be monitored.

In 1992, under 11 *Ganophyllum* focal trees, 168 seedlings were found and labelled. In 1993, it was noticed that a proportion of *Ganophyllum* seeds exhibited delayed germination, germinating in April rather than January. One cohort of newly-germinated seedlings was labelled in February (74 seedlings under 8 trees and 98 seedlings found away from focal trees, resulting from scatter-dispersal) and another in May (140 seedlings under 8 trees and 80 seedlings away from parents).

Only those *Cola* seedlings growing under conspecific canopies were labelled in 1992 (200 seedlings under 7 trees). In 1993, when there was a general *Cola* fruit failure, it was possible to label 100 seedlings growing away from parents, but in a forest fragment that had no herbaceous ground cover, and a closed canopy. The dormancy and staggered germination of *Dialium* seeds (see Chapter 2) allowed seedlings under 7 conspecific canopies to be labelled at various times during the year, but each time only newly-emerged seedlings were labelled. A total of 141 seedlings were labelled. Under each of the three focal *Uapaca* trees in the forest interior, 300 seedlings 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.

As an alternative method to labelling seedlings, some quadrats containing seedlings were established under 3 focal *Uapaca* trees. Quadrats of 50x50cm were marked out on the eight principal compass points, half way between the trunk of the tree and the edge of the crown. The number of seedlings in each and the range of their heights was recorded every three months. This allowed us to compare their survival and growth with that of seedlings with labels, to see whether labelling had any discernable effect on growth or survival.

Use of the camp nursery

A nursery was established in camp originally to grow seedling specimens of a range of species for the herbarium collections, but it was used to investigate the germination strategies of the study species. Seedlings of the four focal species grown in the nursery permitted experimental re-planting in the forest to consolidate data on seedling survival. Seeds were placed in individual pots or on trays containing a mixture of fibrous elephant dung and forest soil. All the pots and trays were placed on a platform 50cm off the ground screened from direct sunlight, and were regularly watered. Germination trials carried out in the nursery used seeds from washed gorilla dung or from underneath the fruiting tree.

A total of 154 *Ganophyllum* seeds from washed gorilla dung and 100 seeds spat out by monkeys were placed in the nursery and their germination success was recorded. Additionally, 111 seeds from gorilla dung that had been in the forest during the atypical dry period (see Chapter 2) were collected and put in the nursery. The germination of 120 immature *Cola* seeds dropped by mandrills and other monkeys was also tested. The germination of 190 'soft' (immature) *Dialium* seeds taken from washed gorilla dung and 50 from immature fruit was compared. Ripe, 'hard' *Dialium* seeds are small enough to be buried by dung beetles, and burial was thought to be one possible influence on germination. In one trial, 65 seeds from fruit collected in May 1992 that had been kept on soil in the nursery and watered, but had not germinated, were buried at depths of 0, 1, 2, 4, and 8cm, in rows of 13 at each depth. In another trial run concurrently, 185 *Dialium* seeds recovered from gorilla dung and stored in a sealed container during the dry season, were planted in the same conditions as the first trial but in rows with 37 seeds at each of the five depths. Germination was recorded for 39 weeks after planting. Both of the trials began in January 1993.

Two trials were made to compare the germination of *Uapaca* seeds from ape dung and those dropped under the parent canopy were made. In the first, 99 seeds from chimpanzee dung and 167 seeds from gorilla dung were used. In the second, seeds from chimpanzee dung (32 seeds), gorilla dung (32 seeds), and seeds spat out by monkeys under two focal trees (90 and 60 seeds) were used. All the seeds used sank in water, so were apparently viable (see Chapter 3).

Planted seedlings

Some seedlings that had been grown in the nursery in camp were planted out in the forest. All the seedlings had at least their first leaves. In 1992, a total of 94 *Ganophyllum* seedlings were planted out in 17 groups (4 or 6 seedlings in each, spaced 5cm apart) away from parent canopies. In 1993, with most seeds lost to predation (see below), 49 seedlings from the nursery were planted in 3 nest sites at 19 dung locations that had been monitored but had no remaining seeds or seedlings. This artificially gave a particular clump one, 2 or 3 survivors. The seedlings were monitored in the same way as those growing from dung. A small number of *Dialium* seedlings were also planted out in the forest, a total of 30 in 6 groups of 5 seedlings.

Other seedlings and stem densities of herbs

In order to establish the 'background' densities of seedlings in the forest, an existing line transect running through the central study zone was used to record the densities of seedlings of some of the species classed as important gorilla foods and others in the 'top ten' tree species in terms of basal area (calculated for this transect, see Chapter 2 and Tutin *et al* 1994). Quadrats of 10 x 1m at 15m intervals (40% sampling) were surveyed along 1850m of the transect, with seedlings of the different species counted and recorded.

Attempts were made to relocate old nest sites made in previous fruiting seasons of the four study species in order to look for seedlings that might have been associated with them. A number of nest sites were chosen, found during the years 1989-1991. Two criteria determined the choice of sites: they had to be relatively straightforward to find and the dung (containing seeds of the study species) had to have been left *in situ*.

The densities of stems of plants belonging to the two dominant families of understorey herbs, Marantaceae and Zingiberaceae, were already known from the forest transect (White *et al* 1995). I wanted to compare this with the typical stem densities found around dung piles at nest sites and under fruiting canopies of the four study species. At each monitored nest site, stem densities of herbs were recorded in the same way as White *et al* (in press), by counting the number of stems of each species in 1x1m quadrats. The species of Marantaceae surveyed were *Haumania liebrechtsiana*, *Hyspelodelphis violacea*, *Megaphrynium* spp (principally *M.velutinum*, and some *M. machrostachyum*) and *Marantochloa cordifolia* and *M. purpurea*. The Zingibers surveyed were *Aframomum* sp ?nov and *Renealmia* spp (predominantly *R. macrocolea* and some *R. cincinnata*). At nest sites the quadrats were placed over each dung pile or clump of surviving seedlings, with the clump in the centre. Under the focal trees, quadrats were placed on the eight principal compass points midway between the trunk and the canopy edge.

Analysis of results

Non-parametric statistical tests were used in almost all cases, due to the sample sizes, large variation and skewed distributions. Tests were 2-tailed unless otherwise stated. Sources were Siegel & Castellan (1988) and Fowler & Cohen (1990).

5.3 RESULTS

Explanation of terms

In this section, the performance and survival of clumps of seedlings are presented in a variety of ways in the tables and figures relating to each species. Some terminology requires an explanation. The "cover score" is the value arrived at from the assessment of vegetation cover described above (section 5.2.1). The performance of a seedling or clump of seedlings can be expressed in different ways. "Lifespan" is the length of time that seedlings persist in a clump. In this case, the maximum was the end of the study, although some were surviving at this time, and their true lifespan could be many years or even decades beyond this. The "maximum height" is the height of the tallest seedling in each clump.

Growth can be quoted as the maximum percentage height gained, which is given by: [(max.height - original height) / original height] x 100. The overall percentage height gain can be summed for a sample of clumps at a nest site, or of seedlings under a tree, by [(Σheights at time1 - Σoriginal heights) / Σoriginal heights] x 100. This was the method used by Hladik and Blanc (1987) in north-east Gabon. Using the % height gain alone will positively bias those clumps that persist for longer, *i.e.* have longer lifespans, so a measure of the average growth of a given clump was derived by dividing the maximum percentage height gained (%HG) by its lifespan. Hereafter, "growth" will be taken to mean %HG/lifespan unless otherwise stated.

From an ecological point of view, the success of a location can be viewed in terms of the proportion or number of deposition sites that still contain at least one potential adult. The number of seedlings remaining (the contribution to the seedling bank), and the number of separate clumps they persist in, is an important aspect of seedling survival or performance. This will be referred to as "clump persistence".

Rationale for the presentation of data on seedling survival

An important feature to explain is the way in which seedling survival is presented in the figures. At the start of the monitoring period, the number of *seeds* were counted in each dung pile, but thereafter it was the number of *seedlings* that was recorded. A total recount to include ungerminated and predated seeds was not done, to avoid disruption of the pile of seeds and young seedlings. Thus the *proportion of the original number of seeds deposited that were surviving as seedlings* was recorded each time.

The graphs of survival therefore combine two processes: a recruitment to a seedling population as the seeds germinate (and concurrent seedling mortality); and the loss of intact seeds (by predation, to germination, or a failure to germinate). From the values of proportional survival in each dung pile at a nest site, on trail, or in each seed quadrat, a median value was calculated. The small sample sizes and large variation were the reasons for using the median value. The survival of seedlings in the nest sites (or at other locations) is therefore shown as the *median* proportion of the number of seeds originally deposited, that survive as seedlings over time.

Another important aspect of the presentation of seedling survival is that, within each group of locations (e.g. a nest site, on trail, or quadrats), any clump that had no seedlings left at all, *i.e.* became demographically dead, was excluded from the analyses. The median value quoted is thus derived *only from those seedling clumps still with seedlings.* As time progressed, and some clumps lost all their seedlings and were thus excluded, the remaining sample size changed. One result of a shift in sample size was that the median value of survival after week *d* could in fact be higher than after week *a.* The inclusion of zero values (from those clumps with no seedlings left) was found to dominate the results, in that a large number of zeros distorted the typical survival in a clump with seedlings, and made statistical analyses problematical at best and meaningless at worst. A series of graphs is shown in Appendix D as an example of the alternative ways of displaying the data. It can be seen that retaining zero values makes the differences less clear, to the point that some positive survival appears to be practically zero.

The loss of all seedlings in some clumps is an important aspect of survival however, as it is part of the overall survival of seedlings at a particular site. For this reason, the persistence of clumps with seedlings (see above) was also shown in the results section.

The intention behind the approach described above was to communicate what I thought to be an ecologically meaningful result, and to avoid the mathematical pitfalls of small samples with many zero values. The method might be regarded as statistically dubious by the purists, but it was thought to reflect the important ecological aspect of survival, *i.e.* the continued existence of potential adults.

5.3.1 *Ganophyllum*

Seed deposition sites

The features of the nest sites in 1992 and 1993, and the performance of seedlings growing in them, are shown in Table 5.1. The details for dung piles found on trail are also given. In 1992, one nest site (G2/5) had smaller aggregations of seeds than the other (G2/6), and more cover, particularly at ≤4m, although stem density of herbs was lower. The difference in cover score for the two sites was not significant. Nearly 500 seeds were deposited at site G2/5, whereas over 2000 were deposited at G2/6, and the largest number of seeds in a clump at this site (391 seeds) was nearly as many as the total for the other site. Nests at these sites were made by the same group of gorillas within days of each other.

The herbaceous cover at site G2/5 was predominantly comprised of *Haumania* whereas it was mostly *Megaphrynium* at G2/6. The growth form of these two species is very different. *Haumania* sprawls and climbs, with up to 100 leaves per stem, whereas *Megaphrynium* has thinner stems, grows in clumps and has one large leaf per stem. Consequently the kind of shade created by equivalent numbers of stems of the two species can be quite different, which might explain the difference in cover score and stem density figures. Site G2/5, in a valley basin with denser ground vegetation, was shadier and moister than site G2/6, which had more sparse herbaceous growth and was on more of a slope. Although stem densities were not recorded for dung piles found on trail, they were predominantly found on or at the edge of elephant paths, so had less herbaceous cover.

In 1993 the dung piles monitored had broadly similar seed aggregations, although site G3/9 had more seeds per clump. The total number of seeds deposited at the sites ranged from 600 to 1100, with a maximum clump size of nearly 300 seeds. The four nest sites displayed a range of vegetation conditions, from quite sparse herb cover (G3/9) or little canopy cover (G3/5), to more densely vegetated sites (G3/6). The median cover score at site G3/5 was significantly lower than for site G3/6 (Kruskal-Wallis 1-way ANOVA by ranks $K_{df3}=8.1$, $P<0.05$). Again, there was variation in the density of stems of the principal herb species, with site G3/6 rich in *Megaphrynium* and G3/8 richer in *Haumania* and *Aframomum*.

Survival and growth 1992

Survival from dung

In site G2/5, 43% of the clumps suffered some seed predation, ranging from an estimated 0-20% of the original number of seeds (median for those clumps predated = 6.6%). At site G2/6, seed predation was noted for 77% of the clumps, with predation levels estimated to be 0-17% within clumps (median for those clumps predated = 5.9%). Predation affected 63% of the dung piles left on trail, and a higher proportion of seeds

Table 5.1 Summary data on gorilla dung piles containing *Ganophyllum* seeds, and the performance of seedlings in the growing clumps. (See text for an explanation of terms).

		1992			1993					
		G2/5	G2/6	trail	G3/5	G3/6	G3/8	G3/9	trail	quadrats
Seeds per clump										
	median	23.2	139	29	45	41	59	114	76	36
	range	5-143	65-391	14-76	13-115	9-238	9-274	52-296	24-163	
	total seeds	495	2073	285	634	690	580	1110	1358	504
	n clumps	14	13	8	11	8	7	8	13	14
Vegetation cover										
	median cover score	7	4	4	6	9.5	7	4	4	
	range	1-10	0-10	1-10	0-6	4-10	0-10	4-10	1-10	
	% of clumps with cover at									
	≤4m	79	15	12.5	50	80	57	38	7.7	
	5-20m	50	85	87.5	0	100	43	100	77	
	>20m	79	62	87.5	0	70	86	100	85	
Herbaceous stems										
	mean stem density (m-2)	7.36	8.73	ND	9.6	12.1	10.7	12.6	ND	
	median	4	6	ND	9	8.5	11.5	12	ND	
	n clumps	11	11	ND	9	8	6	7	ND	
	% of total stems as									
	Haumania	40.7	32.3	ND	73.3	5.2	50	21.6	ND	
	Megaphrynium	30.9	65.6	ND	23.3	92.8	10.9	73.9	ND	
	Aframomum	18.5	2.1	ND	3.5	2.1	14.1	3.4	ND	
	Hypselodelphis	9.9	0	ND	0	0	25	1.1	ND	
Performance										
lifespan (weeks)	median	83	4	1	3	3	0	8	3	4.5
	range	1-92+	3-92+	0-6	2-8	2-16	0-2	0-44+	0-16	0-44+
max ht (cm)	median	17.5	8			10		11.5		
	range	12-34	8-15			9-12.5		9-14		
max %height gain	median	70	18.2			5.3		0		
	range	4.3-278	0-50			4.2-6.7		0-55.6		
%HG/lifespan	median	0.973	0.543			0.096		0		
	range	0.113-3.02	0-0.876			0.26-1.67		0-3.47		
longest leaf (mm)	median	66	42			45		52		
	range	31-120	22-50			35-55		51-57		
max no. lvs	median	7	4			2		3		
	range	3-13	2-6					3-5		

Figure 5.1 Survival of *Ganophyllum* seedlings from dung in two nest sites and on feeding trail in 1992.

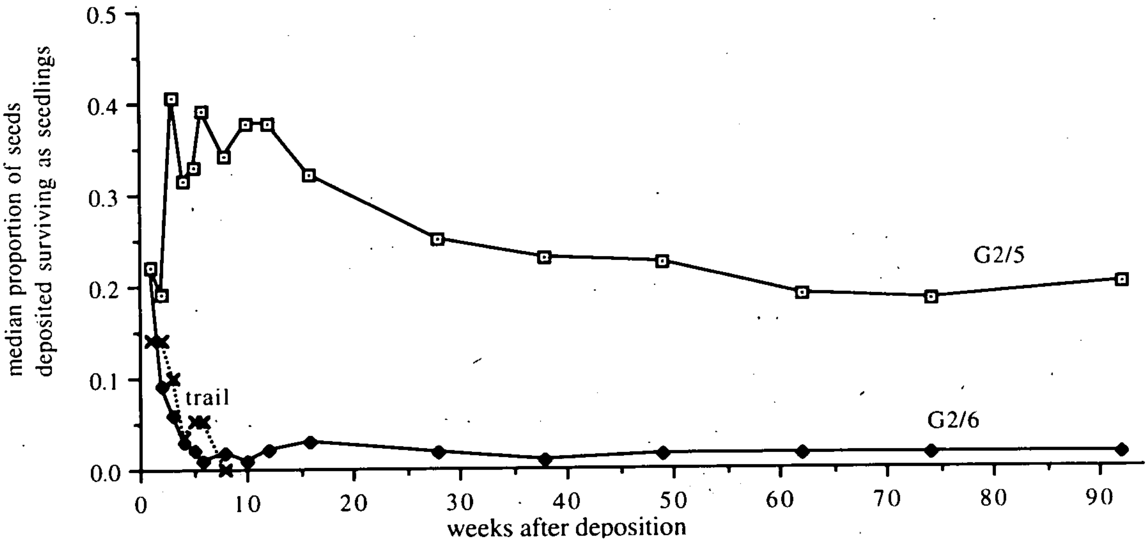


Figure 5.2 Persistence of clumps of *Ganophyllum* seedlings germinating in 1992.

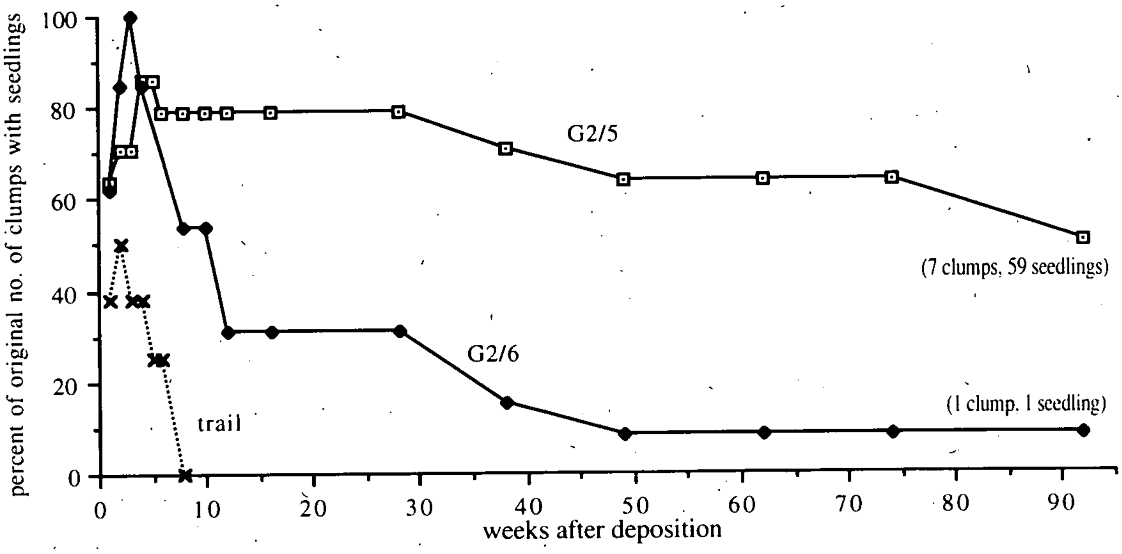
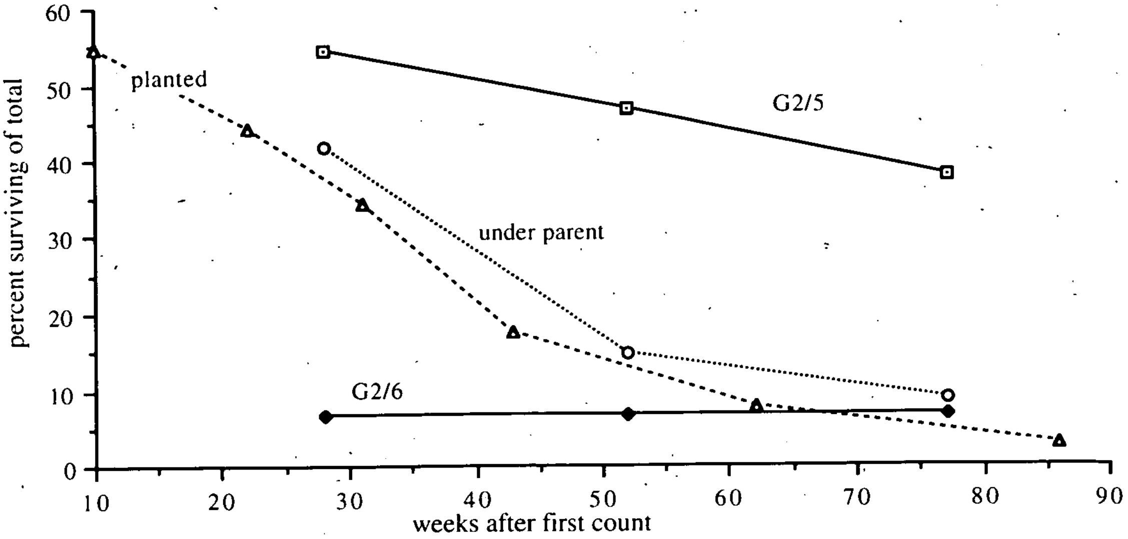


Figure 5.3 Survival of *Ganophyllum* seedlings from age 16 weeks in nest sites and under parents; nursery-grown seedlings planted away from parents (at 6 weeks old) also shown.



were predated, ranging from 0-100% (median of those predated = 50%). No significant difference was found between the three groups (Kruskal-Wallis, K_{df2}=3, P>0.1). Predation was probably by small rodents, judging from the remains left behind, which mostly consisted of broken seed cases.

Figure 5.1 shows the survival of seedlings growing from dung piles over time. Most mortality occurred in the first weeks. The initial increase shown on the graph is a result of the staggered germination of seeds during the first few weeks. Seedlings survived better in site G2/5 than in site G2/6 or on feeding trail. This difference was already significant after 3 weeks (Kruskal-Wallis K_{df2}=12.54, P<0.01), with median survival in site G2/5, G2/6 and on trail 41%, 6% and 10% respectively. Ungerminated seeds and those with emerging radicles appeared to suffer desiccation. Data from the two sites were subsequently tested statistically only at 4 and 28 weeks, because there were too few clumps remaining in site G2/6 beyond 28 weeks. At 4 and at 28 weeks, seedling survival in G2/5 was significantly higher than in G2/6 (Mann-Whitney U-test: 4 weeks, U=8, P<0.001; 28 weeks, U=0, P<0.001). It is clear that seeds and seedlings on trail did not last long. Median 'lifespans' of the clumps (see Table 5.1) were 83 and 4 weeks for sites G2/5 and G2/6 respectively, and one week for clumps on trail. The 'lifespans' of clumps at site G2/5 were significantly longer than at G2/6 and on trail (Kruskal-Wallis K_{df2}=13.82, P<0.01). The persistence of seedling clumps is shown in Figure 5.2, which illustrates the better survivorship in site G2/5. At the end of the study, there was a bigger contribution to the seedling bank at G2/5, where 59 seedlings in 7 clumps survived, but only one seedling remained in site G2/6.

There was no association found between the number of seeds in a clump and the proportion of seedlings surviving at any stage thereafter.

Survival of seedlings from dropped seeds

Figure 5.3 shows the survival of seedlings under focal canopies that were labelled at about 16 weeks of age, alongside the survival of seedlings of an equivalent age at nest sites. For comparison, the survival of 6-week old nursery-grown seedlings planted away from conspecific canopies is included. Survival of seedlings in site G2/5 was significantly better than that of seedlings growing under parent canopies at all time intervals (Mann-Whitney U=12, P<0.01). Site G2/6 was not included in the test for reasons of sample size (see above). The nursery-grown seedlings that were planted out showed similar levels of survival to the seedlings under parent canopies, which was not worse than that of the 'poor' site but significantly poorer than at the 'favourable' site.

Growth and performance

The various aspects of seedling performance are summarised in Table 5.1. The maximum height of a seedling in a clump was found to correlate significantly with the length of the longest leaf (Spearman Rank Correlation, r_s=0.773, P<0.01, n=11) and with the maximum number of leaves (Spearman r_s=0.823, P<0.01, n=11) within the clump. Seedlings in site G2/5 were taller, and had more leaves and longer leaves, than seeedlings in site G2/6. The median heights of seedlings growing in the two sites and under parents, and those planted out from the nursery, are shown in Figure 5.4. Seedlings growing from dung on trail did not last long enough to be measured (measuring was first possible usually about 10 weeks after deposition). Seedlings had developed enough to be measured after 8 weeks in G2/5 but only after 10 weeks in site G2/6. Heights of the tallest seedlings in clumps at sites G2/5 and G2/6 did not differ significantly 10 and 12 weeks after deposition, but those in site G2/5 were significantly taller than those at G2/6 by weeks 16 and 28 (Mann-Whitney U=5.5 and U=2.5, respectively, P<0.05).

Of those seedlings growing under parent crowns, no significant difference was found in the heights of the seedlings under different trees. Comparing the heights of seedlings at site G2/5 and the tallest ones under each of the parent canopies, no significant difference was found, although seedlings at site G2/5 were generally taller (range = 12.5 - 34cm at G2/5; 10 - 20.5cm under parent crowns).

The maximum height gain of seedlings at site G2/5 was significantly larger than at G2/6 (Mann-Whitney U=5.5, P<0.05). This was probably due to the longer lifespans of clumps at this site. Using height gain divided by lifespan ('growth'), there was no statistically significant difference between the sites, suggesting that surviving seedlings at G2/6 grew as fast as those at G2/5 for the length of time they survived. The overall height gain of seedlings at site G2/5 was greater than seedlings growing under parent canopies, but the difference was not statistically significant. However, when the height gain for different time periods was calculated, some difference was detected. The height gain from 16 to 49 weeks of seedlings at site G2/5 was 27.5%, and only 12.5% for seedlings under parent canopies. Height gain from 16 to 92 weeks was 46.4% and 38.8% respectively, suggesting that the undercanopy seedlings 'catch up' to some extent.

There were no consistent associations between seedling height and survival. None of a series of correlations between height at a particular time and survival at that time or thereafter were significant, with one exception. However, a significant correlation emerged between the 'growth' of seedlings and survival at the end of the study (see Figure 5.5; Spearman r_s=0.59, P<0.05, n=16), suggesting that those clumps that contained more vigorous seedlings survived better.

Vegetation and performance

No significant correlation was found between cover score and 'growth', but those clumps that had cover at ≤4m showed poorer growth than those without cover at ≤4m (Mann-Whitney U=5, P<0.05). Using the stem density of herbs around each clump, no significant correlation was found with survival, nor actual height, but stem density did

Figure 5.4 Heights of the tallest seedlings in clumps at nest sites, planted seedlings and those labelled under parents.

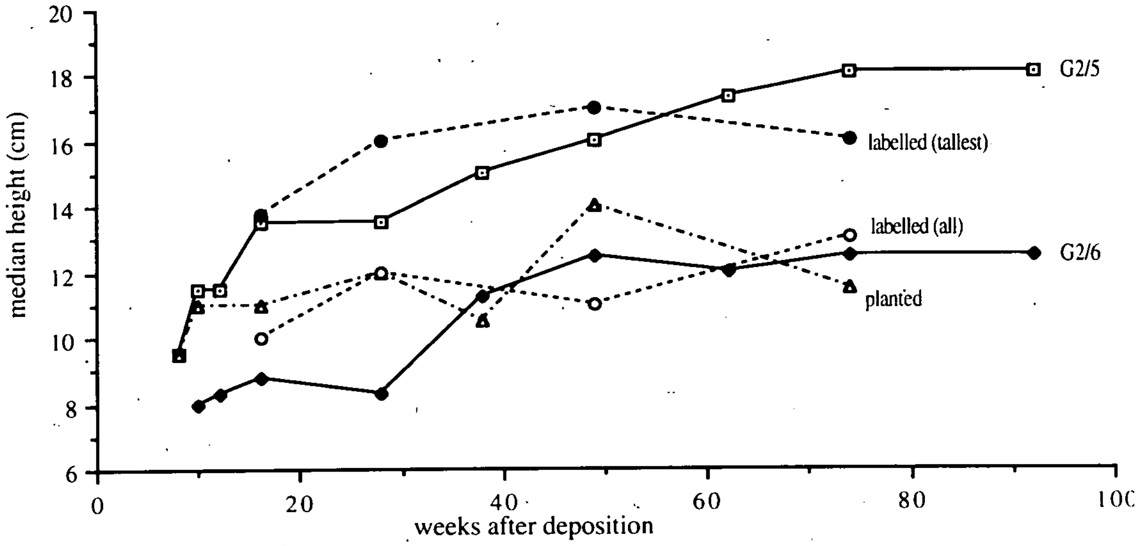


Figure 5.5 Correlation between growth and survival of *Ganophyllum* seedlings in two nest sites, 1992 (r_s=0.590, P<0.01, n=16).

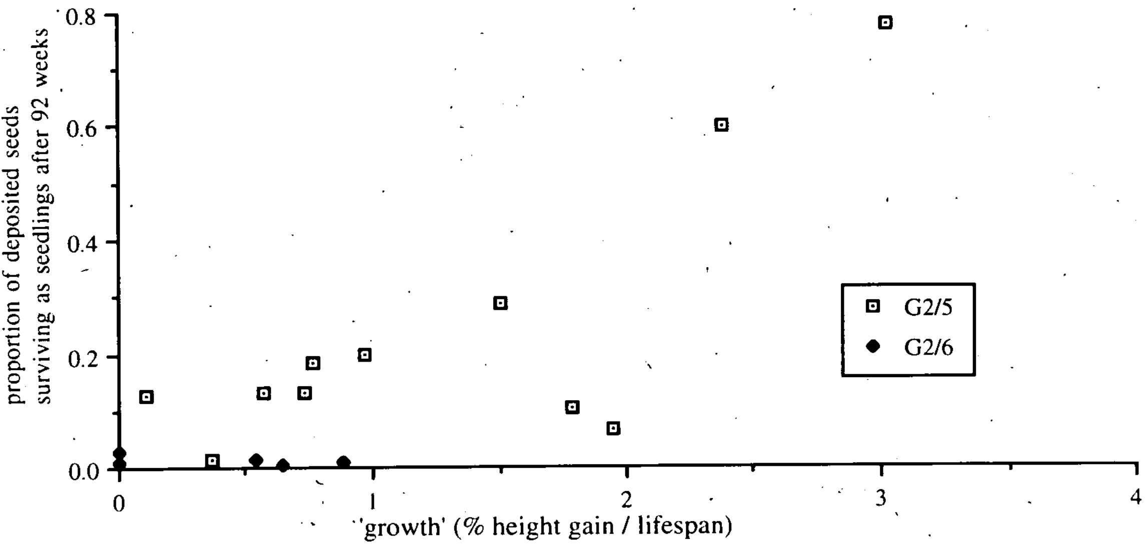
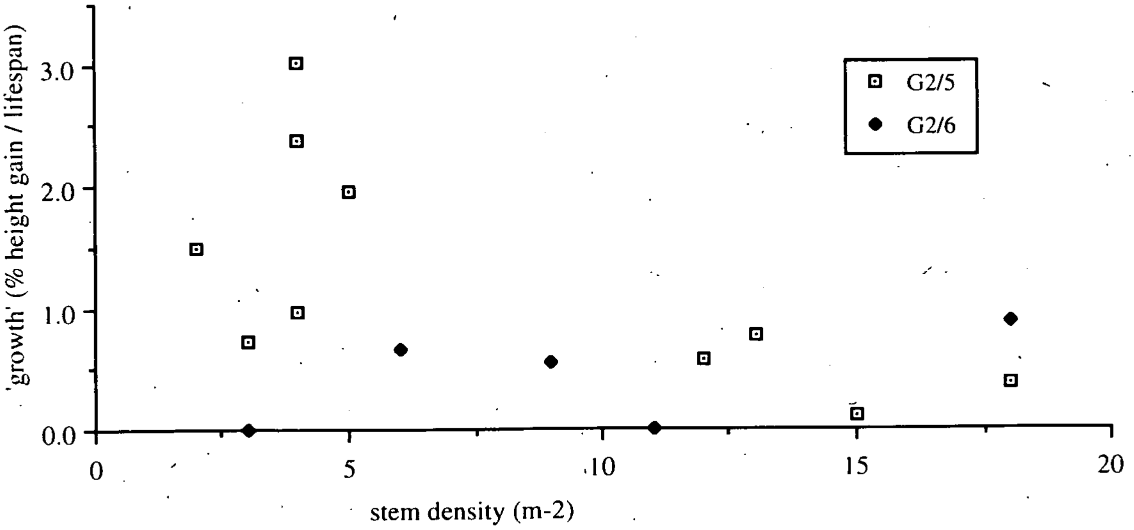


Figure 5.6 Stem density of herbs and growth of *Ganophyllum* seedlings in two nest sites, 1992 (r_s=0.611, P<0.02, n=15).



correlate significantly and negatively with growth (Spearman r_s= -0.611, P<0.02, n=16, 1-tailed test). Figure 5.6 shows this correlation between growth and stem density, indicating that seedlings in clumps with more herbaceous vegetation around them grew less well than those seedlings in clumps with fewer surrounding herbs. Clumps in site G2/6 did not tend to fit the correlation, possibly because desiccation was a more important factor influencing growth.

Survival and growth 1993

Survival from dung

Severe seed predation occurred on *Ganophyllum* seeds deposited in 1993. Every dung pile that was located and marked for monitoring suffered predation, whether it was on trail or in a nest site. Not only did 100% of dung piles suffer predation, but losses were high. Median predation levels at the four nest sites and in dung on trail ranged from 96% to 100%, and the difference between them was not statistically significant (Kruskal-Wallis K_{df4}=3.18, P>0.1). Seed quadrats (dropped and scatter-dispersed seeds) were also severely affected. Predation was high irrespective of either the size of seed aggregation or the location.

Early survival was very low as a consequence, as shown by Figure 5.7, being typically 1-3% after the first 4 weeks, as compared to nearly 40% for site G2/5 in 1992 (Figure 5.1). The survival of seeds in dung left on feeding trail was higher than in some nest sites (e.g. G3/9) but the differences were not quite significant (Kruskal-Wallis K_{df4}=8.89, 0.10>P>0.05). There were too few surviving seedlings thereafter to allow for statistical tests, and only one seedling at site G3/9 survived at the end of the study (49 weeks after deposition), a mortality of 99.98% of the 4372 seeds deposited in dung. The persistence of clumps of seedlings is shown in Figure 5.8, indicating that seed predation of this intensity acted equally among the dung piles at the different locations.

Survival of dropped seeds

The fate of seeds placed in quadrats is also shown in Figure 5.7. There was no significant difference in survival between seeds placed under conspecific canopies and those placed away from conspecifics. Three weeks after deposition, there was a significantly higher proportion of seeds surviving in quadrats than in dung piles in site G3/9 (Kruskal-Wallis K_{df4}=12.9, P<0.02) but after 4 weeks, this difference was no longer significant (Kruskal-Wallis K_{df4}=6.16, 0.1<P<0.2) although the trend was still the same. Only one seedling in each of two quadrats survived at the end of the study, an overall mortality after 49 weeks of 99.6% of the dropped or scattered seeds. Some escape from seed predation evidently did occur.

Of those seedlings that were labelled under or away from parent canopies, a difference in survival was found between those that had germinated promptly and those exhibiting delayed germination, but not between those under parents and those away

Figure 5.7 Survival of *Ganophyllum* seedlings growing from gorilla dung and from scatter-dispersed seeds, 1993.

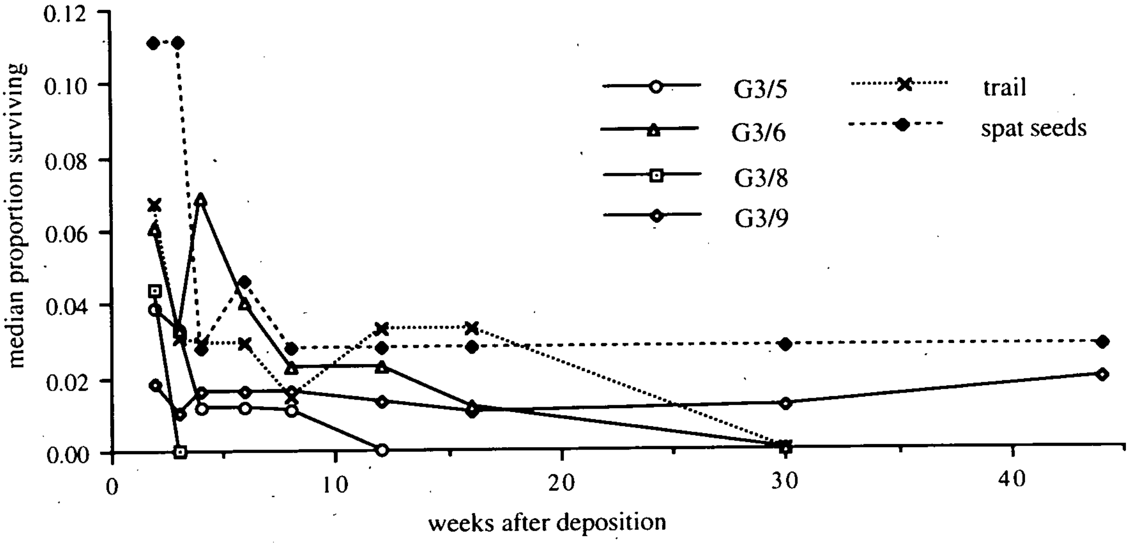


Figure 5.8 Persistence of clumps of *Ganophyllum* seedlings in 1993.

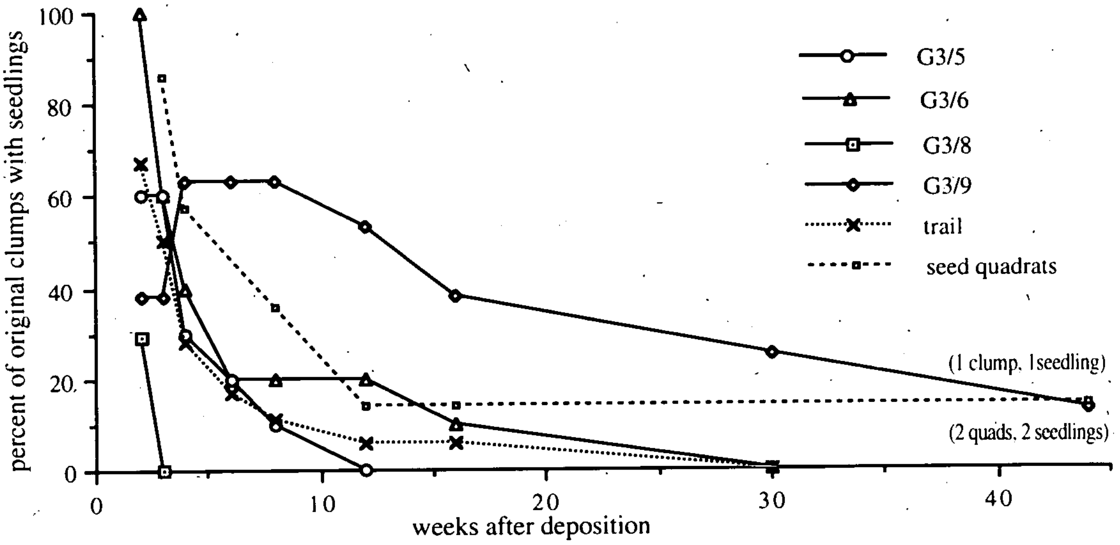
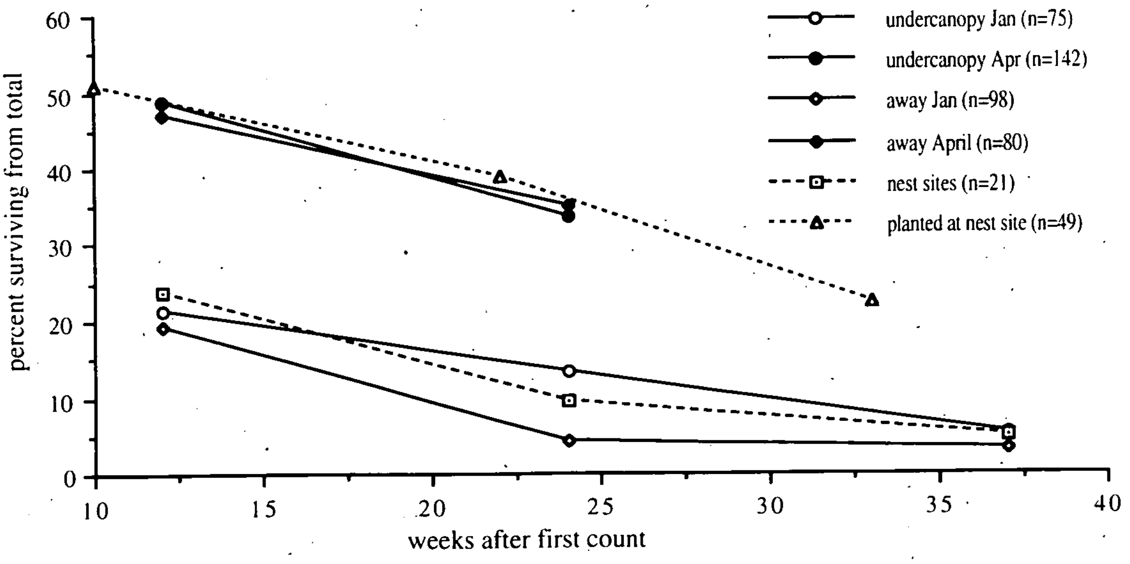


Figure 5.9 Survival of 4-week old *Ganophyllum* seedling with prompt and delayed germination, under and away from parents, at nest sites, and nursery-raised seedlings planted in nest sites, 1993 (n=original number).



from parents. The results are shown in Figure 5.9, where seedlings surviving in nest sites, and nursery-raised stock planted into nest site locations, are also shown. Twelve weeks after they were labelled, survival was higher among seedlings with delayed germination than among prompt-germinating ones (Mann-Whitney U=7, P=0.053). After 24 weeks, the difference was greater, and statistically significant (Mann-Whitney U=5, P<0.05). The small sample size of seedlings in nest sites precluded a statistical test, but there seemed little difference between the survival of prompt-germinating seedlings and those surviving in nest sites. The survival of nursery-raised seedlings planted into nest site locations was similar to that of delayed-germinating ones.

A search for seeds under focal trees 10 days after the end of fruiting indicated that up to 68% of the estimated seed fall was located (Table 5.2), indicating that seeds dropped under conspecific canopies may, at least initially, have a greater escape from predation than those (see also Figure 5.7).

Performance

In terms of lifespan, clumps at site G3/8 had significantly shorter lifespans than all other clumps (Kruskal-Wallis K_{df4}=22.73, P<0.001). In fact all seeds at this site were predated within the first week after deposition. No significant difference was found between the lifespans of seeds in quadrats under or away from conspecifics, nor between the other nest sites and dung on trail, and seed quadrats (Kruskal-Wallis K_{df4}=7.46, P>0.5).

There were too few survivors from any dung pile or quadrat to use in comparisons of heights. For those seedlings labelled under parent canopies, there were no significant differences in the heights of seedlings under different trees (Kruskal-Wallis K_{df4}=4.85, P>0.3), so there was no apparent 'tree' effect. The height of seedlings under and away from parents was very similar when first labelled (undercanopy mean height=10.74cm ±2.73, n=215; away mean=10.16cm ±2.89, n=175). Figure 5.10 shows the median heights of the labelled seedlings, those planted into nest sites, and those seedlings originally deposited in the nest sites. Sample sizes for the latter two categories precluded statistical tests. Of the prompt-germinating seedlings, those growing under parents were taller than those growing away 12 weeks after labelling (Mann-Whitney U=85, P<0.05) but not after 24 weeks (U=11, P>0.1). No significant difference was found in height between delayed germinating seedlings growing under or away from parents (z-test, 12 weeks: z=1.87; 24 weeks: z=1.31, both P>0.05).

Prompt-germinating seedlings growing under parents were taller 12 weeks after labelling (about 20 weeks old) than delayed seedlings under parents (z-test z=2.2, P<0.05). The small sample of prompt-germinating seedlings after 24 weeks precluded a test. This was the same pattern for seedlings growing away from parents: 12 weeks after labelling, prompt-germinating seedlings were significantly taller than delayed seedlings (z-test z=2.44, P<0.05).

Figure 5.10 Heights of labelled *Ganophyllum* seedlings (prompt/delayed germination; under/away from parents) and nursery-raised ones planted in nest sites, 1993.

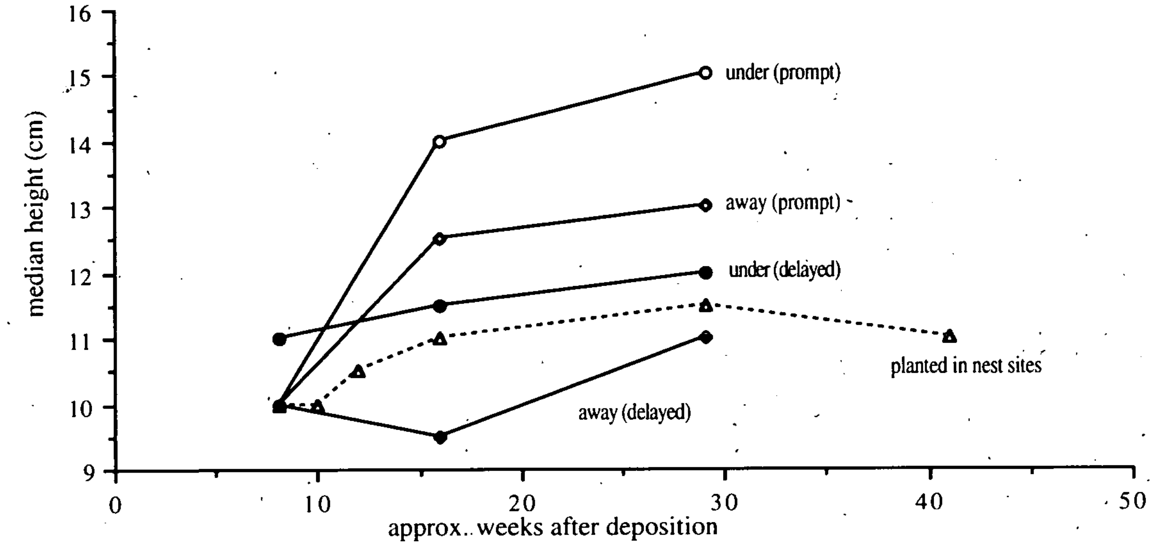


Table 5.2 Results from a search for *Ganophyllum* seeds in 12 (0.25m^2) quadrats under 4 focal trees in 1993. Seed fall estimated from fruitfall counts (see Chapter 4).

tree #	germinated seeds	un-germinated seeds	total seeds found	mean	SD	median	range	n	area sampled (m2)	(median) no. per m2	estimated seed fall (n/m2)	% found
G18	4	1	5	0.42	0.67	0	0-2	12	3	0	1.4	0
G6	23	9	32	2.67	2.35	2	0-5	12	3	8	11.7	68
G8	11	3	14	1.17	1.4	1	0-3	12	3	4	9.6	41
G19	8	3	11	0.92	1.08	1	0-4	12	3	4	7.9	51

Prompt-germinating seedlings were labelled in February and checked in May, delayed ones were labelled in May and checked in August, 2 months into the dry season. When the difference in height of each cohort 12 and 24 weeks after labelling was tested, prompt germinating seedlings growing under parents were not significantly taller after 24 weeks than they were after 12 weeks (Wilcoxon's matched pairs test, T=9.5, n=7, P>0.5), although the sample size was small. Delayed seedlings however were significantly taller after 24 weeks than after 12 weeks, in spite of growing during the dry season (t-test for matched pairs, undercanopy: t=2.11, P<0.05; away: t=3.31, P<0.01).

Vegetation and performance

Too few seedlings survived to investigate any associations with microsite. It would appear that seed predation of this severity affected seeds wherever and however they were deposited.

5.3.2 *Cola*

Seed deposition sites

Table 5.3 gives the details of the 66 gorilla dung piles that were monitored, and their immediate environments, as well as the performance of the seedlings at different locations. From 97-844 *Cola* seeds were deposited at the four nest sites, with a maximum clump size of 113 seeds. Site G2/19 had an open aspect, with a low cover score and little herbaceous vegetation above the clumps, although recorded stem density was not low. Site G2/26 was only a few hundred metres away from G2/19, but had denser cover. Some of the dung piles were located under towers of *Haumania*, in which case cover was very dense and humans had to crawl underneath to reach them, but the stems were not necessarily within the 1m quadrat used for sampling density. This was also the case for clumps located in G2/23, which had the most cover of the four sites. Site G2/22 was adjacent to an old forestry road, with little tree cover. This site had the fewest seeds in the dung piles. The differences in cover score between sites were not statistically significant (Kruskal-Wallis K_{df3}=5.92, P>0.1). Dung piles located on trail generally had no herbaceous cover.

Survival and growth

Survival from dung

All the *Cola* seeds germinated immediately. Seed predation was not recorded as a common cause of mortality. The cotyledons were sometimes nibbled but rarely did this kill the whole seed or seedling. The survival of seedlings growing from gorilla dung in nest sites and on trail is shown in Figure 5.11, which also includes the survival of seedlings growing from quadrats of spat seeds under conspecifics. The bulk of mortality occurred in the early weeks, with typically 20-30% of seeds surviving as seedlings after

Table 5.3 Summary data of the gorilla dung piles containing *Cola* seeds in nest sites and on feeding trail, and 'dropped' seeds, and the performance of growing seedlings (see text for explanation of terms).

		G2/19	G2/22	G2/23	G2/26	trail	seed quadrats
Seeds per clump							
	median	17	7	47	54	19.5	25
	range	3-113	1-17	28-95	10-84	7-106	
	total seeds	284	97	377	844	740	200
	n clumps	9	11	7	17	22	8
Vegetation cover							
	median cover score	3	3	7	7	4	ND
	range	1-10	0-9	1-10	1-10	0-4	
	% of clumps with cover at						
	≤4m	22	46	86	71	0	ND
	5-20m	78	55	29	65	71	ND
	>20m	56	0	86	53	77	ND
Herbaceous stems							
	mean stem density (m-2)	6.1	ND	6.9	3.1	ND	ND
	median	7	ND	3.5	2	ND	ND
	% of total stems as						
	Haumania	64	ND	85	91	ND	ND
	Megaphrynium	36	ND	15		ND	ND
	Aframomum				9		
Performance							
lifespan (weeks)	median	84+	6	84+	84+	47.5	36
	range	3-84+	3-6	21-84+	10-84+	1-84+	10-34
max ht (cm)	median	24.5	ND	23	23.5	12.5	13
	range	12-27		9-24	9.5-27	7-28	7.5-15
max %height gain	median	60.7	ND	50	19	30	14
	range	15.4-194		28-85	0-90	0-155	-20-44
%HG/lifespan	median	0.725	ND	1.01	0.44	0.41	0.378
	range	0.18-2.3		0.42-2.4	0-2.2	0-12.5	-0.67-1.22
longest leaf (mm)	median	110	ND	100	108	95.5	ND
	range	80-134		58-111	23-134	51-150	
max no. lvs	median	5	ND	2.5	3	2.5	ND
	range	3-6		2-4	1-7	1-4	

Figure 5.11 Survival of *Cola* seedlings in nest sites, on feeding trail, and in seed quadrats ('dropped' seeds).

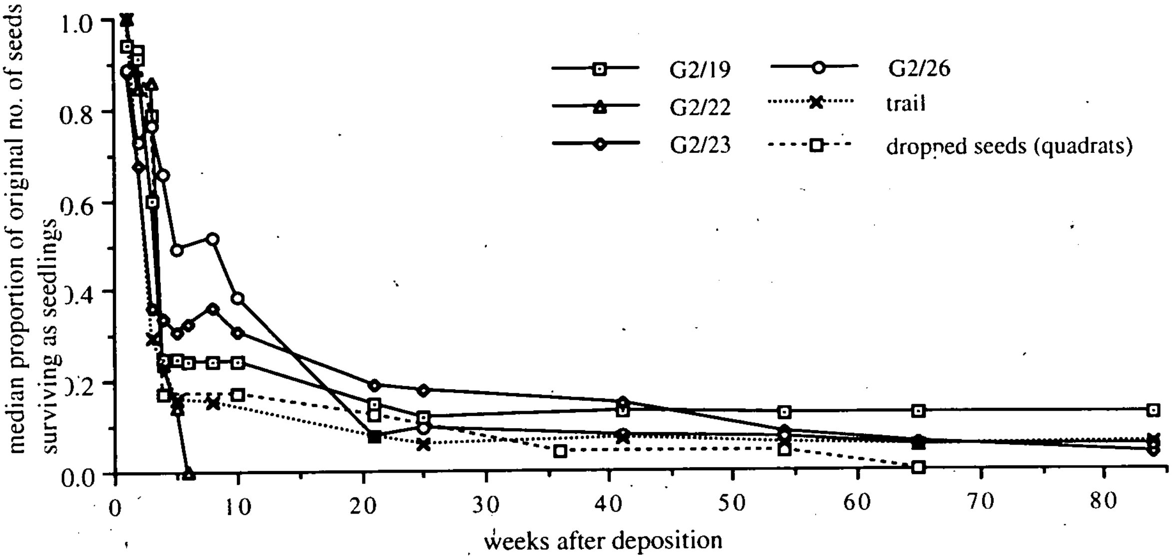


Figure 5.12 Persistence of clumps of *Cola* seedlings in nest sites, on feeding trail, and 'dropped' seeds. n=no. of clumps (& no. of seedlings) remaining after 84 weeks.

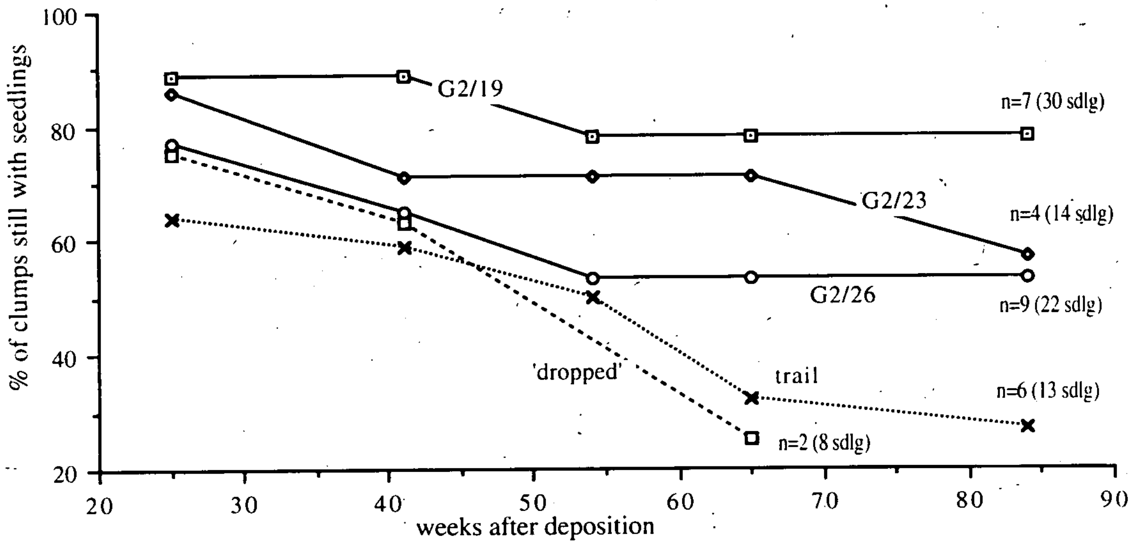


Figure 5.13 Survival of *Cola* seedlings beyond 10 weeks, in nest sites, on feeding trail and under parent canopies.

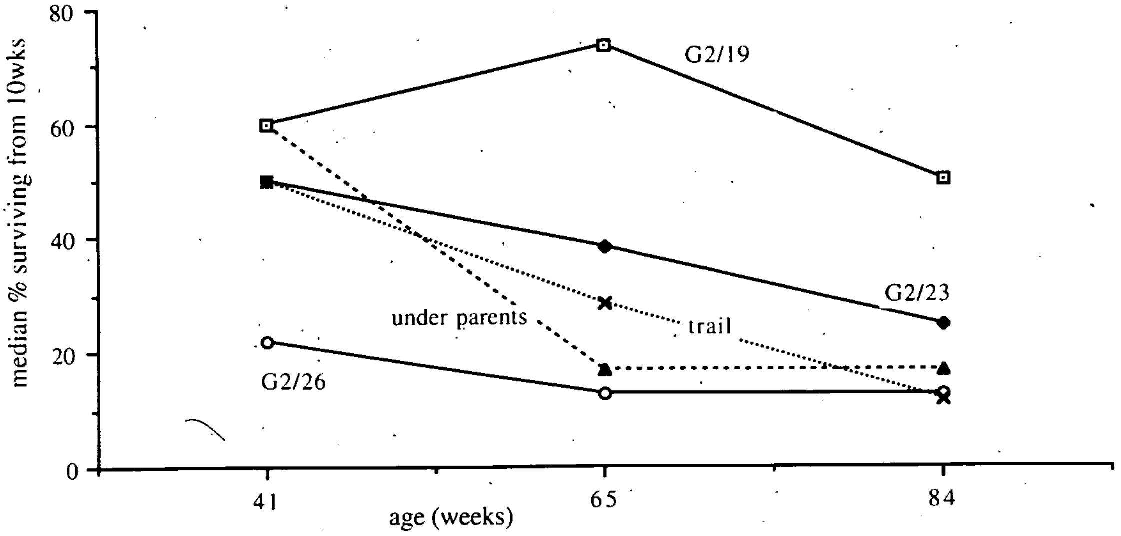


Figure 5.14 Median heights of *Cola* seedlings at nest sites, on feeding trail, and in seed quadrats.

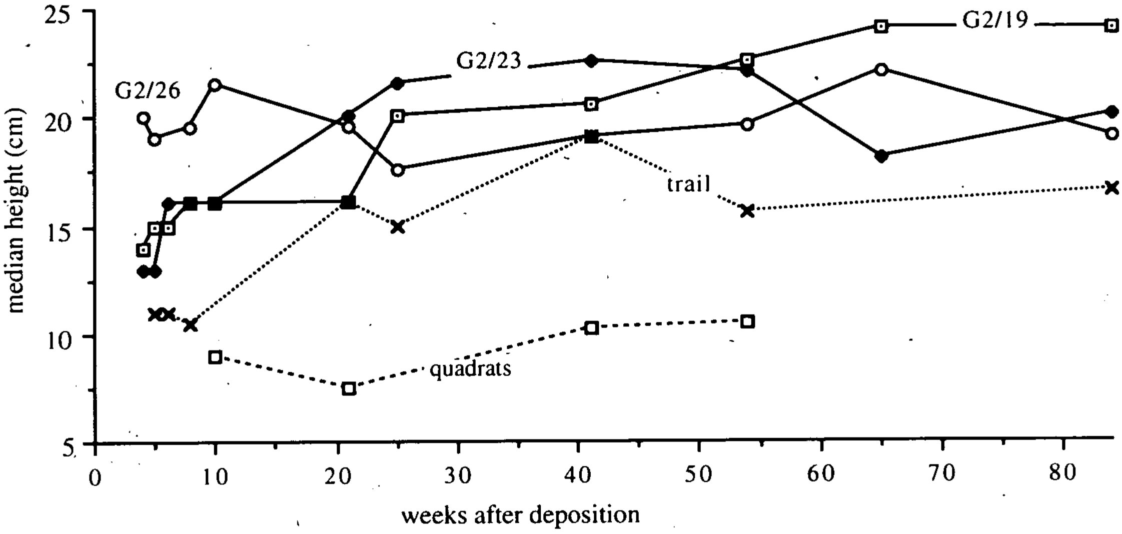
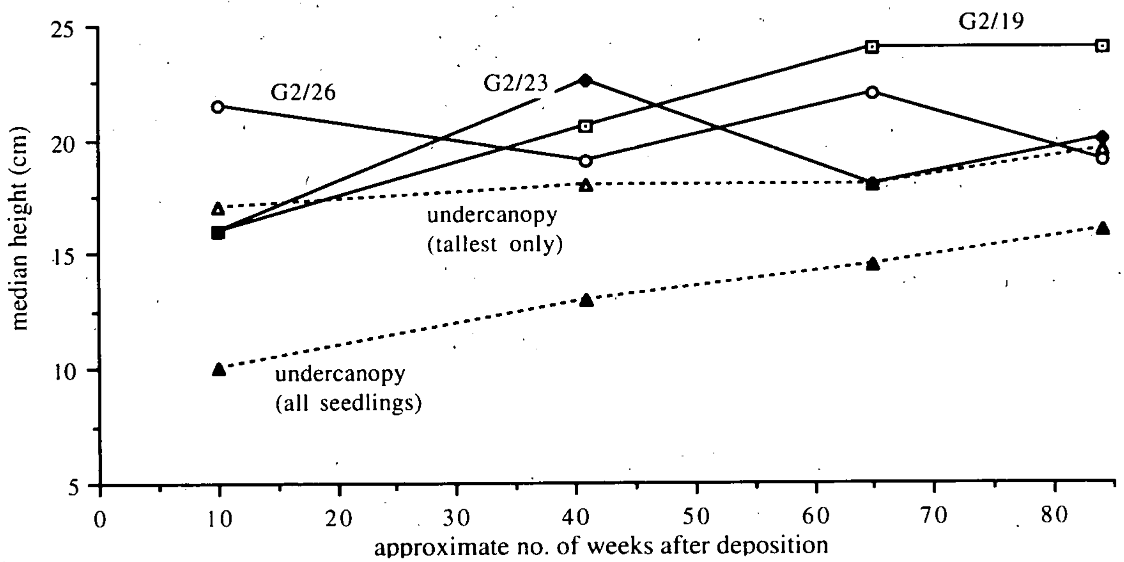


Figure 5.15 Heights of seedlings growing from dung in nest sites (solid lines) and under parents (broken lines).



5 weeks. Apart from the dramatic mortality of all seedlings in site G2/22, there were no large differences in survival among nest sites and dung on trail after the first few months.

At 5 weeks, G2/22 had a significantly lower survival than G2/26 (Kruskal-Wallis $K_{df4}=19.71$, $P<0.001$), and after 8 weeks there was significantly poorer survival of seedlings in dung on trail than those in site G2/26 (Kruskal-Wallis $K_{df3}=10.56$, $P<0.05$). Beyond 25 weeks, there were no significant differences in survival (25 weeks: $K_{df3}=7.38$, $0.1>P>0.05$; 54 weeks: $K_{df3}=2.9$, $P>0.1$; 84 weeks: $K_{df3}=4.25$, $P>0.2$).

The persistence of seedlings in clumps is shown in Figure 5.12, which shows that nest sites had higher survival, in terms of the proportion of clumps remaining, than did dung left on trail or quadrats under parents. Persistence was highest in site G2/19, which also had the highest number of seedlings at the end of the study. Seed predation was rare: only six dung piles were noted to have suffered the loss of some seeds to predation.

Survival of seedlings from dropped seeds

When tested at 4 and 21 weeks, no significant differences were found between the survival of *Cola* seedlings growing from spat seeds in quadrats under conspecific canopies and those growing from gorilla dung in any nest sites, or on trail (Kruskal-Wallis $K_{df5}=7.17$ and $K_{df4}=4.76$ respectively, $P>0.2$ in both cases, Figure 5.11). Too few quadrats had seedlings after this point to allow a test. Nonetheless, from an ecological or demographic aspect, the fact that no seedlings survived in quadrats after 65 weeks is important. The survival of seedlings that were labelled under parent canopies is shown in Figure 5.13, along with that of seedlings of a similar age that had survived from gorilla dung. No significant differences were detected after 7 months nor 17.5 months ($U=8$, $P>0.1$ and $U=15$, $P>0.5$ respectively). These data suggest that in terms of survival alone, seeds dropped under the parent fared worse than those dispersed in gorilla dung, but once seedlings were established under parents they survived as well, although the highest proportion of surviving seedlings was nonetheless at a nest site.

The survival of the seedlings growing from scatter-dispersed seeds that were labelled in 1993 was of a similar magnitude to 1992. Although not shown in Figure 5.13, there were 68% and 48% of the original number labelled still surviving after 13 and 26 weeks respectively.

Performance

If the 'lifespan' of clumps of seedlings is considered (see Table 5.3), then clumps in site G2/22 had significantly shorter 'lifespans' than all other nest sites or on trail (Kruskal-Wallis $K_{df4}=23.98$, $P<0.001$). The median 'lifespan' of seedlings in quadrats was significantly shorter than that of clumps in sites G2/19 and G2/23 (Kruskal-Wallis $K_{df3}=11.51$, $P<0.01$). There was no apparent association between the number of seeds in a clump and the subsequent height of seedlings.

No significant correlations were found between the height of the tallest seedling, and the length of the longest leaf or the maximum number of leaves.

Seedlings growing from dung

Initial differences in height between the tallest seedlings at the different nest sites diminished over time (Figure 5.14). At the first measuring, seedlings at G2/26 were significantly taller than at the other sites (Kruskal-Wallis $K_{df2}=6.82$, $P<0.05$), even though they were deposited and subsequently measured within days of each other. Seedlings growing from dung left on trail were significantly shorter than those at site G2/26 after 8 weeks (Kruskal-Wallis $K_{df3}=14.65$, $P<0.01$), but after 54 and 84 weeks, no differences in height were significant ($P>0.5$ and $P>0.2$ respectively), although seedlings in G2/19 were clearly taller than those at other locations. No association was evident between the height or growth of seedlings in clumps at site G2/19 and their survival; sample sizes at the other sites were too small to test. Clumps at site G2/19 were the only ones that also contained *Celtis* seeds, which produced dense clusters of small seedlings with leafy cotyledons.

Nearly all seedling clumps were browsed at some point during the study period, some of them repeatedly. 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 positions.

Seedlings from dropped seeds

The heights of seedlings growing from seed quadrats are also shown in Figure 5.14. They were significantly shorter than those at G2/26 initially (10 weeks, Kruskal-Wallis $K_{df3}=16.25$, $P<0.01$) and significantly shorter than those at sites G2/19 and G2/23 later on (36 or 41 weeks, Kruskal-Wallis $K_{df3}=10.62$, $P<0.02$). For those seedlings growing under different parent canopies that were labelled, no differences in height were detected between trees after 28 weeks (1-way ANOVA, $F_{6,89}=2.13$, $P>0.05$) nor 75 weeks (Kruskal-Wallis $K_{df4}=7.3$, $P>0.1$). The median height of all seedlings growing under parents, as well as the median height of the *tallest* seedlings growing under parents, are shown in Figure 5.15, with the height of seedlings of the same age growing at nest sites and on trail included for comparison. No significant differences between the median heights of the tallest seedlings in clumps at nest sites and all those under parents were found, although the tallest were those growing from gorilla dung. This suggests that, for seedlings that manage to establish, some may be as tall under parents as in nest sites. Insufficient samples precluded a test using just the tallest seedlings under parents.

The only significant differences in maximum height gain were between G2/19 and G2/26. Seedlings at G2/26 were already relatively tall when first measured, and their subsequent height gain was less than those in G2/19 (Kruskal-Wallis $K_{df3}=11.06$,

$P<0.02$). This difference only occurred in the first 21 weeks: the height gain from 10 to 41 weeks was significantly less for G2/26 (Kruskal-Wallis $K_{df3}=22.2$, $P<0.001$); after that, from 41-65 weeks and 65-84 weeks, there were no significant differences in height gain of seedlings at the two sites (Kruskal-Wallis $K_{df3}=4.42$, $P>0.2$ and $K_{df3}=3.03$, $P>0.3$ respectively). Seedlings growing under parents did not differ significantly from those at nest sites. The 'growth' (%HG/lifespan) of seedlings growing from dung at nest sites was greater, but not significantly so, than those growing from dung on trail and those growing from dropped seeds (Kruskal-Wallis $K_{df3}= 6.03$, $P>0.1$ and $K_{df3}= 7.53$, $P>0.05$ respectively).

The rate of growth of seedlings during different periods varied between sites, with slower growth after the initial 6 weeks at the sites with more cover. When the height gain per week from 4-10 weeks, 10-25 weeks (during the dry season) and 24-41 weeks was tested for each site, seedlings in G2/19 showed no difference between periods, whereas growth at G2/23 was significantly greater from 4-10 than 10-25 weeks (Kruskal-Wallis $K_{df2}=6.9$, $P<0.02$). At site G2/26, growth of seedlings during the first 6 weeks was greater than growth during both subsequent periods (Kruskal-Wallis $K_{df2}=20.83$, $P<0.001$).

Microsite and performance

Bearing in mind the variation in seedling performance at the different locations described above, and summarised in Table 5.3, there were no significant associations found between measures of vegetation cover and performance. No significant correlation was found between cover score and 'growth', either within each site or using pooled data from all clumps. This was the same result when the presence of cover at ≤4m or herbaceous stem density were used in the correlation.

Table 5.4 Summary of the vegetation conditions and associated performance of clumps of *Cola* seedlings in nest sites and on feeding trail. Arrows indicate the direction of the difference.

vegetation	trend	**performance**	trend
cover score	G2/19 < /23 = /26 > trail	lifespan	G2/19 > /23 > /26 > tr
% of clumps +cover ≤4m	G2/19 < /26 < /23	max height	G2/19 > /26 > /23 > tr
stem density	G2/26 < /23 < /19	max %HG	G2/19 > /23 > tr > /26
% of stems as *Haumania*	G2/19 < /23 < /26	%HG/lifespan	G2/23 > /19 > /26 > tr
		% total seeds surviving	G2/19 > /23 > /26 > tr
		clump persistence	G/19>/23>/26>tr>quads

Nonetheless, the trends were clear and consistent, even for what can be regarded as a shade-tolerant species: seedlings at site G2/19, which scored the lowest in terms of canopy cover (especially at ≤4m) and was, when visually assessed, the most 'open' site, outperformed seedlings at other locations, with those deposited on trail 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, or growth. This result is summarised in Table 5.4. A question mark remains over site G2/22, which had similar herbaceous cover to site G2/19 but less tree cover, and showed the poorest survival and performance of seedlings. It was at the edge of an old forestry road, and four of the dung piles were on the rim of the nest constructions, which may have limited the seedlings' ability to root properly.

5.3.3 *Dialium*

Seed deposition sites

Features of the one nest site that was monitored are listed in Table 5.5, along with information on the seed quadrats placed under and away from conspecific canopies. Only two dung piles found on trail were monitored, but the seeds from both disappeared within a month.

Survival and growth

Germination and survival

Two main restrictions which affected sample size apply to the analysis of the results. One arises from finding only one nest site to monitor, and the other from the staggered germination shown by the dormant seeds. Figure 5.16 shows the survival of seeds in dung at the nest site and those placed in quadrats (pooled data for quadrats under and away from conspecifics). A slightly higher percentage germination occurred from seeds deposited in dung than in quadrats (1.45% and 1.26% respectively), and the subsequent survival of seedlings was higher from dung (14.3% and 5.6% of germinated seeds, respectively). In both instances, most seeds were not observed to germinate. Seeds were removed from dung piles: some were possibly predated by rodents, but others may have been buried by dung beetles or washed into the leaf litter by rain. Some of these may have survived in a viable state, germinating at a later stage, making precise assessment of survival of seeds difficult (hence the 'unknown' category in Table 5.5).

The number of seeds placed in quadrats that germinated varied between treatments ('soaked': soaked for 36 hours; 'dry': unsoaked; and 'away': soaked seeds placed away from conspecific canopy) and between locations. This is shown in Figure 5.17, which also includes the number of seedlings that were found and labelled under different focal tree canopies. Searches for seedlings, if not exhaustive, were thorough, so these data are likely to reflect the relative sizes of young seedling populations under the different trees.

Table 5.5 Summary data of the gorilla dung piles containing *Dialium* seeds and seeds in quadrats, and the performance of growing seedlings (see text for explanation of terms).

	G2/39	trail	quadrats			G2/39	trail	quadrats
Seeds per clump				**Performance**				
median	59	100	36	lifespan of	median	uk*	uk	uk
range	20-154	83-117		seedlings (weeks)	range			
total seeds	484	200	1512					
n clumps	7	2	42	max ht (cm)	median	8	ND	9.5
					range	7-10		5-16.5
Vegetation cover								
cover score (median)	7.5	ND		max %height gain	median	4.8	ND	101
% of clumps with cover at					range	-11-25		29-174
≤4m	50	ND						
5-20m	88	ND		%HG/lifespan	median	ND	ND	
>20m	75	ND			range			
Herbaceous stems				longest leaf (mm)	median	50	ND	[63]
mean stem density (m-2)	4.3	ND			range	48-52		
median	3.5	ND						
% of total stems as				max no. lvs	median	6	ND	6.5
Haumania	46.2	ND			range	5-7		5-8
Megaphrynium	42.3	ND						
Aframomum	11.5	ND						

*uk: unknown, due to seed dormancy

Figure 5.16 Survival of *Dialium* seedlings growing from dung in nest sites, and from seed quadrats.

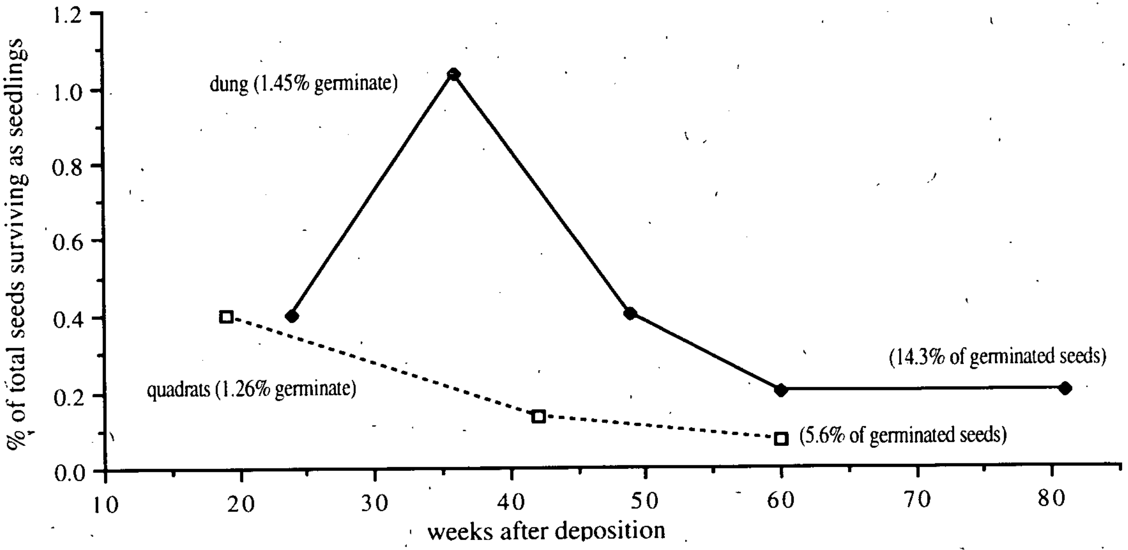


Figure 5.17 Numbers of *Dialium* seedlings germinating after different treatments or labelled under different focal trees.

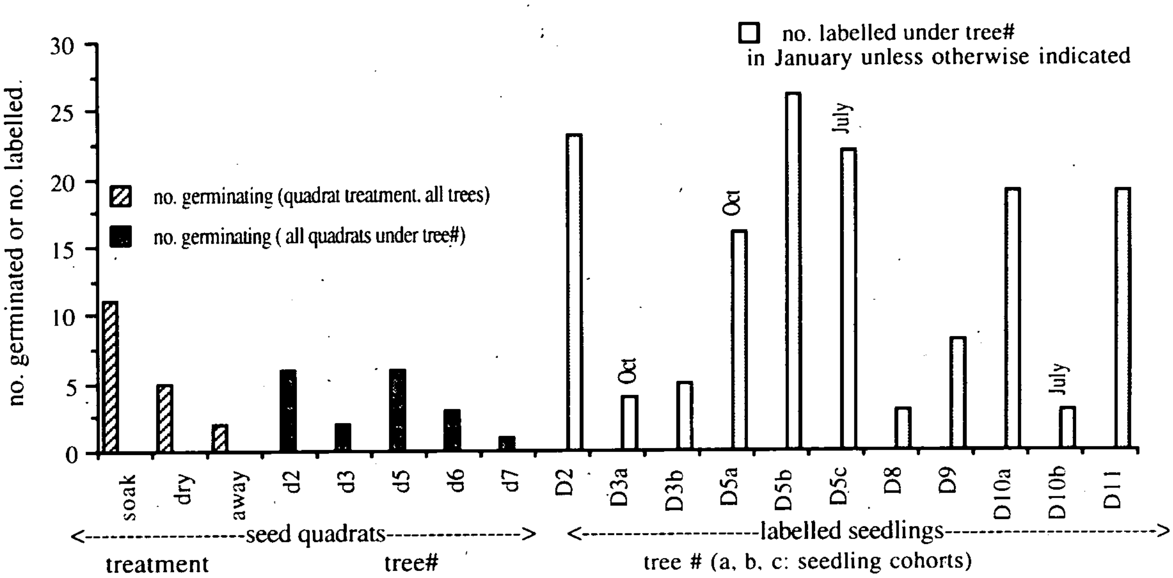


Figure 5.18 Survival of 148 seedlings labelled under parent canopies in October (dotted lines) and January (solid lines). The first census was 20 (October cohort) or 25 (January cohort) weeks after they were first labelled (when survival was 100%).

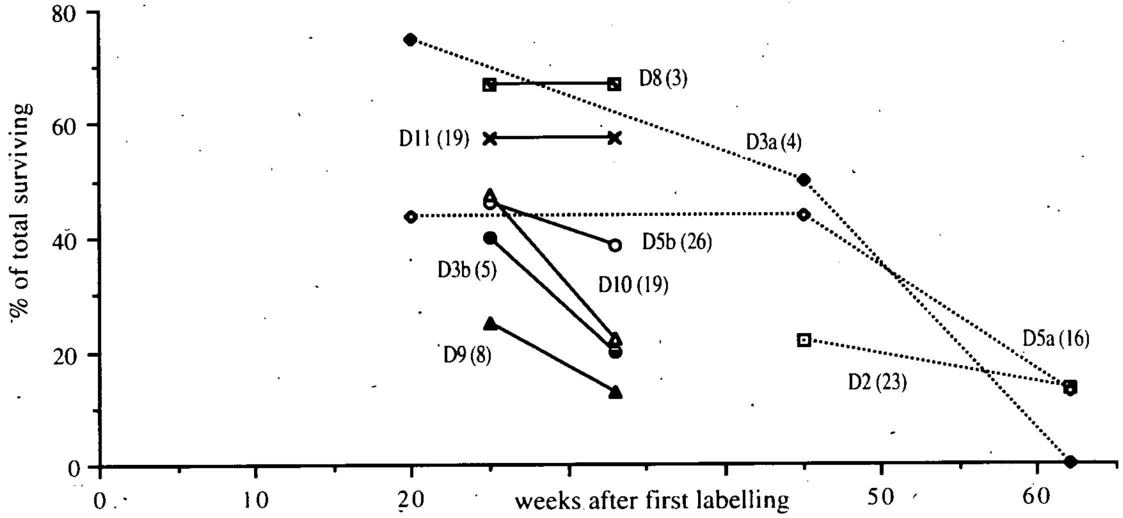
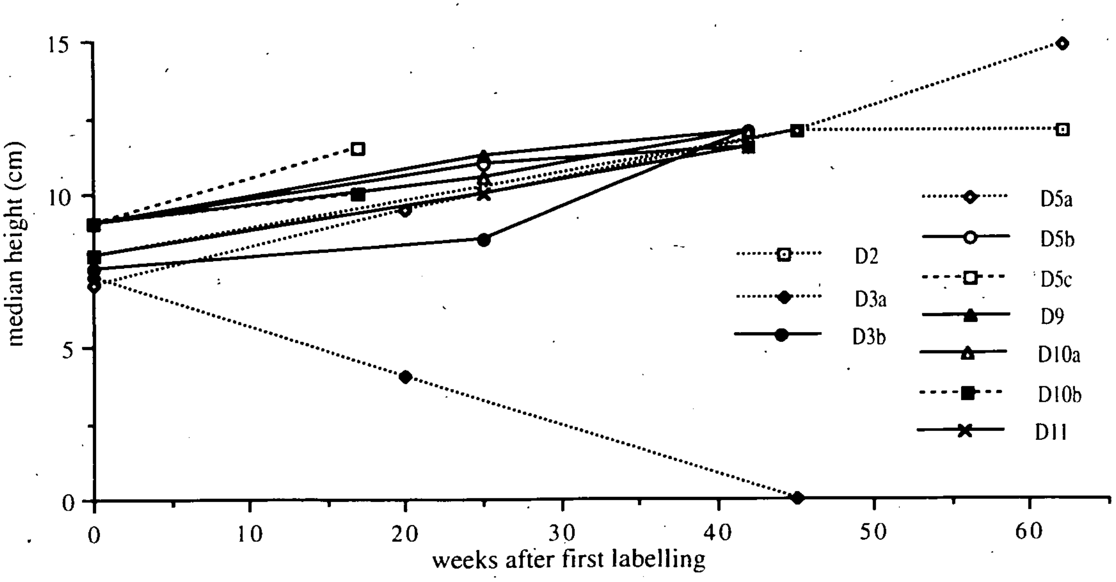


Figure 5.19 Heights of *Dialium* seedlings growing under parent canopies labelled in October (dotted lines), January (solid lines) and July (broken lines).



More soaked (2.2%) than dry seeds (0.99%) germinated under focal trees, but the lowest germination rate was from soaked seeds placed away from focal trees (0.40%). In terms of germination of seeds in quadrats under different canopies, more germinated under trees #D2 and #D5, even though tree #D5 only had 2 rather than 3 quadrats (*i.e.* 72 seeds) underneath it. These two trees were also the ones under which most seedlings were found. They also were estimated to have had the largest crops (see Chapter 4).

The survival of the labelled seedlings growing under focal trees varied considerably (Figure 5.18). Survival 34 weeks after emergence was anything between 10 and 62%, but after 64 weeks this figure was more likely to be in the order of 0-15%.

Performance

Only one seedling survived at the nest site, and one in a seed quadrat, beyond one year. Their heights were 10 and 16.5cm respectively, which was within the range of labelled undercanopy seedlings. The heights of the cohorts of seedlings growing under focal trees are shown in Figure 5.19. Although the staggered germination makes ages approximate, only those seedlings that had obviously recently emerged and were at the same stage of growth were tagged. No statistically significant differences were found between the median heights of seedling cohorts under different trees (October: P>0.1; Jan: P>0.3; July: P>0.05). Tree #D5 (which had the most seedlings) had the tallest seedlings, and the few under #D3 were small. The median height under #D3 declines due to the mortality among the small sample.

If the height gain is considered, then there was no significant difference between those seedlings that germinated early and those that germinated later. Nor was there any difference in height gain between the periods January to July and July to November.

When the last census of the study was carried out in mid-November 1993, it was noticed that a large number of *Dialium* seedlings were emerging under tree #D5, but not under the other trees. This was 18 months after the previous fruiting season, although some seedlings could have been from earlier fruiting events.

5.3.4 *Uapaca*

Seed deposition sites (1992)

The five nest sites from 1992 that were marked out and monitored, occurred in a range of habitat types and thus gave a variety of local conditions for germination and seedling growth. Information relating to the sites, and to dung piles on trail and seed quadrats set away from conspecific canopies, is given in Table 5.6. Sites contained anything from 110 to over 3000 seeds, with clump sizes ranging typically from 8 to 500 seeds, although the largest aggregation was in a silverback dung pile which contained nearly 1200 seeds. Site G2/81 was in grass savanna at the edge of a narrow strip of gallery forest. The nature of the grass and other herbaceous growth suggested that the

Table 5.6 Summary data of the gorilla dung piles containing *Uapaca* seeds, and the performance of seedlings in the growing clumps, 1992 (see text for explanation of terms).

		Nest sites 1992						seed
		G2/81	G2/83	G2/84	G2/89	G2/90	trail	quads (away)
	date deposited	29-Oct	3-Nov	5-Nov	18-Nov	9-Dec		
Seeds per clump								
	median	72	8	15	41	469	13	36
	range	50-198	1-67	5-77	20-50	129-1196	5-190	
	total seeds	728	112	225	152	3002	327	360
	n clumps	7	7	11	4	6	8	10
Vegetation cover								
	cover score (median)	0	10	4	6	1	3.5	6
	% of clumps with cover at							
	≤4m	0.14	57	45.5	75	16.7	37.5	88.9
	5-20m	0	100	63.6	0	33.3	87.5	66.7
	>20m	0	100	54.6	0	83.3	37.5	100
Herbaceous stems								
	mean stem density (m-2)	0	4.5	1.2	19	10.7	ND	ND
	median	0	5.5	0	20	9.5	ND	ND
	% of total stems as							
	Haumania	0	100	0	40.8	15.6	ND	ND
	Megaphrynium	0	0	0	0	14.1	ND	ND
	Aframomum	0	0	0	57.9	56.3	ND	ND
	Hypselodelphis	0	0	0	1.3	14.1	ND	ND
	Renealmia			100				
Performance								
lifespan (weeks)	median	54+	11	53+	38	47+	30	40
	range		1-21	11-53+	24-52+		5-47+	21-47+
max ht (cm)	median	20.8	8.5	12	15	28.5	11	12
	range	12-24.5	7-9	10-15	12-24	16-34	4.5-12.5	5-19
max %height gain	median	104.2	0	21.1	18.8	119.23	29.41	30.2
	range	33.3-176.5	0-6.67	5.26-62.5	9.1-118.2	23.1-157.7	0-100	0-90
%HG/lifespan	median	1.93	0	0.481	0.464	2.54	0.626	0.434
	range	0.62-3.27	0-0.222	0.10-1.56	0.38-2.27	0.49-3.36	0-2.128	0-2.1
longest leaf (mm)	median	116	40	66	57.5	170	82	66
	range	62-144	40	48-108	20-105	58-222	63-106	26-105
max no. lvs	median	9.5	1	4	1.5	7.5	6	2
	range	5-11	1	2-7	1-6	3-9	2-6	1-5

area had not been touched by savanna fires for some time. Fires are set annually, but rarely reach all the parts of the savanna, with some unburnt patches eventually being recolonised by woody species. This site had the least vegetation cover of all the sites monitored. Site G2/83 was under relatively dense tree cover, with some herbaceous vegetation, resulting in relatively dark conditions at the forest floor. Site G2/84 was close to the forest/savanna edge and also had relatively small seed aggregations. There was practically no herbaceous ground cover but extensive dense woody liane tangles overhead. Site G2/89 had considerable herbaceous cover but the surrounding tree cover was very sparse. The lowest cover among the forest nest sites was at site G2/90, where seed aggregations were particularly high. This site was 20m from the edge of the main stream that runs through the study site. Only one dung pile had herbaceous cover above it, and most herb stems at the site were *Aframomum* rather than *Haumania*. The cover at this nest site was even less than was estimated over the dung piles marked on trail. The scores for cover differed significantly between nest sites. The savanna site, G2/81, had perhaps not surprisingly less cover than sites G2/83 and G2/84 (Kruskal-Wallis $K_{df4}=16.36$, $P<0.01$), but was not significantly different from site G2/90. Excluding the savanna site, then site G2/83 had significanlty less cover than site G2/90 ($K_{df3}=8.68$, $P<0.05$). The seed quadrats placed away from conspecifics to mimic scatter dispersal by monkeys were located under relatively dense (herbaceous) cover.

Survival and growth 1992

Survival from dung

No evidence of seed predation was noticed in 1992 at any of the dung locations. Figure 5.20 shows the survival of seedlings growing from dung deposited in the nest sites and on trail, until the end of the study. The survival of seedlings from the seed quadrats, under and away from conspecifics, is also shown. There was a gradual germination of seeds, such that maximum germination occurred at about 5-8 weeks after deposition, which explains the initial increases in the graphs. Most mortality occurred in the first few weeks of growth, with survival rates after 12 weeks typically 10-30% of the seeds deposited. On average, one third of the seeds would have been empty and thus inviable (see Chapter 3), so the germination rate of *viable* seeds would have been higher than that for all seeds deposited. Predation of seeds from dung piles was not detected.

In general terms, seedlings in the savanna nest site (G2/81) had relatively low survival, as did those growing under conspecific canopies. Site G2/83 was evidently not favourable for the few *Uapaca* seedlings growing there, as none remained after 38 weeks. After 4 weeks, seedling survival at site G2/90 was significantly higher than at site G2/81 and in seed quadrats (Kruskal-Wallis $K_{df5}=17.13$, $P<0.01$), whereas after 20 weeks it was site G2/84 that had significantly higher survival than seedlings growing from dung on trail and those 'dropped' in quadrats (Kruskal-Wallis $K_{df5}=13.2$, $P<0.05$). This reflects the changing fates of seedlings at different locations through time. At the

Figure 5.20 Survival of *Uapaca* seedlings growing from nest sites, from dung on trail (dotted line) and from 'dropped' seeds under and away from conspecifics (broken lines), 1992

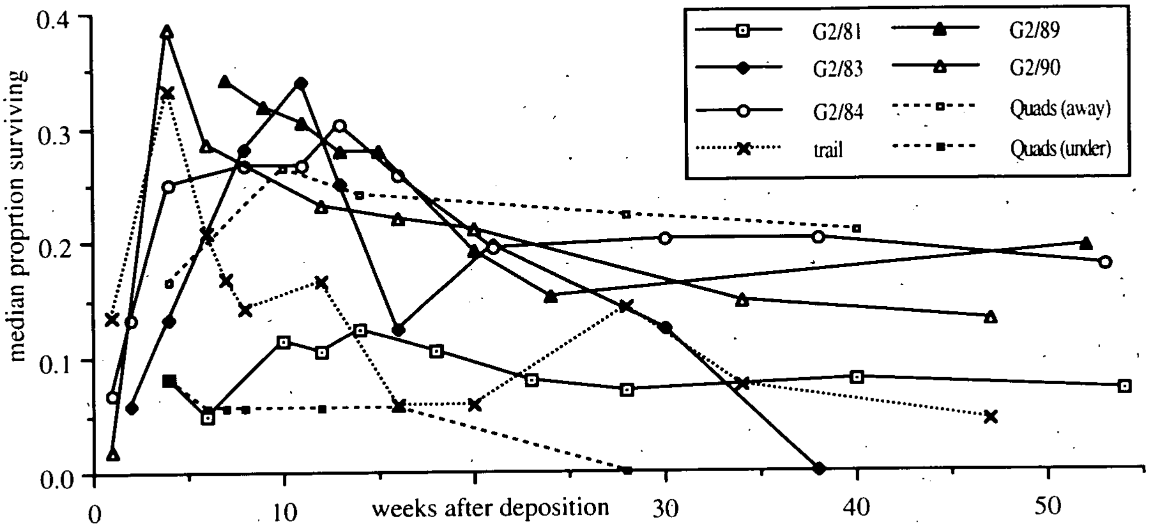


Figure 5.21 Correlation between the survival of *Uapaca* seedlings after 11 weeks and survival at the end of the study (r_s=0.544, P<0.02)

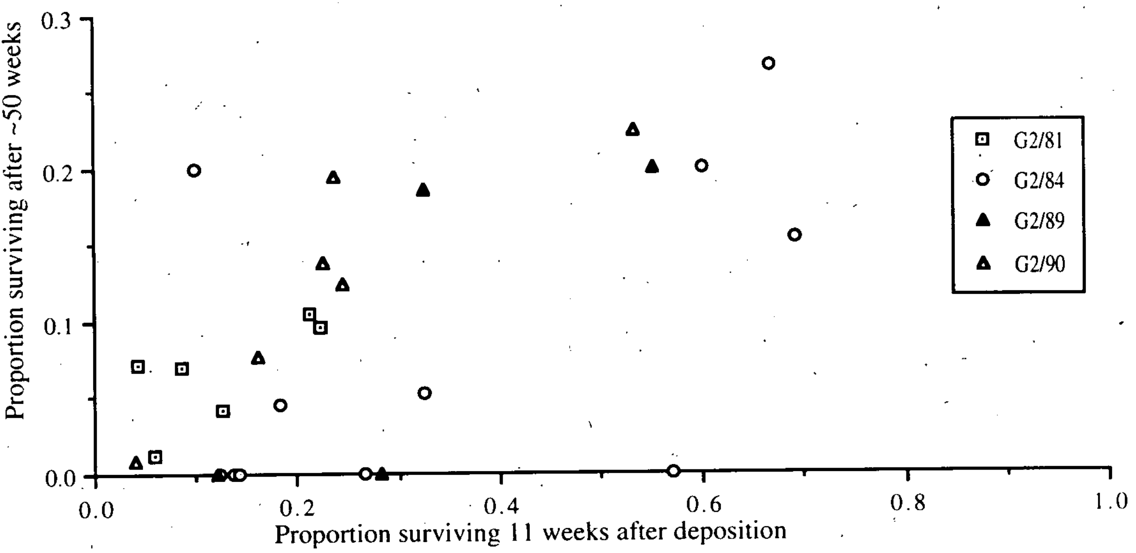
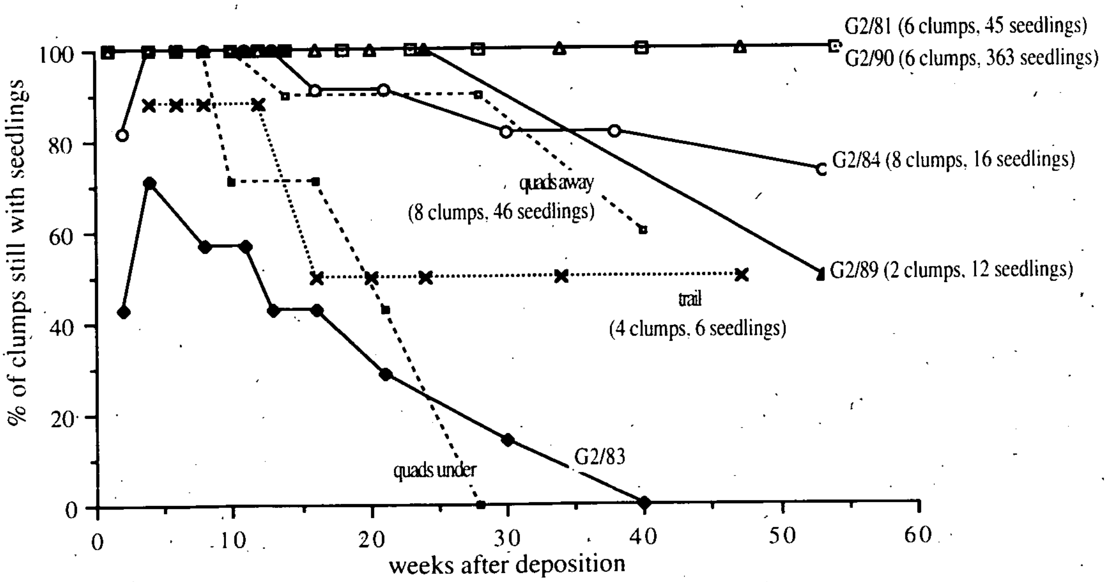


Figure 5.22 Persistence of *Uapaca* seedling clumps. The number of clumps and remaining seedlings are shown in brackets.



end of the study (47-54 weeks after deposition), the differences in survival for those locations still with seedlings (excluding G2/83, quadrats, and G2/89 due to small sample sizes) were not significant.

It was found that the clumps of seedlings that had a higher proportion of seedlings surviving initially were more likely to have higher survival at a later date. There was a significant positive correlation between survival after 11 weeks and after 50 weeks ($r_s=0.544$, $P<0.02$, $n=12$), indicating that seedlings surviving to 11 weeks were more likely to survive thereafter. The correlation is shown in Figure 5.21. This would suggest that survival during the early weeks is critical, and where most seedling mortality occurs. This association was stronger between 30 and 50 weeks, as might be expected ($r_s=0.634$, $P<0.01$, $n=21$).

The persistence of seedling clumps through time is shown in Figure 5.22. Although a low proportion of seedlings at site G2/81 survived, all the clumps originally deposited still had seedlings in them at the end of the study, as did site G2/90 which had the largest seedling 'bank'. Seedlings from dung located on trail did less well, but the loss of seedlings was greatest from quadrats under conspecifics and at nest site G2/83. There was no correlation between the number of seeds in a clump and the survival of seedlings.

Survival of seedlings from dropped seeds

The survival of seedlings growing from 'dropped' seeds under and away from conspecific canopies, in relation to those at nest sites, has been discussed above (and see Figure 5.20). Initially (up to 10 weeks), there was no significant difference in survival between quadrats located under and away from conspecifics. After 21 weeks however, seedling survival was significantly higher at those locations away from conspecific canopies (Mann-Whitney U=2, $P<0.05$).

Seedlings growing under three focal trees were labelled in two cohorts, the first in mid-January and the second at the end of May. The survival of these seedlings is shown in Figure 5.23. Ages of the seedlings were not known precisely, because seedfall occurred over several months, but they were labelled at the same stage of above-ground growth. It is clear that seedlings in the second cohort survived better than those in the first cohort, with larger differences between focal trees in the second cohort. Seedlings growing under a focal tree canopy that did not have labels but were in marked quadrats, showed similar survivorship, suggesting that the act of labelling did not seriously affect survival.

When the survival of seedlings labelled under parents is compared with those of a similar age growing in nest sites, as shown in Figure 5.24, it can be seen that seedlings in sites G2/90 and G2/81 survived better than first cohort seedlings under parent canopies (Figure 5.24A), but there seemed to be little difference between the other sites and first cohort seedlings at the end of the study. No major differences were apparent between second cohort seedlings and similar-aged ones in nest sites (Figure 5.24B),

Figure 5.23 Survival of *Uapaca* seedlings growing under 3 focal canopies: 1st and 2nd cohorts of labelled seedlings, and unlabelled seedlings in quadrats (see text).

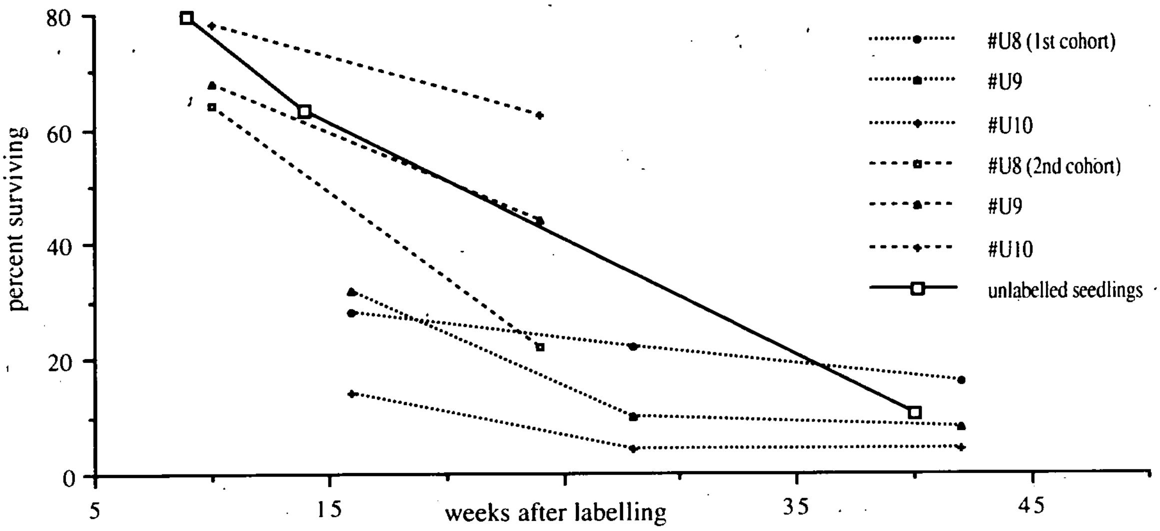


Figure 5.24A Survival of *Uapaca* seedlings: 1st cohort under parents (broken lines); in nest sites (solid lines); and from dung on trail (dotted line).

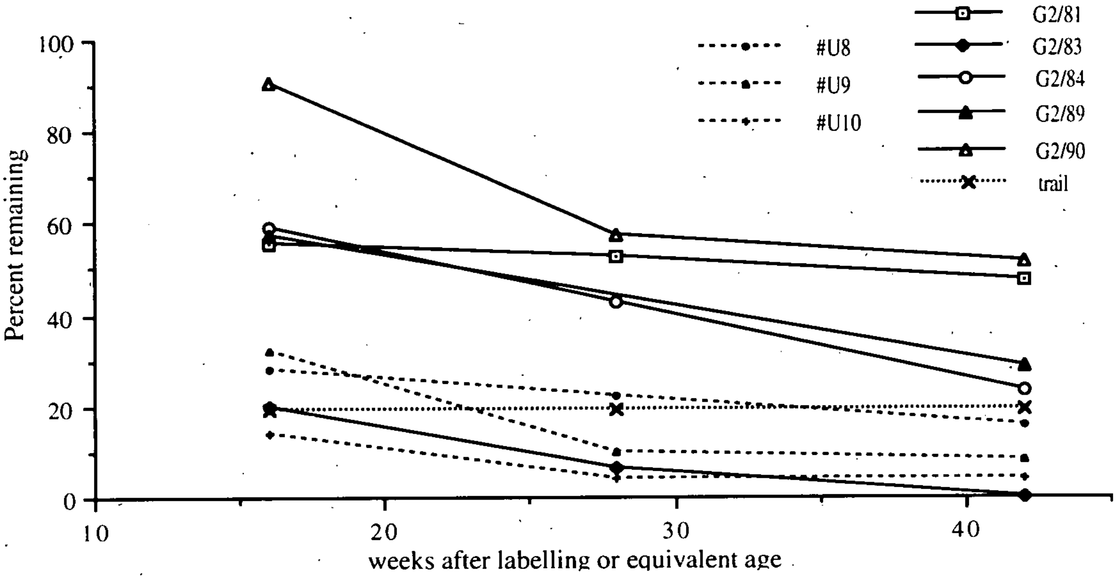
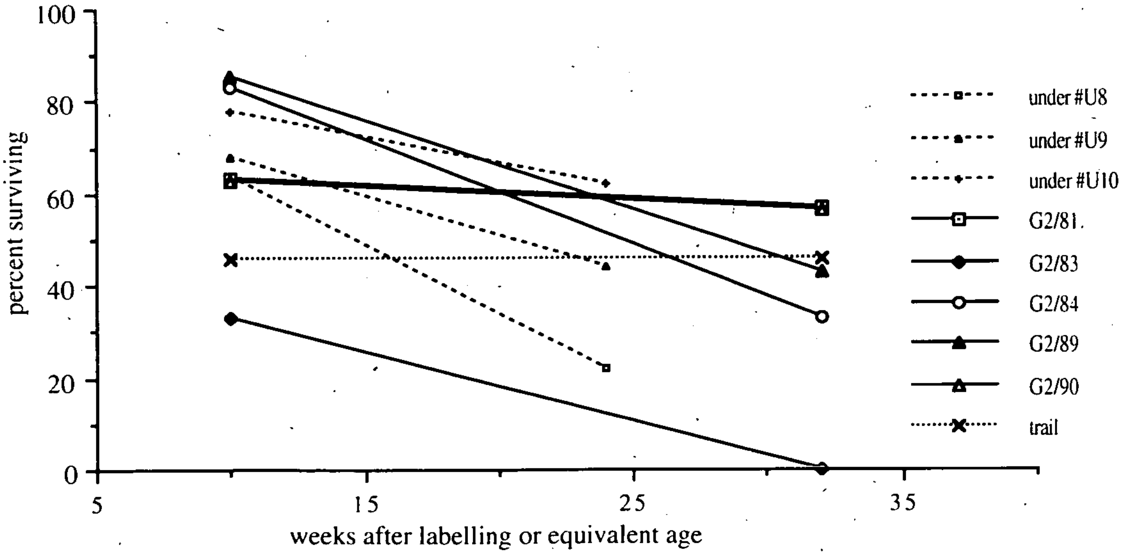


Figure 5.24B Survival of *Uapaca* seedlings: 2nd cohort under parents (broken lines); in nest sites (solid lines); and from dung on trail (dotted line).



although the poor survival of seedlings at site G2/83 is clear.

Performance

Clumps of seedlings at site G2/83 had a significantly shorter median 'lifespan' than those at the other sites (Kruskal-Wallis K_{df4}=74.8, $P<0.001$). It was found that the dimensions taken as measures of performance, *i.e.* maximum height, length of the longest leaf, and the maximum number of leaves, were all closely associated (Kendall's coefficient of concordance W=0.876, chi-sq=65.7, df=25, $P<0.001$; average r_s=0.814). The tallest seedlings were thus likely to be the most vigorous in terms of leaf production. Seedlings in the savanna site (G2/81) however tended to invest in leaf growth whereas those in the better forest site (G2/90) tended to be taller (Table 5.6).

The heights of seedlings at the nest sites, those from dung on trail, in quadrats and those that were labelled as the 1st cohort under canopies are shown in Figure 5.25. It is evident that seedlings at site G2/90 grew particularly well, and those in site G2/83 and G2/84 were consistently poorer. Seedlings at site G2/90 were consistently and significantly taller than seedlings in some of the other sites, those from dung on trail, and those from 'dropped' seeds. The precise differences at the various stages of the study are summarised in Table 5.7. The height of seedlings in quadrats away from conspecifics was not significantly different from those in quadrats under conspecifics initially (after 10 weeks), but after 21 or 27 weeks seedlings away from conspecifics were significantly taller (Kruskal-Wallis K_{df2}=6.76, $P<0.05$). By the end of the study, undercanopy seedlings were the smallest of any location.

The 'growth' (%height gain/lifespan) of seedlings differed between locations. Seedlings at site G2/83 showed significantly poorer growth than seedlings at sites G2/81 and G2/90 (Kruskal-Wallis K_{df7}=19.48, $P<0.01$). Excluding site G2/83 from the analysis, site G2/84 had a lower growth rate than sites G2/81 and G2/90 (Kruskal-Wallis K_{df3}=11.69, $P<0.01$). Including data from dung on trail and all quadrats, the only significant difference was between sites G2/84 (poorest growth) and G2/90 (best growth) (Kruskal-Wallis K_{df6}=13.5, $P<0.05$).

The height gain of seedlings over a specific period was compared between nest sites, dung on trail, quadrats and labelled seedlings of the first cohort. Differences were not statistically significant, but for the 12-week period from May-August, the ranking for height gain was (highest first) G2/90, G2/81, trail, G2/84, and labelled seedlings. From August to November the rank was G2/90, G2/81, trail, labelled and G2/84. This was the trend for the 26 week overall period. The same rankings applied when the second cohort of labelled seedlings were compared. Performance then was consistently best in sites G2/90 and G2/81.

For the seedlings labelled under parent canopies, no significant differences were found in the height of first-cohort seedlings between different trees, although sample sizes were small. In the case of the second-cohort seedlings, no significant difference in

Figure 5.25 Heights of *Uapaca* seedlings growing from dung at nest sites and on trail, from seed quadrats (Quads /a /u: quadrats away from or under conspecifics) and labelled seedlings under parents (1st cohort only).

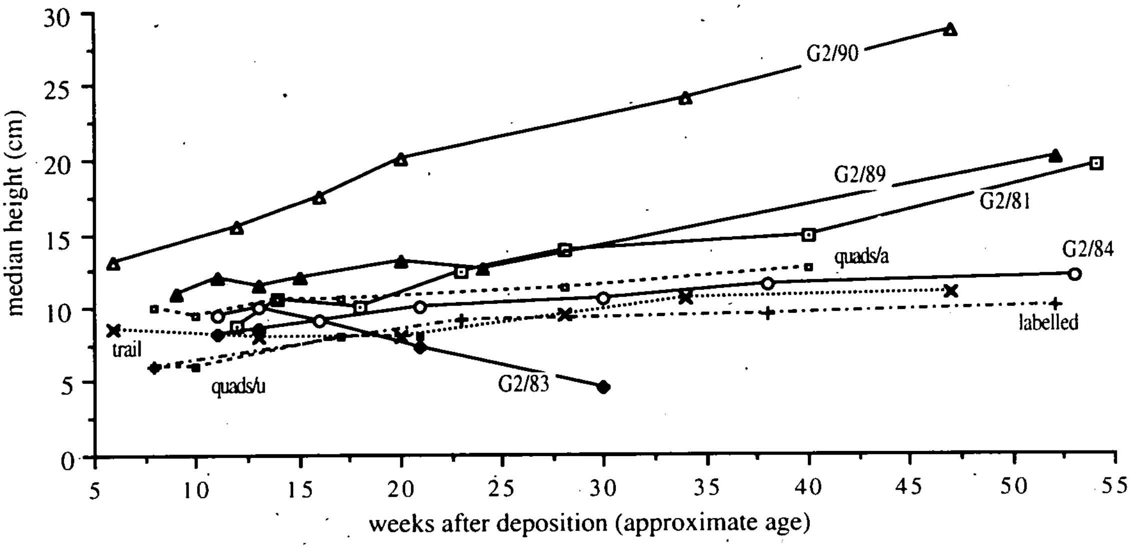


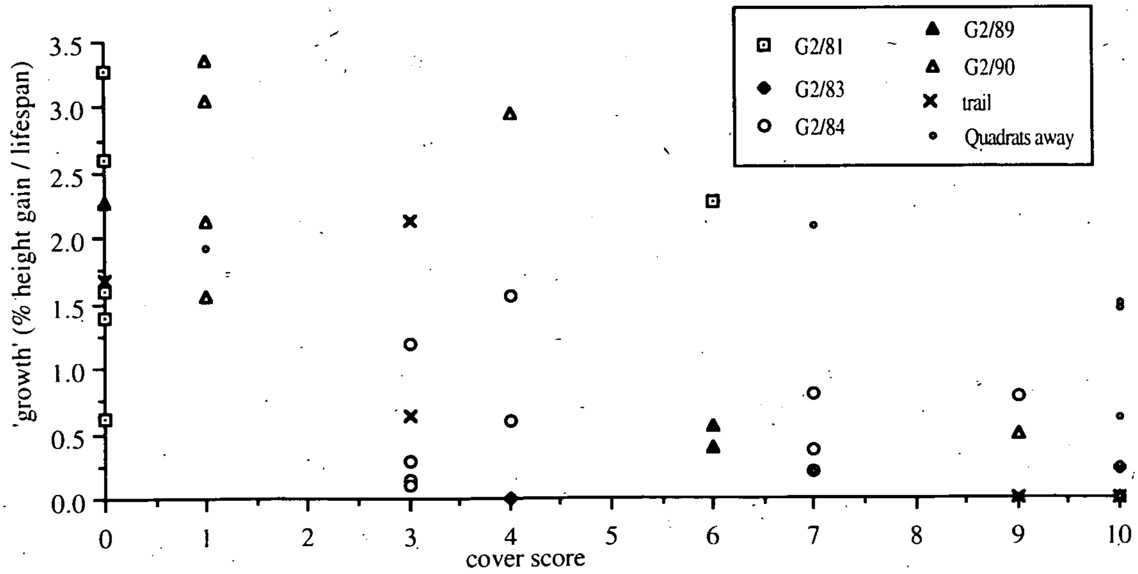
Table 5.7 Summary of height differences between clumps of *Uapaca* seedlings at different locations. (Q /a /u: quadrats away from or under conspecifics; labelled seedlings are the 1st cohort only)

weeks after deposition	grouping tested	nest sites for which height difference is significant*	test statistic K**	df	probability
11 or 12	5 sites & trail	90 > 81, 83, trail	19.6	5	0.01
	sites, trail & quadrats	90 > 83, trail, quadrats	22.2	6	0.01
20+	4 sites & trail	90 > 84, 81 & trail	17.85	4	0.01
	sites & qaudrats/a	90 > 84, quadrats	17.5	4	0.01
	sites, trail, quads/a + /u, & labelled	90 > trail, quads/u & labelled	34.81	7	0.001
40	3 sites & trail	90 > 84 & trail	13.09	3	0.01
	sites, trail & quadrats /a + /u	90 > 84 & trail	16.07	4	0.01
	sites, trail, quads/a + /u & labelled	labelled < 90, 81 & quadrats/a	29.26	5	0.001
47/54***	3 sites & trail	90 > 84 & trail	13.05	3	0.01
	3 sites, trail & labelled	90 > labelled (1st cohort)	19.41	4	0.001

* arrows indicate direction of difference; sites are referred to by number alone

** Kruskal-Wallis 1-way ANOVA by ranks   ***end of study; no quadrats of this age

Figure 5.26 Cover score and growth of *Uapaca* seedlings growing from dung at 5 nest sites and on trail, and from seed quadrats (r_s=0.560, P<0.001, n=48).



height was apparent after 20 weeks, but after 30 and 44 weeks, those under tree #U10 were taller than those under the other 2 focal trees (1-way ANOVA $F_{2,102}=13.58$, $P<0.01$ and $F_{2,60}=5.395$, $P<0.1$ respectively).

Vegetation and performance

Performance was consistently and negatively correlated with measures of vegetation cover. Figure 5.26 shows the cover score of individual seedling clumps and the associated growth. Data from all locations were pooled, because sample sizes at individual sites were too small. The correlation was significant (Spearman's $r_s= -0.560$, $P<0.001$, $n=48$), indicating that seedlings with least cover overhead grew the most vigorously. Comparing the growth of seedling clumps with cover at ≤4m to those without, it was clear that those without vegetation cover immediately overhead showed a better 'growth' (Mann-Whitney $U=79.5$, $P<0.05$, $n=16$ and 22). Cover score was not significantly associated with survival or maximum height. Stem density of herbs showed no significant association with performance or survival. Pooling data from all sites showed no association between height or 'growth' and survival, but in the savanna nest site, seedling height after 28 weeks correlated significantly and positively with survival after 54 weeks (Spearman Rank Correlation $r_s=1$, $P<0.01$, $n=6$), suggesting that the more vigorous seedlings were more likely to survive.

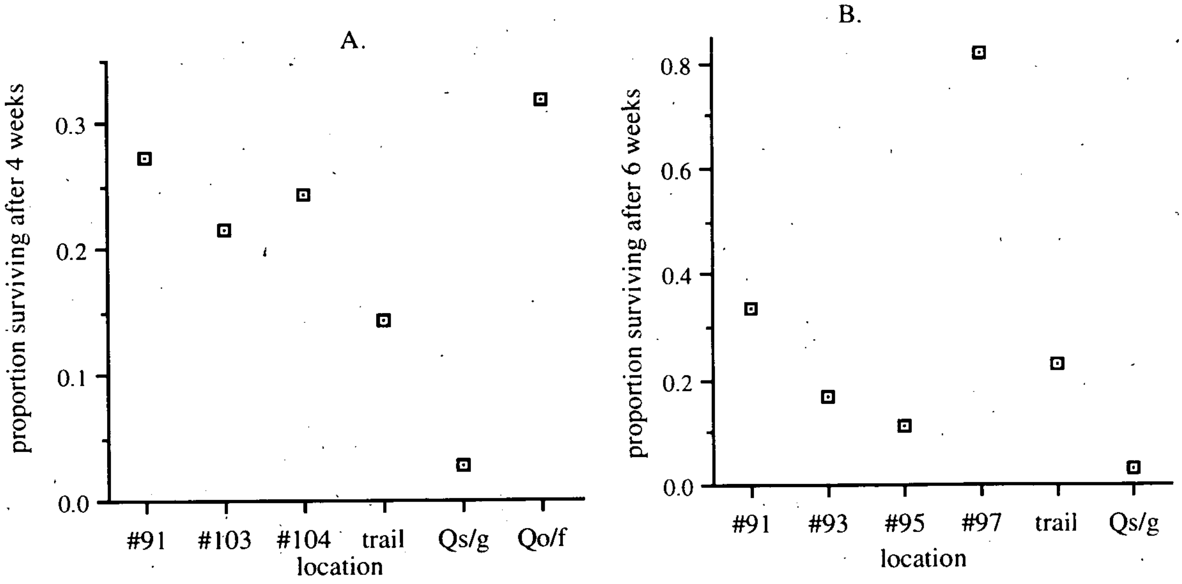
Seed deposition sites (1993)

No data on performance are included for these sites in Table 5.7, because they were monitored for insufficient time before the study ended for performance to be assessed. Nest sites in 1993 showed a similar range of cover conditions to those of 1992, and seed aggregations were similar to monitored sites of the previous year, other than site G2/90. Two of the sites, G3/103 and G3/104 were in 'closed canopy forest' (see Chapter 2) at the western edge of the study area, due to the presence there of fruiting *Gambeya africana* trees which attracted gorillas. Site G3/103 was completely without herbaceous cover under a closed tree canopy, on a steep-sided bluff above a gulley, and G3/104 was in a valley basin covered in dense herbaceous growth of *Ataenidia conferta* (Marantaceae). Site G3/97 was at the edge of a savanna pocket within the forest, among dense, sprawling colonising vegetation. Site G3/95 was among thick herbaceous vegetation in an open site of an old treefall gap. Site G3/93 was at the edge of a stream liable to flooding, with some herbaceous vegetation and woody cover limited to small *Cryptosepalum staudtii* (Caesalpiniaceae) trees. Site G3/91 was under nearly closed canopy with some herbaceous cover as well. Dung piles deposited on trail tended to have little herbaceous cover but frequently had overhead tree cover.

Table 5.8 Summary data on gorilla dung piles containing *Uapaca* seeds, and the performance of seeds from the growing clumps, 1993 (see text for explanation of terms).

				1993			
	G3/91	G3/93	G3/95	G3/97	G3/103	G3/104	trail
Seeds per clump							
median	18	9	56	12	30	37	48
range	5-68	3-17	11-127	5-71	7-56	8-88	6-110
total seeds	237	95	725	127	158	274	362
n clumps	9	9	13	5	5	7	7
Vegetation cover							
cover score (median)	7	6	6	9	4	10	3
% of clumps with cover at							
≤4m	55.6	55.6	75	63.5	0	100	14.3
5-20m	44.4	44.4	50	87.5	100	62.5	85.7
>20m	88.9	0	8	25	100	87.5	42.9

Figure 5.27 Survival of *Uapaca* seedlings in 1993, (A) after 4 weeks and (B) after 6 weeks from dung in nest sites and on trail, and from 'dropped' seeds (Qs/g: quadrats set in gallery forest in September; Qo/f: quadrats set in the forest interior in October).



Survival and growth (1993)

Note: The length of the monitoring period was limited to a few weeks, because these sites were marked shortly before the end of the study period. Emerging seedlings were counted twice and measured only once.

Survival

No seed predation was recorded at the dung piles in this season either. The survival of seedlings from deposited seeds after 4 weeks is shown in Figure 5.27A. The survival of seedlings in quadrats put out in gallery forest early in the season (September) was significantly lower than seedlings in site G3/91 and those in quadrats set in the forest interior in October (Kruskal-Wallis K_{df4}=18.35, P<0.01). The survival of seedlings from dung left on trail was significantly lower than seedlings in quadrats set in October (Kruskal-Wallis K_{df4}=10, P<0.05). The survival at the sites that were monitored after 6-7 weeks is shown in Figure 5.27B. Seedling survival was significantly lower at site G3/95 than at site G3/97 (Kruskal-Wallis K_{df4}=11.3, P<0.05). Site G3/95 was the only site with considerable numbers of large seeds of *Gambeya africana* (Sapotaceae) in the same dung piles as *Uapaca* seeds, which may have influenced survival. The quadrats set in September had significantly lower survival than sites G3/91, G3/93 and G3/97 (Kruskal-Wallis K_{df4}=21.3, P<0.001).

Performance

No significant difference in height was found between locations, perhaps because growth was at a very early stage. Most seedlings were still at the cotyledon stage and only some showed the emergence of the first leaf. Similarly, there were no apparent associations between cover score and height or survival at that stage.

5.3.5 Germination trials

The camp nursery enabled the germination of the four species under study to be investigated. Data from the germination trials undertaken are shown in Table 5.9.

Ganophyllum

Seeds taken from gorilla dung and washed, and seeds dropped by monkeys (*i.e.* with no gut passage) had very similar germination success in nursery conditions (78% and 76%, n=154 and n=100 respectively). A sample of 111 seeds from gorilla dung that had been exposed to unusually dry conditions in the forest (see Chapter 2) showed very poor germination in nursery conditions, with only 1.8% germinating during the trial. The seeds apparently were unable to withstand desiccation. Some fruit that was judged by human eye to be immature using colour as a cue contained some viable seeds, as 40% of the 20 seeds germinated.

Cola

Trials were only undertaken using seeds from immature fruit (full size but green) that monkeys (including mandrills) had spat out while feeding. Of the 120 seeds used in the trial, not one germinated (ripe seeds germinate within days of deposition), confirming that feeding on immature fruit is effectively seed waste.

Dialium

Hard and soft seeds

The soft, swollen seeds that were found in immature fruit and in gorilla dung germinated immediately, but were vulnerable to fungal attack. Those that went through a gorilla gut succumbed rapidly to fungus (0.7% germination, n=140) whereas 70% of those that were taken from intact immature fruit germinated. These did not last long, and only 50% of the seedlings survived after 5 weeks.

An initial trial (A in Table 5.9) used hard (ripe) *Dialium* seeds from gorilla dung and from intact fruit. A higher percentage germinated from those that were from dung in the 13 weeks of the trial (6.5% from dung and 1.3% from fruit). An additional group of seeds from dung were soaked in rainwater for 36 and 72 hours, but no difference in germination was apparent after 6 weeks. These seeds were all discarded, but it was noted that an additional 21.6% germinated over the following 9 months. It was not possible to run an exhaustive trial, for these seeds may not germinate for years.

Experimental seed burial

Germination of hard *Dialium* seeds from gorilla dung occurred from depths of up to 8cm below the soil surface, and fewest germinated at the soil surface. In the initial trial (B in Table 5.9), 15.4% of 65 seeds germinated over a 21-week period, with those buried deepest emerging during the latter part of the trial, and none germinating at the surface itself. During the subsequent 2 months, an additional 1.5% germinated. In the second trial (C in Table 5.9; n=185 seeds), 10% germinated within 18 weeks. As many germinated at 8cm depth as at 2cm and only 1 germinated at the soil surface. It would seem that burial may in fact enhance germination by providing suitable conditions such as sufficient moisture.

Uapaca

An initial trial ('October' in Table 5.9) indicated that seeds deposited by gorillas germinated more quickly and with a higher percentage than those deposited by chimpanzees. This was confounded by a subsequent trial ('November') that indicated little difference in the effect of the two apes' guts on germination. Seeds from underneath 2 focal trees, spat out by monkeys, showed a large difference in germination (46% and 72% respectively). In one case seed germination was just as successful, if not quite as rapid, as that of seeds from ape dung.

Table 5.9 Germination trials carried out for the four study species. FRI: seeds from immature fruit; FRR: ripe seeds.

source		n seeds	% germination	week of trial	time to first germination	time to 50% germination
Ganophyllum						
gorilla dung		154	78	ND	<1 wk	ND
gorilla dung (dry)		111	1.8	ND		
spat undercanopy		100	76	4	<1 wk	2wks
FRI		20	40	4		
Cola						
FRI		120	0			
Dialium						
Soft seeds						
Gorilla dung		140	0.7	1	<1 wk	all rotted < 1wk
Gorilla dung		50	0	2	<1 wk	all rotted < 1wk
FRI		50	70	2	<1 wk	1-2 wks
Hard seeds A						
Gorilla dung		77	6.5	3-13		
FRR		77	1.3	3		
dry		20	10	6		
soaked 36h		20	5	6		
soaked 72h		20	10	6		
total		214	5	1-13		
additional germination			plus 21.6%	plus 9mths		
Hard seeds B	depth		n germinated			
gorilla dung/FRR	0cm	13	0			
	1	13	2	11-18		
	2	13	3	10-18		
	4	13	3	1-13		
	8	13	2	19-21		
total		65	10 (15.4%)			
additional germination			plus 1.5%	plus 2mths		
Hard seeds C						
gorilla dung	0	37	1	8		
	1	37	6	3-22		
	2	37	5	12-18		
	4	37	2	11-18		
	8	37	5	5-18		
total		185	19 (10.2%)			
Uapaca						
A (October)		n seeds	% germinated			
chimp dung		99	65.7	6	<1	4
gorilla dung		167	75.5	4	<1	1
B (November)						
chimp dung		32	87.5	6	<1	<2
gorilla dung		32	71.9	6	<1	<2
spat a (#U53)		90	45.6	6	<1	
spat b (#U55)		60	71.7	6	<1	4

5.3.6 Seedlings in Marantaceae Forest

The species of seedlings that were found on the transect in mid-1993 are listed in Table 5.10, ranked in order of abundance. Data on the basal area and abundance of trees ≥10cm dbh of the same species along the same transect are also given. The more common species of tree generally had the most abundant seedlings. One remarkable exception is the Caesalpiniaceae *Hylodendron gabunense*, which had a much higher seedling population than other species, despite the fact that the survey was done in the middle of a year following a community-wide high seed production. This would suggest that *Hylodendron* seedlings are able to tolerate the difficult establishment conditions of dense herbaceous growth in Marantaceae forest and suffer mortality at a later stage. All the seedlings were of a similar growth stage, suggesting that they were from the last major seed crop.

It is interesting to note that some species that are not uncommon as adult trees (*e.g. Dacryodes buettnerii, Pycnanthus angolensis, Trichoscypha acuminata*) were absent as seedlings, suggesting that current conditions do not favour the establishment of seedlings of these species, or that they recruit rarely in good years. This one-off survey, although representing the seed fall and establishment of possibly several fruit crops, cannot convey the shifting dynamics of seedling populations in the forest . With such variable growth and vegetative conditions over time and space, the fate of seedlings will doubtless shift in a pattern that reflects this changing environment. A search along 2km of linear transect in 1990 yielded only 1 *Dialium* seedling(R. Parnell, pers. comm.)

5.3.7 Seedlings in old nest sites

Attempts were made to relocate nest sites built by gorillas during 1989-1991 where it was known that seeds of the four study species had been deposited, in order to look for seedlings associated with them. In only a few sites were seedlings found that might have originated from dung. No *Ganophyllum* seedlings were found in the area of 2 nest sites (16 dung locations) that were searched. Seven sites that dated from *Cola* deposition seasons were searched (54 dung locations). Of these, 4 were found to have *Cola* seedlings, although only in one site could the 4 seedlings be said with any degree of certainty to have originated from dung. In the other sites, which included the one that was the subject of an earlier study of seedling survival (Tutin *et al* 1991a), the few seedlings that were found could not be distinguished from those that may have been from older or more recent 'background' seed fall (*i.e.* from scatter dispersal by monkeys). They were of similar heights to the seedlings that were monitored in this study.

Searches at 4 old *Dialium* nest sites yielded no seedlings, but some were found at two others, 2 in one and 6 (of various ages) in the other. The latter site had been monitored for a short time after deposition (R. Parnell, pers. comm.), so was well

Table 5.10 The densities of seedlings ≤50cm high of 23 species found in mid-1993 along a 1.85km transect in Marantaceae forest. Sample area was 500m^2. Stem densities and rank basal area of trees ≥10 cm dbh are also shown.

			seedlings ≤50cm in ht		trees ≥10cm dbh°		
Species	Family	dispersal mode*	no. of seedlings/ha	rank	rank basal area	no. stems per ha	rank (no. stems)
Hylodendron gabunense	Caesalpiniaceae	W	7420	1	8	3.28	
Diospyros polystemon	Ebenaceae	A	1360**	2	7	12.80	5
Diospyros dendo	Ebenaceae	A				11.40	6
Cola lizae	Sterculiaceae	A	840	3	2	74.68	1
Lophira alata	Ochnaceae	W	800	4	3	28.30	3
Aucoumea klaineana	Burseraceae	W	680	5	1	37.10	2
Pentaclethra eetveldiana	Mimosaceae	B	280	6	6	6.54	10
Dialium lopense	Caesalpiniaceae	A	180	7		2.82	
Celtis tessmannii	Ulmaceae	A	180	7		0.08	
Uapaca guineensis	Euphorbiaceae	A	180	7		0.30	
Lecaniodiscus cupanoides	Sapindaceae	A	80	10		1.00	
Irvingia spp	Irvingiaceae	A	60	11		3.12	
Uvariastrum pierreanum	Annonaceae	A	60	11		0.26	
Ganophyllum giganteum	Sapindaceae	A	40	13		1.00	
Pentaclethra macrophylla	Mimosaceae	B	20	14	4	7.36	9
Dacryodes buettneri	Burseraceae	A	0		5	5.92	
Dacryodes normandii	Burseraceae	A	0			1.80	
Parkia bicolor	Mimosaceae	A	0			0.26	
Pycnanthus angolensis	Myristicaceae	A	0		10	1.84	
Santiria trimera	Burseraceae	A	0			0.20	
Tricoscypha acuminata	Anacardiaceae	A	0			4.60	

*W = wind; A= animal; B = ballistic

** data for the two Diospyros spp are pooled due to uncertain identification

° from Tutin et al 1994

known. It was several hundred metres from the nearest known *Dialium* tree, so the seedlings were likely to have originated from the dung at the nest site. Three sites (11 dung locations) containing *Uapaca* seeds were searched but no seedlings were found.

This sample is small compared to the number of deposition sites that must accumulate over time in the appropriate seasons. The exact locations of the original nests were difficult to establish, but the area was thoroughly searched. The above points, coupled with the high mortality that seeds and seedlings experience, meant that the lack of success of the searches was not entirely surprising.

5.3.8 Stem densities of herbs

Data on the density of herbaceous stems recorded in nest sites, under focal trees, and along a forest transect are shown in Table 5.11. Most of these herbs are patchily distributed and may be extremely dense, with *Haumania liebrechtsiana* occurring locally at densities of 40 000 stems per hectare or more. Densities were broadly similar between nest sites and under focal canopies of the four species, and along the forest transect,

Table 5.11 Stem densities of herbaceous vegetation under focal trees, at gorilla nest sites and on a transect in Marantaceae forest.

	Family	MARANTACEAE				ZINGIBERACEAE	
	Species	*Haumania liebrechtsiana*	*Hypselodelphis violacea*	*Marantochloa spp*	*Megaphrynium spp*	*Aframomum sp ?nov*	*Renealmia spp*
Ganophyllum							
nest sites	stems/m2	3.46	0.43	0	4.89	0.63	0
	range	0.63-7.38	0-2.67		1.17-11.25	0.15-1.5	
	n	6	6		6	6	
trees	stems/m2	3.21	0.34	0	5.18	0.31	0
	range	1-6.25	0-1.25		0-14.25	0-1.5	
	n	10	10		10	10	
Cola							
nest sites	stems/m2	4.11	0	0	1	0.11	0
	range	2.92-5.86			0-2.5	0-0.25	
	n	3	3		3	3	
trees	stems/m2	3.99	0.84	0	2.55	1.36	0
	range	2.5-6.88	0-3.13		0-7.13	0-4.5	
	n	10	10		10	10	
Dialium							
nest site	stems/m2	2	0	0	1.83	0.5	0
	range	n/a			n/a	n/a	
	n	1	1		1	1	
trees	stems/m2	3.2	0.29	0	3.59	0.36	0
	range	0.13-7.5	0-0.75		0-7.88	0-2.13	
	n	10	10		10	10	
Uapaca							
nest sites *	stems/m2	2.52	0.33	0	2.96	0.26	0.22
	range	0-6.2	0-1.5		0-8.8	0-1	0-0.6
	n	4	4		4	4	4
trees							
forest interior	stems/m2	4.42	0.13	0.5	3.17	0	0.33
	range	2.25-6.5	0-0.38	0-1.5	0-5.25	n/a	0-0.75
	n	3	3	3	3	3	3
gallery/edge	stems/m2	0	0	0	0.63	0.16	0
	range				0-2.5	0-0.63	
	n				4	4	
Marantaceae forest transect°	stems/m2	2.52	1.64	0.82	2.53	0.28	0.18

* excluding a nest site located in open savanna ° from White et al (1995)

suggesting that there are no major differences in the herbaceous vegetation density in these different locations. There may however be differences in cover at the level of tree canopies. In some respects the forest transect represents a number of ancient and recent gorilla nest sites, in that the some areas must have had nest sites built in them for a very long time. The two species of *Marantochloa* included in the survey are largely restricted to marshes, which explains their absence from nest sites or under the study tree species other than *Uapaca*.

5.3.9 Post-script: seedling performance since the end of the study

Many of the clumps of seedlings at nest sites have been monitored since this study ended, with two censuses carried out in June 1994 and February 1995 (C.E.G.Tutin & R.J. Parnell, pers. comm.). These additional data are shown in summary form in Appendix E, along with the results from the end of theis study (November 1993). The general trends in survivorship and performance discussed in this chapter are still evident: there are favourable and less favourable sites. The other interesting feature is that *Cola* seedlings seem to have reached a plateau in height, perhaps adopting a 'sit-and-wait' strategy, whereas the tallest *Uapaca* seedlings in the favourable forest site (G2/90) are now over 1m in height.

5.3.10 A summary of the principal results

Ganophyllum

1. The location of one nest site (G2/6) with less dense herbacous vegetation exposed the seeds to desiccation during an atypical 6-week dry period in 1992. Those in a moister, more densely-covered site (G2/5) survived much better. Seeds and seedlings left on trail did not survive well.
2. At the end of the study, site G2/5 had 59 seedlings in 7 clumps, and site G2/6 had one seedling only.
3. Most seeds germinated within the first 2 weeks after deposition, but a number of seeds displayed a delay in germination of about 8 weeks.
4. Survival and growth of seedlings in site G2/5 were both significantly better than in site G2/6, on trail, and better than those from 'dropped' seeds (in seed quadrats or labelled undercanopy seedlings). The best survival and growth were in a nest site.
5. At site G2/5, clumps with the most vigorous seedlings showed the highest survival.
6. Herbaceous stem density at site G2/5 correlated negatively with performance: clumps with more stems showed poorer growth.
7. Severe seed predation occurred in 1993. Predation rates of 95-100% were recorded for most seed aggregations, irrespective of their size. All seed locations appeared to be equally affected, although a shortlived initial 'escape' for scatter-dispersed seeds

was indicated. Site G3/8 was so rapidly raided that all seeds were lost within the first week.

Cola

1. Seeds germinated within a few days of deposition, and most mortality occurred within the first five weeks.
2. There were consistent trends suggesting that seedlings in locations with less cover survived and grew better, although they are able to establish in less favourable conditions. The biggest seedling 'bank' was at the nest site with the least cover and the most vigorous seedling growth.
3. Survival and growth of seedlings from seeds dropped under conspecific canopies was poorer than for seedlings at nest sites.
4. Seedlings labelled under parents survived as well as in some nest sites, but growth was poorer.
5. Seedlings at site G2/26 were already taller than elsewhere when first measured, but they gained less in height through time. The tallest seedlings were in site G2/19, the smallest under conspecifics and from dung on feeding trail.
6. Many seedlings suffered browsing, which sometimes led to the death of the seedling.

Dialium

1. Seeds were dormant, and displayed a staggered germination which resulted in some seeds germinating beyond 18 months after deposition.
2. Seeds 'disappeared' from deposition sites, either removed by predators or buried by dung-beetles or litter. Gorillas indulged in coprophagy to remove some of the seeds in their dung.
3. Within the period of study, a slightly higher percentage of seeds germinated from dung at the nest site than seeds washed from dung and put out in quadrats, and the subsequent survival of seedlings over 14 months was higher from dung at the nest site.
4. Germination from seeds soaked in water was better than unsoaked seeds under parents, but soaked seeds away from conspecifics had the lowest germination.
5. Certain focal trees were found to have larger seedling populations under them than others. These were the trees that were estimated to have had the largest crops.
6. No clear differences in growth were evident between seedlings under different focal trees.

Uapaca

1. Seeds germinated generally within the first week, although some took 2-8

weeks to germinate. On average, one third of seeds deposited were inviable, having no cotyledonar material within their cases. There was no effect of clump size on survival.

2. Seedling clumps at some nest sites showed better survival and/or performance than seedlings growing from dung on trail or from dropped or scatter-dispersed seeds. Seedlings in sites G2/90 and G2/81 showed the best growth. Initial differences in survival between sites evened out over the period of a year.
3. Seeds/seedlings under conspecifics ('dropped') fared less well, in terms of survival and growth, than those away from conspecifics ('scatter-dispersed'). The best success in terms of a seedling bank was at nest sites.
4. Seedlings labelled under parents earlier in the season (first cohort) survived less well than those in nest sites. Those labelled later in the season (second cohort) showed much the same survival as seedlings in nest sites but their growth was poorer.
5. Growth was significantly and negatively correlated with cover conditions: those seedlings growing in locations with less cover showed better growth than those where cover was denser.
6. Seed/seedlings deposited in 1993 were not monitored long enough to make any realistic assessments of survival or growth. No association of cover with survival or performance was detected over the short time scale. Seeds deposited early in the season seemed to fare less well than those deposited later.

5.4 DISCUSSION

Where a seed ends up on the forest floor is largely a matter of chance. Although a tree has some control over the manner in which seeds are removed, by attracting certain types of consumer and therefore seed treatment, the actual conditions of a deposition site are for the most part unpredictable. For the four species studied here, the bulk of the seed crop is either dropped under the parent canopy, scatter-dispersed (spat out by monkeys), or clump-dispersed in dung. The extremely high variation in survival and growth was not unexpected. Seeds are deposited over a variable and patchy environment, and a myriad of factors relating to local conditions affect seed and seedling responses in the different locations where they are deposited. With such variation, inherent plasticity on the part of the seedlings and high mortality, the interpretation of the analyses should be made cautiously. On the other hand, results which did come through clearly, either as a statistically significant outcome, or as a consistent trend, have done so in spite of the limitations mentioned above. Certainly it would be a major improvement if larger sample sizes were possible, in terms of the number of nest sites and deposition locations, trees under which seedlings are followed and quadrats of seeds.

5.4.1 Germination strategies, seedling types and causes of mortality

The four species represent a range of seed types and germination strategies. I do not plan to discuss in detail the physiology of germination, which is a complex subject that touches on maternal effects on germination ability, microclimate, soil-seed interactions, chemistry and light. Some of these issues were raised in Chapter 1 and are explored in Fenner (1992), but were not studied in detail during this research.

Seed predation

The fleshy cotyledons of *Ganophyllum* seeds are physically protected by a hard but thin shell. This did not prevent seed predation, as was vividly demonstrated in 1993 when more than 95% of seeds were predated. In the previous year there was community-wide high seed production, which may have provided ample food for rodents and resulted in an increase in their populations. Levels of predation on *Ganophyllum* seeds in dung in 1992 were around 7-10%. The fleshy cotyledons must represent a relatively high-quality meal for granivores. The large seeds of *Cola* are unprotected physically but are probably chemically so (Hallé 1987, Rogers *et al* 1990, Tutin *et al* 1991a), for their size would otherwise make them vulnerable to the attentions of seed predators. The seeds of the congener *C. nitida* are sold commercially because they contain active chemical stimulants, so some form of chemical protection is likely in *C. lizae* seeds. During this study there were few losses of *Cola* seeds to seed predators.

Dialium seeds are incredibly hard, and this may confer some resistence to predation. They are small enough to be buried by dung beetle activity or litter accumulation and tended to 'disappear' from deposition sites, although it was never established whether this was sometimes due to their removal by potential seed predators. Seeds of *Uapaca* have a tough, ridged case that seemed to be resistant to seed predation by small rodents (forest hogs crunch up seeds with ease). It is possible that the reward of the leafy cotyledons within does not merit the effort of breaking the shell for small granivores. They were certainly harder to break open manually than *Ganophyllum* seeds.

Germination

Most *Ganophyllum* seeds germinated within the first week, but some displayed a delay in germination of 8 weeks. *Dialium* seeds, if they ripen to become hard, are dormant and only began to germinate after the dry season, although their staggered germination meant that only a small proportion of seeds germinated within the first year. *Cola* seeds germinated immediately upon deposition, developing a hypocotyl within days. The staggered germination of *Uapaca* was probably a consequence of the time it took for individual seeds to take up moisture.

Staggered germination avoids an "all the eggs in one basket" scenario: in an unpredictable environment, it may be advantageous for some seeds to delay germination. Ungerminated seeds remain at risk of predation and desiccation, but may avoid any initial density-dependent mortality of early seedlings. There was no clear evidence of such density-dependence during the study, but delayed *Ganophyllum* seedlings from dropped or scatter-dispersed seeds were found to survive better than prompt-germinating seedlings in 1993. In a clump, however, later-germinating ones may have a height disadvantage.

Desiccation affected ungerminated *Ganophyllum* seeds and newly-emerging seedlings equally. Attempts to germinate desiccated seeds in the camp nursery all but failed, which suggests that these seeds were unable to withstand desiccation and would be difficult to store. The desiccation of seeds probably explains why delayed germination was not noticed in 1992, because most ungerminated seeds would have died. The poor germination of *Uapaca* seeds put out in quadrats at the very start of the fruiting season in 1993 (Figure 5.27), when the soil was still quite dry and the rains had not begun in earnest, might have been partially a result of desiccation.

Dormancy and quiescence are common features among the Caesalpiniaceae (Murdoch and Ellis 1992). *Dialium* seeds have been easily stored in dry conditions in camp, and there is no reason why seeds should not remain viable in the soil for several years. It would have been instructive to dig underneath individual trees to investigate the existence of *Dialium* seeds in the soil seed bank. They were shown to germinate from depths of at least 8cm, and less germination was observed on the soil surface. It would seem that moist conditions are required to enable *Dialium* seeds to germinate. The seed-soil interface may determine how moisture affects the opening of the hilum, or scarification, that allows imbibition of seeds and thence germination. For a dormant seed, burial probably confers some protection from predation (see above). Estrada and Coates-Estrada (1991) have reported the importance of dung-beetle activity for the protection of seeds from predation, either by burial of seeds or their removal from a dung pile.

Seedling types

As the fleshy cotyledons of *Ganophyllum* uncurl, the first compound leaves appear as a pair, with subsequent leaves growing in a whorl. Vigorous seedlings at the end of the study had up to 13 leaves. The cotyledons may be lost, probably to rodents early on, or along with the leaves to browsing herbivores at a later stage. If most or all cotyledonar material was removed before the first leaves had emerged, the seedling was likely to die. If just the topmost leaves were taken and others (or cotyledons) remained, the seedling could resprout. Repeated or severe browsing either killed the seedlings directly or weakened them such that they were more likely to fail at a later stage.

A similar scenario affected *Cola* seedlings, which suffered most from the attentions of herbivores, both invertebrate and vertebrate. The large seeds give rise to stout, large seedlings but they were more frequently browsed. Seedlings depend on the large cotyledon reserves for considerable initial height growth. This enabled the seedlings in site G2/19 to overcome competition with *Celtis* seedlings deposited in the same clumps. *Celtis* seedlings are small and have leafy cotyledons which create dense shade, but due to their small size the larger *Cola* seedlings rapidly overtopped them. Rodents sometimes nibbled at the cotyledons but this rarely killed the seedling. *Cola* produces fewer, larger leaves than the other species studied, and vigorous seedlings had up to 7 of them after 18 months. Even with both of the first two leaves and part of the stem removed, seedlings with cotyledons could regenerate if not killed outright, but repeated browsing seemed to tip the balance of struggling seedlings such that they failed to resprout or succumbed to pathogens. With hindsight, it was never safe to class a *Cola* seedling as dead unless it had completely disappeared. Some browning of parts of the large leaves was noted, the cause of which was not determined, and insect herbivory on leaves was also noted.

Denslow (1980) suggested that the size of a seed or seedling and its ability to recover from herbivory until it reaches a 'safer' size is an important feature of the regeneration strategy of a species. The large-seeded Bombacaceae species she studied was able to recover from considerable browsing, and from repeated meristem loss due to attack by aphids. Some 22% of seedlings made a new growing point after aphids destroyed the meristem.

Both *Ganophyllum* and *Cola* seedlings were able to grow in more shaded locations at least initially, because their relatively large seeds provided reserves for early growth. Some *Cola* seeds deposited under vine towers grew as well as (if not better than) seedlings elsewhere in the first weeks.

The small green fleshy cotyledons of *Dialium* seeds were able to nourish considerable hypocotyl growth of buried seeds, but seedlings were small and withered easily, even in nursery conditions. First leaves appeared as four simple ones, arranged symmetrically in a cross, and subsequent leaves were observed to be simple. Compound leaves were noted on seedlings approaching 50cm in height. No direct evidence of damage was recorded for *Dialium* seedlings: they were either there, or had been removed completely, due possibly to browsing.

Uapaca seedlings emerged with leafy cotyledons, and leaves did not appear sometimes until a few weeks afterwards. One year after germinating, the more vigorous seedlings had up to 11 leaves. The cotyledons may be nipped off by browsers, in which case the seedling is doomed, but herbivory on older seedlings was not recorded as being frequent or severe, possibly because they had developed mechanical or chemical resistence.

5.4.2 Seedling survival and growth

The proportion of the original number of deposited seeds that survive as seedlings, and measures of growth, should be treated independently. Seedlings at some locations suffered large proportional mortality but the remaining seedlings showed more vigorous growth than in other locations. Proportional survival may not reflect the more ecologically important aspect of survival, *i.e.* the number of potential adults that persist as a seedling bank. For this reason the survival of seedlings in clumps was shown in terms of the persistence of potential adults in clumps, as a contribution to the seedling bank (Figures 5.2, 5.8, 5.12 & 5.22). Success in these terms was always better at a gorilla nest site than from dung deposited elsewhere or from scatter-dispersed or dropped seeds, except perhaps in years of high seed predation for *Ganophyllum*.

Some dung piles were in such proximity that an individual adult tree could not ultimately survive from each one. Clump-dispersal, by creating aggregations of seedlings, creates a situation where a group of seedlings can withstand high proportional mortality and still retain a considerable number of potential adults. A clump of seedlings becomes not just a bank, but an insurance. Smaller groups of seedlings in this study were more likely to suffer complete mortality, and the lifespan of seedling clumps was generally longest at nest sites. Browsing animals might be more likely to nip off the tops of all the scattered individuals they locate (although scattering will provide opportunity for escape) but in a clump of seedlings there were always some that were not browsed.

Height alone was not thought to be an ideal measure of growth, for it was influenced by the length of time that a seedling survived. Instead, the % height gained by a seedling, divided by its lifespan to give a measure of overall growth, was chosen as a better indication of seedling vigour over the study period (see section 5.3). The locations with the tallest seedlings tended also to have the ones with the longest leaves and the highest maximum number of leaves, which together reflect a seedling's photosynthetic area. These three measures of performance were highly correlated in the case of *Ganophyllum* and *Uapaca*. For *Cola* seedlings, they were not correlated, possibly because of the disruptive effects of the frequent browsing they suffered, coupled with a growth form that consisted of few (1-2) large leaves in the early stages of growth. The most vigorous performance of seedlings of the three species for which there are sufficient data, in terms of height, leaf length or number, or 'growth', was always in a nest site.

The component of fitness

The number of surviving offspring, or seedlings, can be regarded as an indication of fitness, as suggested by Crawley (1992). An individual is fitter if it leaves more copies of its genes in the next generation. From a tree's point of view, a frugivore that ensures the biggest contribution of its genes to subsequent generations (*i.e.* one whose dispersal services result in the highest survival of seedlings) is an important disperser. The survival of seedlings is probably a good measure of fitness, because a dead seedling has zero fitness. If, as this study demonstrated, more seedlings survive as potential adults as a result of gorilla-mediated seed dispersal, then gorillas are contributing to the parent trees' fitness.

Janzen (1983) cautions that the timing of dispersal, and the location of dispersed seeds, that result in the highest parental or offspring fitness are practically impossible to determine. The number of surviving seedlings might indicate fitness but it perhaps should be the number of seedlings that survive to reproduce - not a particularly feasible approach with tropical forest trees. Furthermore, a tree contributes genes to the next generation over many years. However, if there are more seedlings surviving at a particular site after 2 years than elsewhere, it is more likely that there will be some left at that site after 4 years, and so on.

Genetic techniques to determine maternity may identify if young trees, seedlings or seeds are related to nearby adults or ones further distant, but are likely only to distinguish between dispersal events at a very coarse scale. The survival of seedlings for as long as they can be monitored after different dispersal events is probably the best solution currently available to most field ecologists.

The growth of seedlings as it was measured in this study is essentially a physiological response to the environment and may or may not have a genetic component, or be related to fitness. Seedlings that are 'suppressed' may grow very slowly, or put resources into root growth, but may have the capacity to perform well once they are released. In this study, however, those that grew slowly or not at all were least likely to survive. Seedlings that persist as small individuals in the shaded understorey remain at risk of repeated herbivory (Howe 1990), which can lead to the death of the seedling. Even if they are not browsed, then they may be close to their compensation point in terms of their carbon balance, which would limit the development of resilience to a range of biotic and abiotic stresses. I found that the growth of seedlings was positively associated with survival, in which case growth can be indirectly related to fitness: a seedling that grows better is more likely to survive in the future. If those that are dispersed grow and survive better than others, there is likely to be a selection pressure for dispersal because it results in increased fitness.

5.4.3 Seed deposition sites and seedling performance

Clump dispersal in dung

The large aggregations of seeds in dung did not seem to have an adverse effect on survival or growth. No associations between the size of seed clumps and subsequent survival or growth were found for any of the species. The effect of the size of seed aggregation on germination success was not assessed. If crowding has a negative effect on survival or growth, individual labelled seedlings should have done better than those in clumps, but this was not the case. Survival in dense clumps of seedlings was high, and they contained the seedlings that grew best, whereas individual seedlings spat out or dropped did not do so well, suggesting that site is more important for these species than clump size. There may also be positive physiological effects of clumping (see Chapter 1). From an ecological point of view, it is clump size that is important (Loiselle 1990), rather than the number of seeds per unit weight of dung.

Although data on the daily faecal output of gorillas is lacking, casual observation at Lopé would suggest that most dung is deposited at nest sites. Dung is left in the evening and in the morning before the gorillas move off. This means that considerable numbers of seeds are left at the sites. For each species, the number of sites found and monitored depended on a range of factors. The ranging behaviour of the gorillas and the ease of tracking, the number of fieldworkers searching for gorilla sign, the collection of dung for routine analysis and the length of the fruiting season all influenced the number of sites that were monitored. In the case of *Dialium*, a combination of factors led to only one nest site being marked out. It was a very rainy part of the year, so many nests were built in trees and dung was fragmented and scattered as it fell; there were fewer fieldworkers searching for gorilla sign, and coprophagy of dung in some sites was so severe that there was insufficient material to use.

Seed predation on a scale suffered by *Ganophyllum* seeds in 1993 seemed to act as an equalising factor, in that all clumps, irrespective of their location or size, were raided. The fact that some seedlings were found both under and away from parents suggests that some scatter-dispersed and dropped seeds escaped in spite of the high predation levels that affected all the seeds deposited in dung. Dung is likely to be easier to locate, and offer a larger reward, for predators using smell for searching. The nature of the vegetation at a site might also influence predation levels, either providing a more secure environment for the predator, as suggested by Schupp & Frost (1989), or making scattered seeds harder to find. In 1992, when predation levels were lower, *Ganophyllum* seeds in dung in the more densely vegetated nest site suffered less predation than in the sparse site or on trail.

Germination *per se* probably does not account for differences in seedling densities, especially for larger-seeded species (Sork 1985). Most seeds of the study species germinated wherever they landed, creating a seedling pool which then was subject to other limiting conditions. I noticed that many seeds germinated even in dry or apparently unfavourable sites, and mortality acted on seedlings at a very early stage, often when only the radicle had developed.

Seeds under conspecific crowns

Howe (1989) proposed that seedlings of species that are clump-dispersed should be able to tolerate competition and disease, and be able to establish in dense aggregations under parent trees as well. This was not altogether the case for the species of this study, for which survival was generally lower under conspecifics. Although seedlings under conspecifics in some cases showed similar survival to those that were clump-dispersed to nest sites, they did not grow as well.

Seedlings of all the species were able to establish under parents, forming a carpet of small seedlings in the case of *Uapaca.* This species however is vulnerable to trampling, as elephants and other terrestrial frugivores and granivores frequently feed under the fruiting canopy. This might be one explanation for the higher survival of the second cohort of seedlings that emerged at the end of the fruiting season under focal trees (Figure 5.23), but those surviving to the next fruiting season were probably doomed to be trampled. Older *Uapaca* seedlings were almost never seen under parents. Several *Dialium* trees on the other hand were found to have considerable numbers of seedlings of a range of growth stages underneath them. *Dialium* saplings were also found on occasion under parental canopies. Under *Ganophyllum* trees, older seedlings were found but none exceeded 50 cm in height. Rarely were young *Cola* individuals found under parents.

These observations suggest that there is little chance of long-term survival under parent canopies of these species, except perhaps for *Dialium,* although seedlings might persist in rare cases under the parent until the opportunity for growth to maturity occurs. Recent analysis of long-term data on forest dynamics on Barro Colorado Island have indicated that there are negative conspecific effects on juvenile trees (Hubbell & Foster 1990). Their results showed that juveniles over 1cm dbh and up to 3m high within a conspecific tree crown showed an impaired growth rate relative to those away from conspecifics. In this study, no differences were found in the growth of young seedlings under different parents, contrary to Howe's (1993b) finding of a "neighbourhood" effect of different trees on the growth of *Virola nobilis* seedlings. The large quantity of seedlings under *Dialium* focal trees #2 and #5 was possibly due to the larger crops and greater knockdown of fruit than other trees, rather than an effect of site, because tree #3 was within 50m of tree #5 yet had very few seedlings underneath it.

Responses to vegetation cover

There are many variables other than light which affect the fate of seeds and seedlings, as discussed in Chapter 1, but light availability or quality has often been suggested as an important limiting factor (e.g. Denslow 1987, Clark 1990). The vegetation environment immediately around or above a seedling clump determines the light conditions they grow in. This is particularly the case in Marantaceae forest, where herbaceous ground cover is extremely dense. For these reasons, and because of the relative ease of assessing vegetation cover, this was the factor that was investigated. One assumption that was made was that the below-ground effects of adjacent herbaceous vegetation were secondary to the effects of shading.

The nature of the herbaceous growth meant that stem density did not always correlate with cover score. Under a dense vine tower there may be an area greater than $1m^2$ which has no stems in it, and gorillas are known to nest under such towers. Several *Cola* seedling clumps were under vine towers. The different growth forms of the herb species have also to be considered (see section 5.3.1).

Apart from *Dialium* (excluded on the basis of a lack of evidence), there were clear and consistent associations between the growth of seedlings and vegetation cover. Those clumps of seedlings with more cover showed the poorest growth. This result was clear despite the relatively crude measure of cover that was used, and the inevitable influence of other biotic and abiotic factors.

The degree of sensitivity to cover varied between species. *Uapaca* was the least shade-tolerant species, with survival and growth of seedlings severely affected by vegetative cover. In the favourable forest site, G2/90, seedlings in the one clump that had dense herbaceous cover over it failed to grow well or survive for long. *Uapaca* was the only species studied to have leafy cotyledons, which has been suggested as a characteristic of shade-intolerant species (Fenner 1985). The distribution of adult trees along water courses and at the forest edge, and the sometimes dense growth of seedlings at the outer edge of a gallery, support this finding. In this respect, seeds dropped near a canopy, or at the edge of gallery forest, may do better than those that are deposited in dung in a densely-covered gorilla nest site in a relatively dim location, such as site G2/83 (Figures 5.20, 5.21 & 5.22). The seedlings in the savanna site (G2/81) tended to divert resources to increase photosynthetic area by growing more leaves, whereas those in the favourable forest site G2/90 tended to invest in height growth (Table 5.6). This plastic behaviour in terms of changes in morphology relating to light conditions has been discussed by Fenner (1985).

Cola seedlings seemed most able to cope with shade; large seeds with fleshy cotyledons are associated with more shade-tolerant species (Fenner 1985). The association between cover and growth for *Cola* were not significant, and seedlings survived and grew under parents and in conditions of dense cover (and thus low light availability), even under towers of vines. Nonetheless the results showed a clear trend, with the best survival and growth in the site that was least densely-vegetated (Table 5.4). Initial seedling growth is fuelled by cotyledon reserves, which are considerable in this species. *Cola* seedlings in the sites with more cover grew more in the first six weeks than in subsequent periods, whereas no difference was evident at the more open site, which suggests that later growth in more covered locations was limited by the availability of light.

Sork (1985) found that the large-seeded *Gustavia superba* was able not only to persist under shade but also to grow, with little difference in height between those in shade and those in gap conditions 17 months after germination. He suggested that large-seeded species may be more susceptible to predation (if they have no defences) than to light conditions. However, Augspurger (1984) found that seedlings of 12 out of 18 species in Barro Colorado Island's forest did better in gap conditions, and many were unable to grow in the shaded understorey. These studies generally refer to "gap" and "non-gap" conditions, but subtle differences in light quality and quantity, determined by the nature of the gap (and often influenced beyond the gap 'edge'), can have considerable effects on the carbon economy of seedlings (Sork 1987, Chazdon 1988).

Ganophyllum seedlings showed a significant negative association with vegetation cover, in this case assessed by stem density, with the most vigorous seedlings in clumps with least surrounding vegetation. It is interesting to note that the denser vegetation at one site (G2/5) contributed positively to survival in abnormal weather conditions by protecting seeds and early seedlings from desiccation (Figure 5.1), but it may have limited later performance (Figure 5.4). Had weather conditions been more typical (i.e. wetter), higher survival and better growth might have been expected in the more sparsely-vegetated site.

When cover was correlated with performance of a particular species (Figures 5.6, 5.26), certain outlying data points corresponding to the particular location of a clump could often be explained using additional information about the microsite of that clump. For instance, the long persistence of a clump of *Ganophyllum* seedlings on feeding trail was apparently the result of physical protection afforded by an exposed tree root; the particularly poor performance of an *Uapaca* clump in a savanna location with little cover was associated with its proximity to the forest edge and the dense fern associated with it; *Cola* seeds in one clump were deposited at the rim of a nest and thus unable to root easily, so survival and growth were poor despite open vegetation conditions. For seeds deposited on trail, if they ended up on or adjacent to animal paths (which may in this area be old forestry skidder trails or roads), then soil compaction seemed to limit the growth of secure roots. This was observed for many seedlings of *Cola*, which seemed to have difficulty rooting in such locations.

Changes in vegetation conditions

The nature of the herbaceous vegetation cover changes through time (Plate 5.1). Gorillas flatten the vegetation in a nest site area, sometimes killing many of the stems, but regrowth of these herbaceous species is rapid and the conditions can recover to their former state in two years. Nonetheless nest-building by gorillas can provide the window that seedlings need to establish. They may then enter a 'waiting' stage. The persistent use of areas of dense herbaceous vegetation by large mammals, particularly gorillas and elephants, may provide sufficient disturbance for successful seedling growth, if they are not trampled. Light quality may be more important than quantity, and the occurrence of sunflecks is likely to be maintained, or their incidence increased, by the feeding activity of these animals. The herbaceous vegetation creates immediate shade over a seedling, so the balance of fate could thus be tipped in favour of survival or growth of a suppressed seedling. Nesting by gorillas in areas of more open tree canopy might be thought to favour shade-intolerant species, but the density of herbs would suggest that shade conditions are rapidly re-established. The paucity of seedlings on the forest transect, and the lack of seedlings located in old gorilla nest sites, are vivid testimony to the difficult establishment conditions faced by seeds that arrive on the Marantaceae forest floor.

Dispersal into nest sites

Nest sites selected by gorillas did not always favour the survival or establishment of seedlings. Factors that influence where nests are built may include: preference for certain habitats in that season; distance travelled during that day's foraging; the nature of the herbaceous vegetation; weather conditions; favoured locations (Tutin *et al* 1994b); and possibly whim and aesthetics. Herbaceous vegetation was used in 62% of night nests (n=2435) found at Lopé, and sites were often made in more open areas such as treefall gaps (Tutin *et al* 1995). The range of possible microsites for deposition is considerable. For example, one site during *Ganophyllum* season was in a sparsely-vegetated location that did not provide protection from atypically dry conditions, some *Cola* seed aggregations were actually under dense towers of *Haumania* vines, and *Uapaca* seeds may even be deposited in open grass savanna.

Nonetheless, for *Ganophyllum*, *Cola* and *Uapaca* (the evidence for *Dialium* was equivocal), it was consistently found that the highest survival and the most vigorous growth of seedlings was from seeds deposited by gorillas in a nest site. Contributions to the seedling bank, in terms of the number of potential adults that persist, were greater at nest sites, as described above. The poorest survival and performance was usually from scatter-dispersed or dropped seeds. This is

Plate 5.1 The change in herbaceous vegetation over time: a) nest site G2/5 when first made (February 1992); b) the same site 92 weeks later.

a)

b)

consistent with the results of other research which suggests that gap conditions are important for the regeneration component of the forest (see Chapter 1). Dirzo and Domínguez (1986) found that *Trichilia* seedlings growing in gap conditions did not show any higher *survival* than those in non-gap conditions, but the height, number of leaves and length of leaves (their performance) were all greater in the gap site. For those seedlings that were followed long enough, De Steven (1988) found that numbers fell considerably in the shaded understorey. The results of this study were of a similar vein.

Growth of *Ganophyllum* seedlings in site G2/5 was better than that of seedlings from scatter-dispersed or dropped seeds initially but not later on, which suggests that seedlings at a favourable site might grow faster at first but if their growth is then checked (e.g. by the regrowth of herbs), seedlings growing elsewhere may catch up (Figure 5.4 & section 5.3.1). The best growth was in a nest site however. The better performance of *Cola* seedlings in site G2/19 was also linked to higher survival: those clumps with the best performance showed the highest survival (Table 5.4). Seedlings growing under conspecific canopies showed poorer growth which probably made them less able to withstand biotic or abiotic stress. Other workers have commented on the positive effect of better growth on the resilience of seedlings to stress (Denslow 1980, Folgarait & Davidson 1989). *Uapaca* seedlings growing in savanna had low survival initially (Figure 5.20), a result of poor germination caused perhaps by drier conditions. The seedlings had to contend with competition from the dense grass growth, but received high insolation levels and were able to grow successfully (Figure 5.22), although the best growth was among seedlings in a forest nest site, G2/90.

5.4.4 Conclusion

The consequences of gorilla-mediated dispersal for the survival and growth of seedlings are certainly varied, and depend to a large extent on the site that is used for nesting. For the three tree species for which sufficient data are available, both survivorship and growth were better in one or more of the nest sites, than under conspecific canopies or as a result of scatter-dispersal. Even with such huge losses of seeds and young seedlings, which is doubtless the normal situation, the differences in the performance of the remaining few can indicate the relative effect of certain modes of dispersal.

If more seeds are likely to survive to adulthood from gorilla dung than from the alternative treatments as a result of better survival and growth in the early stages, then there is a direct beneficial effect of dispersal by gorillas. The first months' or years' survival and growth are no guarantee of ultimate survival to maturity. Seedlings should be followed for much longer, and their performance integrated with information on sapling populations, to determine the relative outcome of different dispersal modes. It is the aggregate results from many night's nesting over many fruiting seasons in many sites that will determine the effect of gorilla dispersal on the populations of these species.

For those species that have a range of dispersers, other large mammals such as chimpanzees and elephants (e.g. for *Dialium* and *Uapaca*) may be as crucial as gorillas, or more so. Nonetheless, the effect of gorillas might be more influential than one would expect from their density, since they are reliable visitors to important food species, and each one disperses large quantities of seeds each season into a range of regeneration sites, some of which provide conditions that result in high survivorship and vigorous growth of seedlings.

This study has shown that seedlings in gorilla nest sites show better performance, linked to higher survivorship, than seedlings growing from scatter-dispersed or undispersed seeds, suggesting that in the long term, gorillas are likely to be important dispersers of these species.

Chapter 6

GORILLAS AND THE DISPERSAL OF SMALL-SEEDED FRUIT

6.1 INTRODUCTION

In the previous chapters I have considered the dispersal of some of the large-seeded tree species of the forest. Gorillas are also able to take advantage of small-seeded fruit. Slightly different circumstances prevail regarding the dipsersal scenario for those species that have very small seeds within small, often multi-seeded, fruit. They are ostensibly "bird type" structures conforming to the 'bird' end of the suite of dispersal syndromes in morphological terms (see Chapter 1). Each fruit represents relatively little investment by the parent: they are cheap and plentiful, and may be removed by a wide variety of animals. To be attractive to large-bodied vertebrate frugivores they must be packaged such that the energetic gains make it worth harvesting them.

Three species were selected in order to investigate the consequences of seed dispersal by gorillas for such types of fruit. They were *Antidesma vogelianum* (Euphorbiaceae), *Psychotria vogeliana* (Rubiaceae) and *Psidium guineense* (Myrtaceae). They are all confined to the savanna-gallery forest mosaïc in the northern part of the Lopé Reserve (see Chapter 2, and Tutin *et al* 1994a). Gorillas use this habitat extensively at certain times of the year when foods such as *Uapaca* fruit are available, or when these species are abundant (see Chapter 4). *Psidium* has been classed as an 'important' food for gorillas (see Chapter 2, Williamson *et al* 1990, Tutin *et al* 1991b, Tutin & Fernandez 1993). The aims were to investigate the interface between such small-seeded plants and one of the large-bodied vertebrate frugivores that feed on their fruit, dispersing the seeds in their dung. The rest of this chapter describes the plant species, their distribution and abundance, their fruiting patterns, the consumption of fruit by gorillas and the fate of deposited seeds.

The species

The three species are illustrated in Plate 6.1. Details of the fruit characteristics of all three species are given in Table 6.1. Results of chemical analyses have been published by Rogers *et al* (1990), but essentially all three species are rich in water-soluble carbohydrates (i.e. are sugary), low in lipids and protein, and have relatively low levels of secondary compounds (tannins and phenols) in the ripe fruit.

Antidesma vogelianum (Euphorbiaceae) is a small, multi-stemmed tree typically less than 5m in height that occurs at the savanna/forest interface, and in the forest interior by water. It is common along the edges of gallery forest close to water, or actually in

Plate 6.1 Three small-seeded species of the savanna/forest mosaïc of the Lopé Reserve: a) *Antidesma vogelianum*; b) *Psychotria vogeliana* ; c) *Psidium guineense.*

Table 6.1 Fruit characteristics of 3 small-seeded plant species of the forest/savanna mosaïc.

Species	av. seed weight	av. fruit weight	no. of seeds per fruit	no. of fruit per cluster	no. of clusters per plant			no. of fruit per plant			n clusters	n plants
					mean	SD	range	mean	SD	range		
Psychotria vogeliana	0.021g	0.17g	2	16-47	33	24.4	9-75	1082	1061	263-3478	93	10
				no. of fruit per panicle								
				mean	SD	range	n					
Antidesma vogelianum	0.05g	0.17g	1	17.1	5.21	8-27	14					
	seed size	fruit weight		no. of seeds per fruit				no. of fruit per plant				
				mean	SD	range	n	mean	SD	n	transect	
Psidium guineense	c.2mm	9.85g		109	28	67-143	7	13.7	13.5	144	P7a+b	
								10.5	15	37	P4a	
								9.6	8.4	24	P5a+b	

marshes. The small (*c.* 8mm) fruit are arranged in dense clusters on a long panicle, and the thin pericarp encloses a single hard seed, which accounts for about 30% of the wet weight of fruit. The fruit change from off-white through red to deep purple when ripe. Not all the fruit on each panicle ripen at the same moment, which means that the larger-bodied consumers take some immature fruit as they feed, either because it is not worth the processing time to exclude it, or because they are physically unable to select individual fruits. Immature fruit have a low sugar content and have twice the concentration of phenols and tannins of ripe fruit (Rogers *et al* 1990).

The sugar-rich, juicy mesocarp attracts not only birds but also the monkey species that regularly use gallery forest for food sources (principally *Cercopithecus cephus* and *C. nictitans*), apes and elephants. The fruit taste good to the human palate as well. *Antidesma* is an important food for elephants (White 1992), which display considerable dexterity in harvesting the fruit with their trunks. They do however cause some damage to the trees, but *Antidesma* resprout readily from the base, and tend to have the appearance of a large, sprawling shrub. Gorillas tend to feed by pulling the panicle through the mouth when it is still attached to the tree, stripping fruit off the panicle with their lips.

The understorey shrub *Psychotria vogeliana* (Rubiaceae) exists at low densities in the forest interior but is abundant along the forest/savanna edge. Rarely growing taller than 1.5m and regularly browsed by large herbivores, plants grow densely together and produce clusters of small berries, each of which contains two seeds. Fruit have a high sugar content but contain very few lipids, and few defensive compounds (Rogers *et al* 1990). The weight of a single fruit, at 0.17g, is similar to that of *Antidesma*, and the seeds make up 25% of the weight of fruit, akin to *Antidesma*. The fruit turn grey-white when ripe, obvious against the shaded dark green background of foliage, and are eaten by birds, apes and elephants. Gorillas pluck whole clusters to eat, chimpanzees tend to wadge some of the fruit they take, spitting out clumps of seeds and skins, elephants take fruit and foliage together, and birds are more likely to take one or a few fruit at a time.

The origins of the guava *Psidium guineense* (Myrtaceae) lie in South America (Mabberley 1987), but it is now naturalised in much of the central African region. A shrub that occurs in open savanna throughout the Lopé, it also grows adjacent to the forest edge. It tends to have a clumped distribution, and may form extremely dense patches. It is resilient to fire which humans use to manage the savanna areas; the above-ground stems burn and the plant rapidly resprouts from the root stock. *Psidium* is not strictly speaking a 'bird' type fruit in structure. Seeds are small and can be removed from ripe fruit when the relatively thick skin softens or splits, but the fruit are relatively large, the seeds are protected and not displayed, the colour change is slight and the biggest changes between ripe and unripe fruit are scent and texture. It has the lowest concentrations of sugars of these three species, has a low protein and fat content, and few secondary compounds apart from the skin, which contains considerable amounts of tannin (Rogers *et al* 1990).

About 100 seeds are tightly packed in the mesocarp within the almost spherical fruit, which usually measure 3-4cm diameter and weigh typically under 10g (see Table 6.1). The exocarp is relatively thick but it softens on ripening and ultimately splits, and the colour change is from green to yellowish. *Psidium* fruits are enjoyed by the monkey species mentioned above, apes and elephants as well as birds and humans. Most birds may not be able to penetrate the fruit until the skin softens or splits. Bulbuls (Pycnonotidae) have been seen feeding on *Psidium*, and holes pecked in fruit are an indication of bird feeding (P. Christy, pers. comm.). Toothed feeders can take fruit before they are fully ripe. Monkeys tend not to venture far from the forest edge to forage for *Psidium*, but chimpanzees and gorillas will feed on guavas extensively, and tend to use the savanna/forest mosaïc when they are available. Gorillas generally eat the fruit entire, but will rake out the flesh with their teeth and discard the skin of less ripe fruit. Chimpanzees tend to discard the skin more frequently, especially of fruit that are not fully ripe. Elephants spend long hours in the savanna, as they eat the abundant herbaceous material growing there, but they consume large numbers of guavas as well (L. White, pers. comm. & pers. obs.). As the fruit ripen they smell stronger, and elephants probably select the riper fruit using olfactory cues (pers. obs.), something the apes probably do as well.

Each of these species fruits twice a year, once in March-April and again in September-October, with *Psychotria* slightly later than the others. In some years, fruiting of *Psychotria* overlaps with that of *Uapaca*, which is abundant in the same habitat.

6.2 METHODS

Distribution and abundance

A total of 2.6km of typical forest edge habitat in the study zone was sampled using 10 linear transects 260m long, and included gallery forest and forest fragments. Figure 6:1 is a map of the forest/savanna mosaïc in the main study area that shows the location of the transects. In the case of *Antidesma*, plants were considered to be at the 'edge' if any of their foliage overhung shrubs lining the edge of what could be classed as savanna. For *Psychotria* and *Psidium*, they were considered to be at the edge if they were the last woody plant rooted before the grasses began. The shift from forest to savanna forms quite a distinct boundary in most areas, especially those which are regularly burnt. The number of plants of each species was recorded in the first 5m of every 20m along each transect. Individuals of *Psychotria* were considered to be those plants which had a group of stems all rooted within a 50cm radius. It is possible that the rooting system of this species meant that an individual might have been classed as several individual plants but generally it seemed to be a workable field definition. Every 50m along each transect, the distance to a watercourse was estimated to the nearest 5m.

At two points, 100m and 200m along 9 of the edge transects, a random bearing (controlled to ensure that it headed into the savanna) determined each of the 18 transects used to sample *Psidium* plants. The savanna transects were 100m long and 4m wide, giving a sample total of 7200m^2 of savanna. Any marshes, rocks, and fern patches were recorded on all transects.

Fruit production

The fruit production of all the plants counted was recorded using the phenology scoring system described in Chapter 4, and the ripe fruit score (a percentage of the theoretical maximum) was derived in the same manner. The transects were first established at the end of February, just before the fruit became ripe. They were re-surveyed in late August, immediately prior to the second season of ripe fruit. For a sample of 10 *Psychotria* plants (327 clumps of fruit) and 205 *Psidium* plants on certain transects, the number of fruits per plant were counted (excluding plants with no fruit). The number of seeds per fruit were also recorded for a sample of 10 whole ripe Psidium fruits. The number of fruits in a 50g sample of *Antidesma* and *Psychotria* fruit was determined. A total of 100 and 106 seeds of each species respectively were extracted, re **6.1** Map of the savanna/forest mosaïc in the study area, ing the location of edge transects (red) savanna transects (green). Stippled are forest. (Approx. scale 1:30000)

cleaned and weighed.

Consumption, deposition and survival

Dung piles left by gorillas that contained seeds of the three species were marked and monitored as described for the forest species (see Chapters 4 & 5). The only difference was that the small seeds were rated on an abundance scale (rare, few, common or abundant) rather than counted. From a sample of the dung containing seeds of these species that was collected for faecal analysis, a small amount of known weight was retained to count the seeds prior to washing. Total counts for the whole dung sample were extrapolated from this, to give an estimate of the typical numbers of seeds represented by the different categories of abundance.

No attempts were made to determine the presence of seeds of these species in the soil seed bank.

6.3 RESULTS

Distribution and abundance

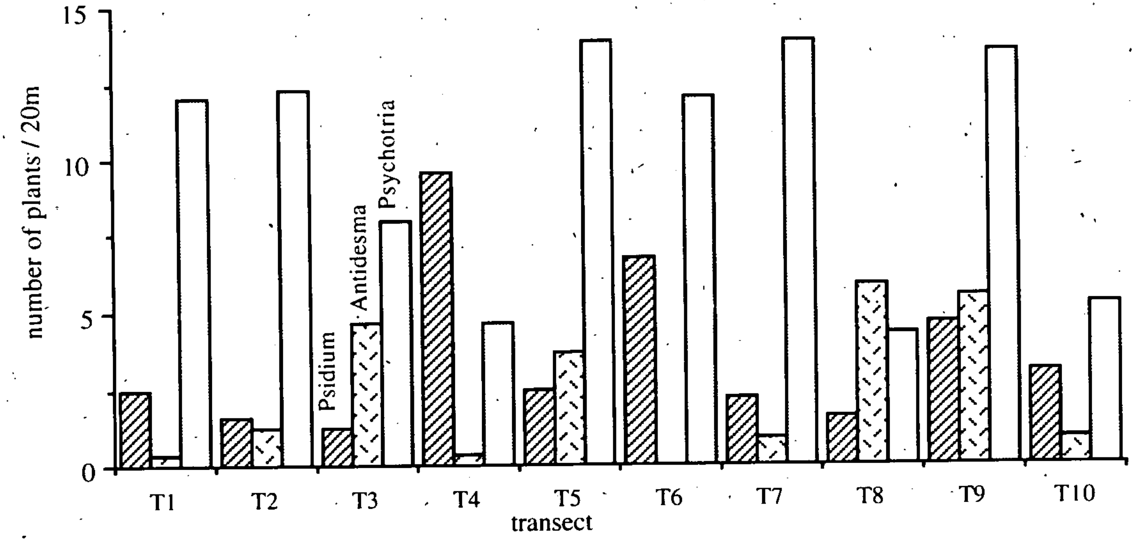
Figure 6.1 shows the location of all transects, and physical information is given in Table 6.2. The normal fire regime is quoted for each transect. Between those that are 'usually' burnt (every year) and those that are never burnt, the frequency with which a given area is affected by the fires set annually is a matter of chance. Densities of the three species along the forest/savanna interface varied greatly from site to site, as shown by Figure 6.2. The average densities (the number of plants per 20m of edge), using the total length of edge surveyed, were 9.97 plants per 20m for *Psychotria*, 2.34 for *Antidesma* and 3.51 for *Psidium*. Median values were 12.0, 1.08 and 2.31 plants per 20m respectively. The presence of *Antidesma* is certainly linked to water: there were none recorded on the transect T6 at a waterless forest patch (not a gallery), and numbers always rose if the edge was close to a watercourse or through a marsh (*e.g.* T3, T8, T9, Table 6.2). The transect T4, where fewest *Psychotria* were recorded, was along a very 'blurred' forest edge. It was in an enclosed savanna that is currently never burnt and probably has not been for many years. Consequently at this edge there were extensive areas of colonising okoumé (*Aucoumea klaineana*) in dense stands. Another cause of few *Psychotria* plants were occasional dense stands of fern (*Gleichenia linearis*), such as on transect T8 (Table 6.2).

Psidium was not abundant along forest edges, although it was more common on transects T4 and T6. It is apparently associated with the open savanna habitat either because it 'prefers' it, or because it are unable to compete with other species at the forest edge. The patchy distribution of *Psidium* is illustrated by Figure 6.3, which shows densities in the savanna (number of plants per m^2). It was not recorded as common on transects P5 and P9b, where a number of factors may have had an influence: slopes were

Table 6.2 Physical characteristics of the forest edge and savanna transects. T: edge transect; P: savanna transect.

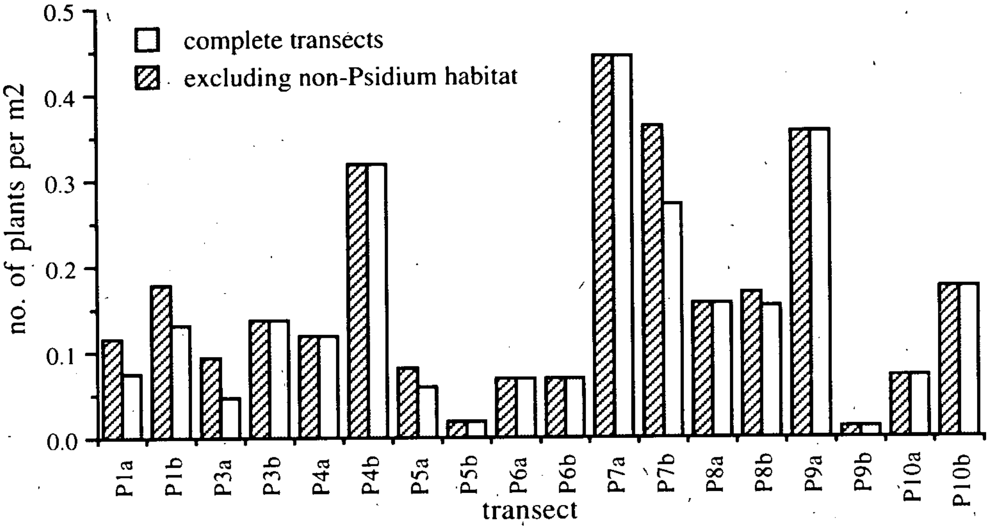
Transect no.	burning regime	% fern	% marsh	mean distance to stream, m (range)	other information
T1	rarely	13.5		30 (25-35)	
P1a			35		
P1b			25		
T2	sometimes			>50	steep slope
T3	never		69.2	24 (10-50)	
P3a			50		
P3b					
T4	never			all >50	okoumé regeneration
P4a					
P4b					
T5	rarely		26.9	17 (5-35)	
P5a			25		slopes
P5b					steep slopes
T6	sometimes			(no stream)	
P6a					
P6b					
T7	sometimes		8.5	31 (0-50)	
P7a					
P7b					rocks 30%
T8	usually	44.2		11 (5-15)	
P8a		10			
P8b					
T9	rarely		11.5	8 (5-15)	
P9a					
P9b	usually		5		slopes
T10	usually			33 (25-40)	slope
P10a					50% old village site
P10b					50% old village site

Figure 6.2 Densities of *Psidium, Antidesma* and *Psychotria* along forest (gallery) edges



steeper, regular burning takes place, and the soil substrate was exposed and rocky. If the areas covered by distinct non-*Psidium* habitat (marsh, bare rock, and fern) are excluded, then calculated densities for some transects are increased (Figure 6.3). In some places, very dense stands of *Psidium* develop, such as on transects P7a and b and P4b. The overall density of *Psidium* in the open savanna (excluding non-*Psidium* habitat) was 1650 plants per hectare (median=1177 plants.ha^{-1}).

Figure 6.3 Density of *Psidium* plants on savanna transects.



Fruit production and consumption by gorillas

Fruit production is shown for the three species, including *Psidium* in the savanna, in Figure 6.4a-d. For all species it is clear that in 1993 the second fruit crop was poorer than the first, although the difference was not significant for *Psidium* (Wilcoxon's Matched Pairs, *Psychotria*: T=0, P<0.002; *Antidesma*: T=1, P<0.02; *Psidium* (edge): T=14, P>0.1, all n=10; *Psidium* (savanna): T=55, P>0.1, n=18). The second fruiting occurs at the end of the 2-3 month dry season. The *Psidium* plants in the savanna (Figure 6.4d) showed a higher productivity than those at the forest edge (Figure 6.4c). The transects that were in areas that were burnt in August were T6, T8 and T10, but this did not appear to affect fruit production of *Psidium* greatly. The lowest figures for *Psychotria* fruit production, however, were on those transects that were in the burnt

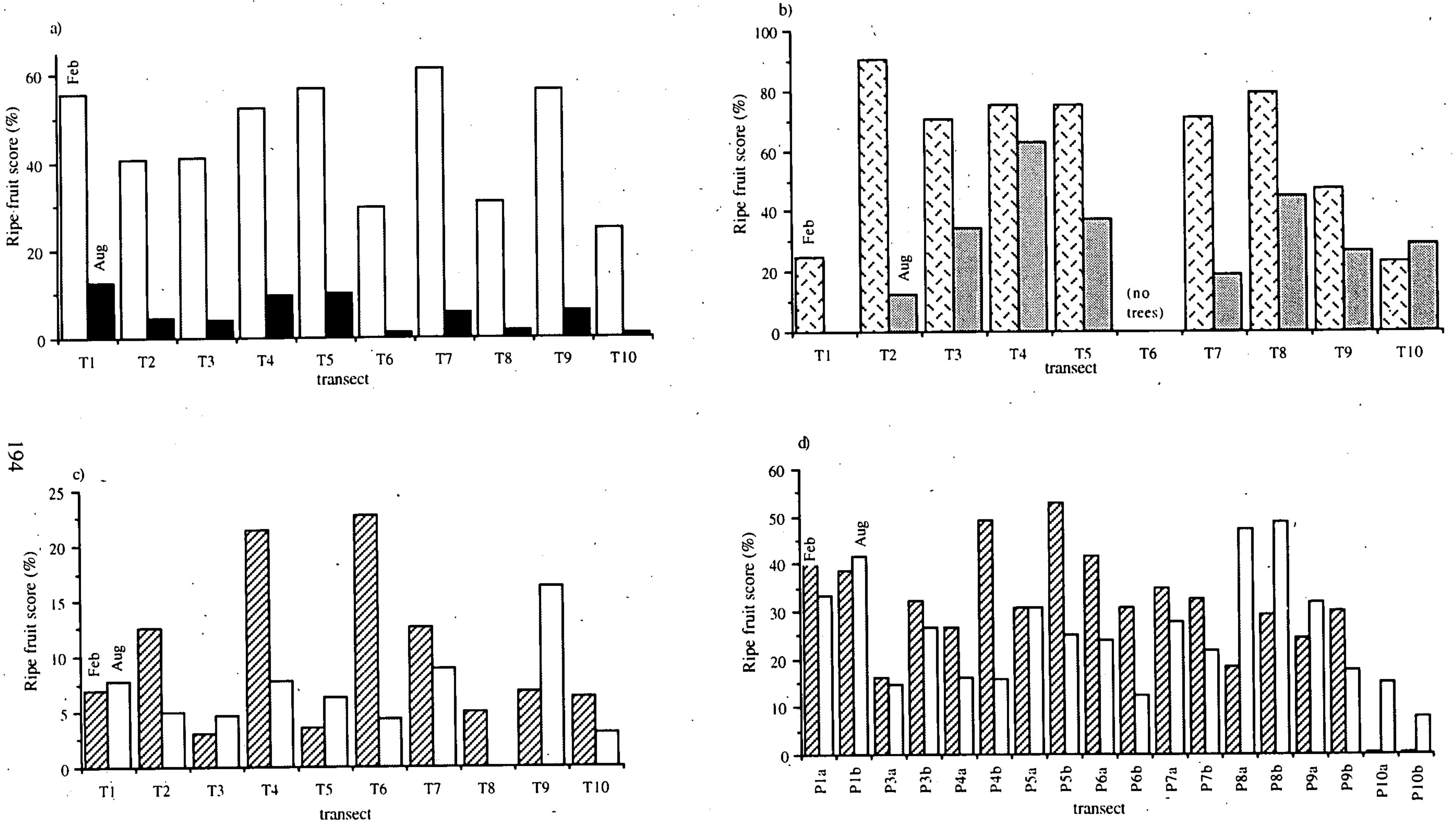


Figure 6.4 Ripe fruit production of a) *Psychotria*, b) *Antidesma* and c) *Psidium* on the forest edge transects in two seasons in 1993; d) *Psidium* fruit production in the savanna.

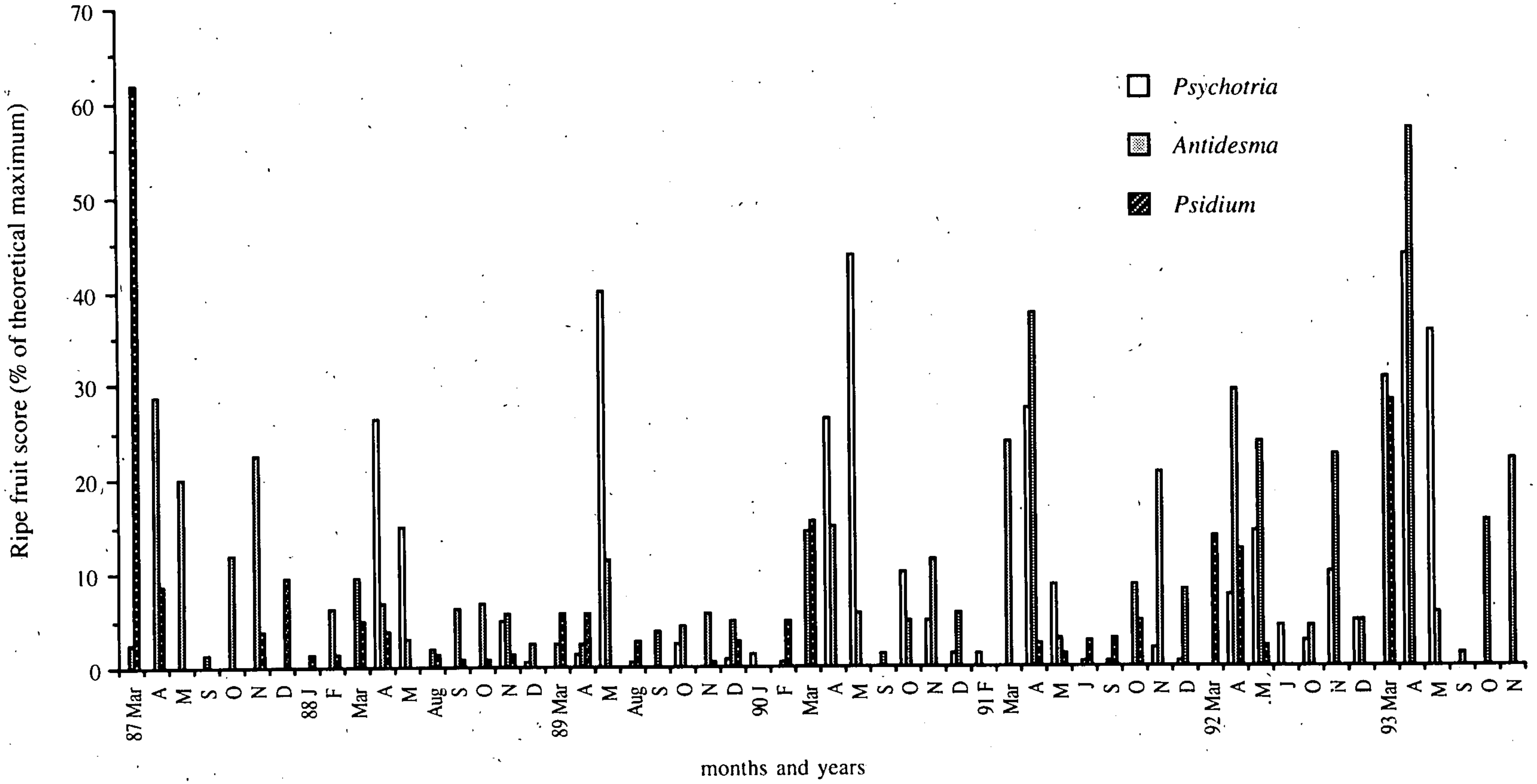


Figure 6.5 Production of ripe fruit over 7 years by *Psychotria*, *Antidesma* and *Psidium*. (Months when none had fruit are not shown).

areas.

The production of fruit for the three species over 7 years, derived from the phenology circuits, is shown in Figure 6.5. It is clear that the second fruiting of each year is poorer than the first for all three species. There was no fruit on the *Psidium* and *Psychotria* plants used in the phenology circuits in the second season in 1993, but these are based on small samples (n=10). Data from the transects (Figure 6.4) and from gorilla dung (Figure 6.6) show that there was some fruit available, but it was not abundant. Compared with all other available ripe fruit foods monitored on the phenology circuits, the availability rank of *Antidesma, Psychotria* and *Psidium* in the 'peak' months was first, first and fourth respectively.

The presence of seeds of the three species in gorilla dung is shown in Figure 6.6a-c as squares. It reflects the availability of these fruit, shown as the percentage ripe fruit scores (circled) calculated from transect data. The mode abundance category of seeds in dung for each month is shown next to the relevant data point. The number of other gorilla food species with ripe fruit that were monitored on the phenology circuit is shown as the other axis in each figure (solid circles). It would seem that gorillas eat *Antidesma, Psychotria* and *Psidium* in quantity even when other (forest) fruits are available, but only if their fruits are abundant.

Deposition and fate of seeds

The abundance ratings of seeds represent anything from under a hundred to several thousand seeds per dung pile. The results from counting seeds in samples of dung are shown in Table 6.3. It can be seen that the rank assigned by visual assessment was not always a reliable indicator of differences in actual numbers, since the categories overlapped, but the median values consistently reflected the assigned categories. The details of the dung piles that were pegged and monitored are given in Table 6.4. Although some nest sites were adjacent to savannas, most were in the forest interior, frequently in habitats apparently hostile to the establishment requirements of the species.

Psychotria seeds remained dormant until several months after deposition, whether they were deposited prior to or after the dry season. Some dung piles that originally were marked for *Uapaca* seeds in early November 1992 became beds of *Psychotria* seedlings in June 1993, seven months later. This pattern was the same for seeds deposited in March 1993, so only one assessment of survival was made of these clumps before the end of the study. There was very little, or no germination of *Psidium* seeds deposited in nest sites, but seeds that were watered in the camp nursery sprouted rapidly. Seedlings of all species were initially tiny and difficult to count accurately, so estimates to the nearest 50 were sometimes used.

The survival of *Psychotria* seedlings is shown in Figure 6.7a. Due to the dormancy of seeds, the main result is from the two nest sites monitored for *Uapaca* that also contained *Psychotria* seeds. The percentage of the estimated original number of deposited

Figure 6.6 The occurrence of seeds in gorilla dung (dotted squares; abundance ranks: R=rare; F=few; C=common; Ab=abundant); and the number of other food species with fruit (solid circles). Encircled figures are the percentage fruit score from transect data.

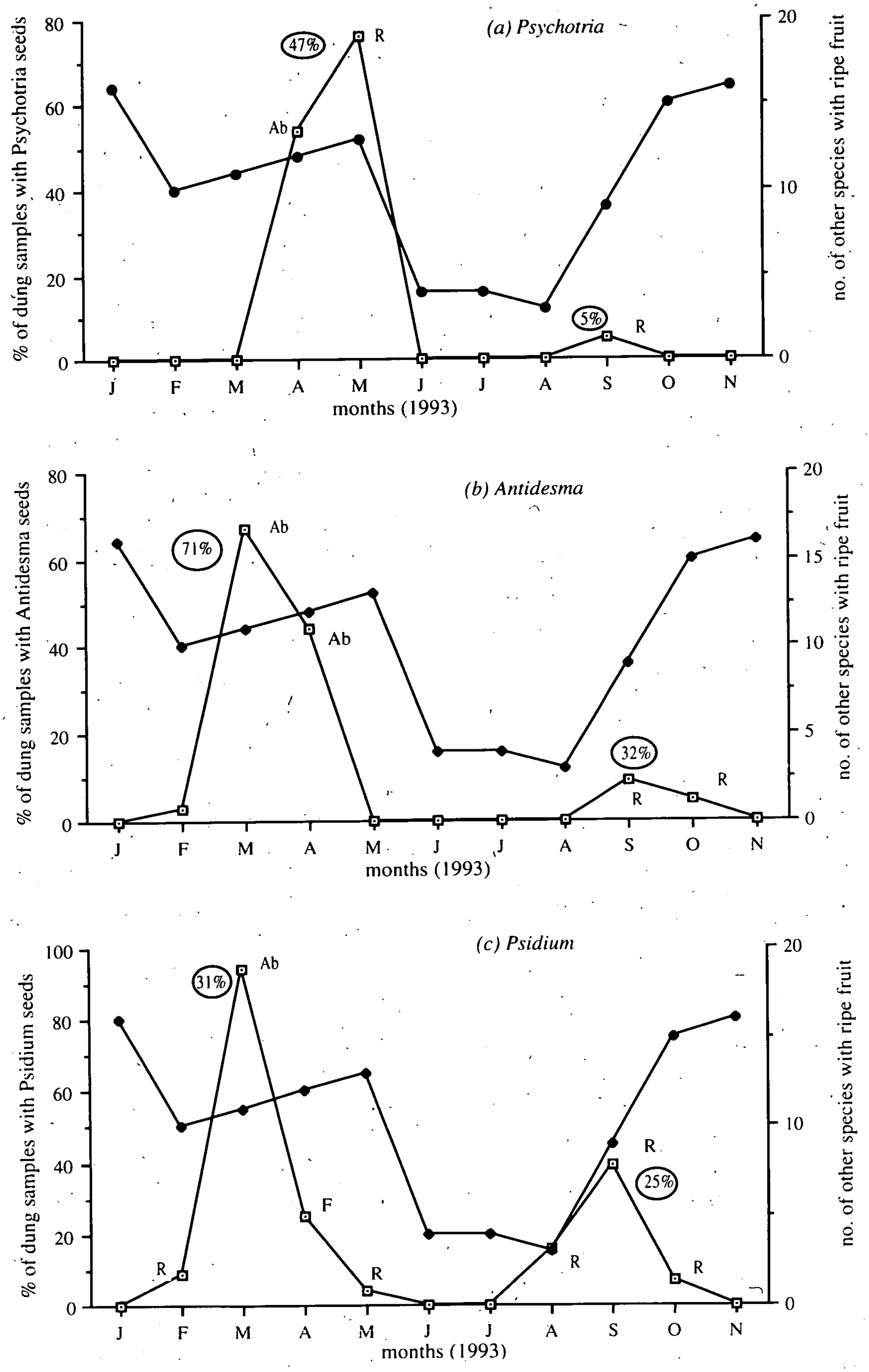


Table 6.3 Abundance ratings and actual numbers of small seeds in gorilla dung samples. (Square brackets: sample n=1).

	no. per 50g				no. per dung sample				
	mean	SD	range	median	mean	SD	range	median	n.
Psidium									
Abundant	715	502	328-1905	551	2684	1369	747-4618	2870	8
Common	362	320	101-828	183	2052	1000	747-3375	1789	5
Few	[56]				[191]				1
Rare	[20]				[172]				1
Psychotria									
Abundant	358	281	159-557	358	[1846]				2[1]
Common	111	81	53-168	111	[315]				2[1]
Few	[40]				[128]				1
Rare	ND				ND				
Antidesma									
Abundant	177	50	128-231	174	1743	624	1250-2633	1545	4
Common	45	22	24-67	43	212	68	145-280	211	3
Few	[20]				[36]				1
Rare	10	8	4-15	10	43	8	37-48	43	2

Table 6.4 Abundance of seeds of *Psychotria, Antidesma* and *Psidium* in monitored gorilla dung, and features of the nest sites.

		nest site code								
		G3/21	G3/23-4	G3/28	G3/31	G3/41	G3/42	trail	G2/83	G2/84
Seed abundance per clump*										
Psidium	median	C/Ab	0	F/C						
	range	C-Ab	0-C	F-Ab						
	n clumps	8	7	6						
	est. no. of seeds**	18 636	7 729	8 102						
Antidesma	median		Ab	F/C	C/Ab					
	range		R-Ab	0-Ab	F-Ab					
	n clumps		16	5	6					
	est. no. of seeds		15 039	3 373	5 093					
Psychotria	median					Ab	Ab	Ab	C/Ab	Ab
	range							C-Ab	F-Ab	F-Ab
	n clumps					3	3	3	6	10
	est. no. of seeds					5 538	5 538	4 007	6 296	12 149
Canopy cover										
median		3	9	8.5	4	7	0	ND	10	4
% clumps										
with cover at	≤4m	25	72	67	67	100	0	ND	57	45.5
	5-20m	75	89	67	100	33	25	ND	100	63.6
	>20m	25	0	100	100	67	0	ND	100	54.6
Marantaceae stems										
mean stem density		none	none	9.8	6.2	none	none	none	5.5	0
median				13.5	7.5				4.5	1.2
% stems as	*Haumania*			11.9	13.5				100	
	Megaphrynium			55.9					0	
	Aframomum			32.2					0	
	Anisotes				86.5					
	Renealmia									100

* seed abundance estimated on a ranked scale: R - Rare; F - Few; C - Common or Ab - Abundant

**seed no. estimated from the median seed number in dung samples of a particular abundance rating

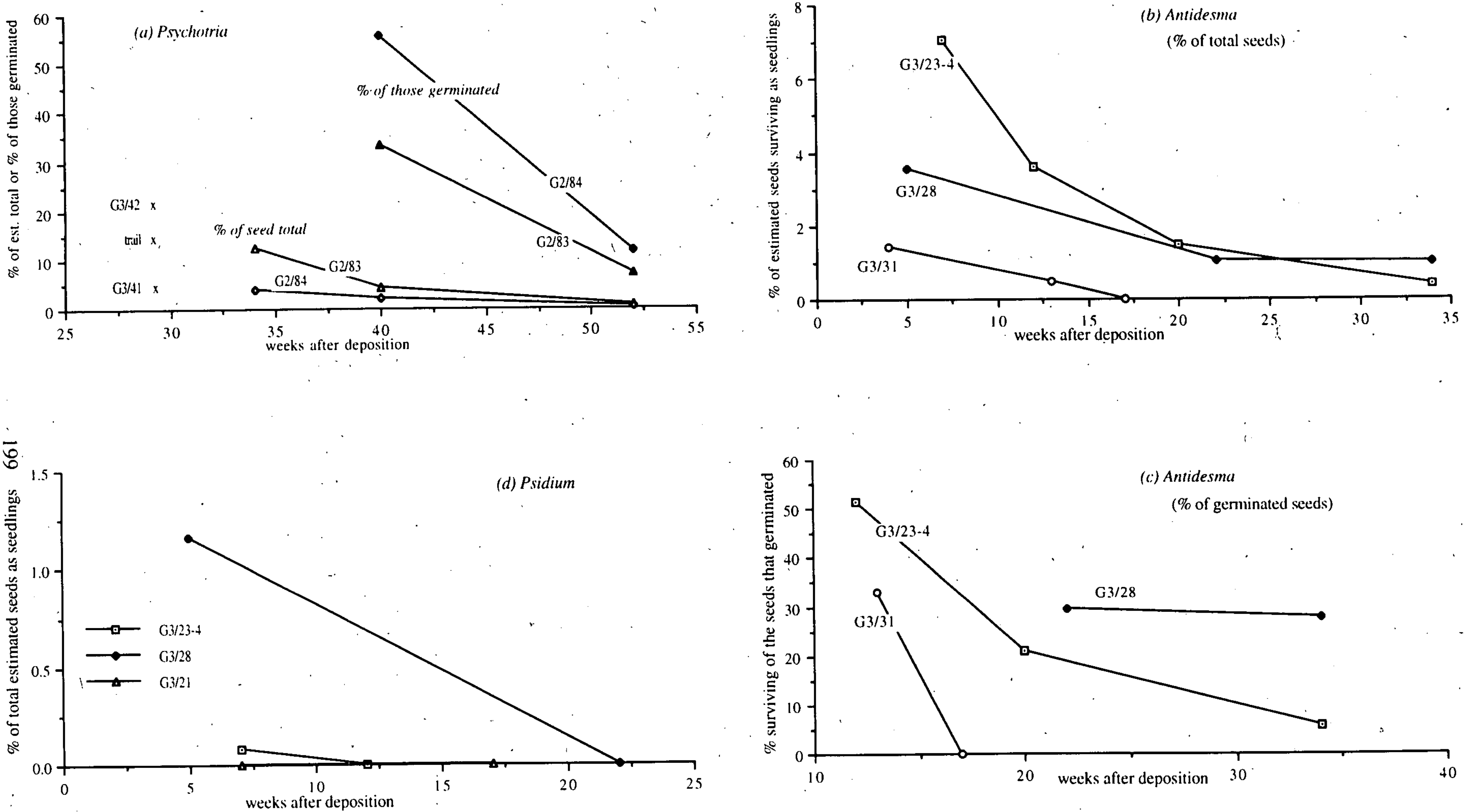


Figure 6.7 Survival of seeds and seedlings (% of estimated total seeds, and % of those seeds that germinated) of a) *Psychotria*, b) & c) *Antidesma* and d) *Psidium*. (In c), site G3/28 was first monitored 22 weeks after deposition).

seeds that survived as seedlings, as in Chapter 5, is shown, but the surviving percentage of the germinated seeds is also included because of the small number that became seedlings. Initially, a dense mat of seedlings emerged, but both nest sites seemed to be in locations that did not favour their establishment. Both were in shaded locations about 20m or more from the forest edge. The single points on the graph are the percentage of estimated seeds deposited in 1993 that germinated and were surviving as seedlings 28 weeks after deposition, when the study ended.

Figure 6.7b) and c) show the same results for *Antidesma*, with b) showing the percentage of deposited seeds surviving as seedlings, and c) the survival of those seedlings. Survival was poorest in site G3/31, in a location densely shaded by herbs and woody lianas, and best in site G3/28, which was in typical Marantaceae forest, but with less shade due to the flattening of the herbaceous vegetation and the sparse tree canopy. Site G3/23-4 (two adjacent sites) was actually under *Antidesma* trees at the edge of a stretch of gallery forest. Figure 6.7d) shows that, although some *Psidium* seeds germinated at certain locations, with most at site G3/28, survival was poor at every site. No seedlings were present after 5 months, and none had germinated from a nest site (G3/21) at the edge of a forest fragment, 5-10m from the savanna.

6.4 DISCUSSION

Annual burning of the savannas takes place usually at the end of the dry season, in August-September. Fruit set of the study species in the second part of the year occurs before the fires are started, but they affect the fruit availability directly. This is particularly the case for *Psidium*, which is burnt completely, but fire also damages *Psychotria* and *Antidesma* if it reaches the forest or gallery edge. Areas that are not burnt regularly, or have remained unburnt for a long period of time, contain higher densities of shrubs and other colonising species (White 1995). Careful management of fire, burning small areas in rotation, controlling the likelihood of it reaching the forest edge, and leaving some areas unburnt, would all improve the availability of food resources for the consumers (Tutin *et al* 1994a, White 1995).

There was no clear indication of fire affecting fruit production, although the poorest *Psychotria* and *Psidium* production was along the edge transects that are "usually" burnt (Table 2, Figure 6.4a). The second fruiting was assessed before fires were lit, and is more likely to be a consequence of natural fruiting patterns of the species. The historical data for fruit production (Figure 6.5) indicate that fruit production in the early part of the year is consistently higher than in the second season. The second fruiting occurs at the end of the dry season, and the length and severity of the dry period might influence fruit set as a result of water limitations. *Psidium* showed the least difference in fruit production between the seasons, possibly as a result of it being less dependent on water than the other species.

There is little doubt that gorillas consume and disperse large quantities of the seeds of these three species. They shift their foraging patterns to feed on *Psidium*, and spend much of their time in the mosaïc of forest, forest patches, galleries and associated savanna when this and the other species are abundant (Tutin *et al* 1994a). Gorillas feed on the three species even when they are less abundant (during the second season of 1993), possibly because they occur in the same habitat mosaïc as *Uapaca*, which had fruit at the same time (see Chapter 4). It would appear that both *Antidesma* and *Psychotria*, as small fruit, are arranged in a way that makes a sufficient meal possible for larger vertebrate feeders such as gorillas, although they might not feed so much on these two species if *Psidium* was not available at the same time. Such 'packaging' is thought to be important in terms of fruit selection by large frugivores (Leighton 1993). The close proximity of individual plants can also contribute to the 'packaging' of small fruit on a larger scale, such that sufficient quantities occur on plants near to one another to attract larger frugivores.

In order to assess the quality of the dispersal by gorillas, their habitat use when nesting and the habitat requirements of the plant species have to be examined. Adult plants of these species are generally confined to open savanna (*Psidium*), forest edge (*Psychotria*, *Antidesma*) and proximity to water (*Antidesma*). Gorillas are known to nest in open savanna at Lopé but do so close to the forest edge (Tutin *et al* 1995, pers. obs.). It is uncommon behaviour and was only recorded during this study in the *Uapaca* season (pers. obs.), when gorillas tend to use this habitat (Williamson *et al* 1988, Tutin *et al* 1995). They deposit some seeds in dung that is left in the savanna while they forage for *Psidium*, but most seeds will be deposited in forest locations, as were all those monitored in this study. Gorillas are probably dispersers of very low quality as a result of this behaviour.

For *Psychotria* and *Antidesma*, there was an indication that the deposition of some seeds does occur in sites that might be favourable for establishment. Gorillas nest in galleries and at the edges of forest when they are using this zone, and some of the nest sites monitored were in potentially suitable locations. The *Psychotria* seeds deposited in dung in 1993 were mostly in what could be regarded as *Psychotria* habitat, *i.e.* at the savanna/forest boundry. Wastage of seeds is likely to be high however, if in general gorillas tend to nest further into the forest. Clumping of thousands of seeds in a single dung pile will incur considerable wastage as well, because ultimately only one individual can survive at that location. The three plant species' strategy however is one of low investment in a large number of seeds, which allows for high seed or seedling losses.

Other consumers may provide better dispersal services than gorillas. Birds probably remove smaller quantities of seeds, but they are more likely to be deposited in smaller clumps, or individually (Loiselle 1990). The seeds that are removed might end up within the same habitat type as the adult plants if birds show a more limited foraging range relative to the time between consuming and voiding seeds (Snow & Snow 1988, Jordano

1992), which would increase their quality as dispersers. On the other hand, rapid regurgitation or voiding of seeds while birds are perched in a fruiting canopy might be regarded as poor dispersal.

Elephants remove huge quantities of *Psidium* seeds, and use the savanna areas for long periods of time because they provide considerable quantities of herbaceous food (L. White, pers. comm.), in addition to guavas. Some dung will inevitably be left in the savanna. Their prolonged use of the gallery forest/savanna mosaïc also means that some of the *Antidesma* and *Psychotria* seeds they remove will also end up in favourable habitats. Gut passage time of an elephant is long and their ranging considerable (Spinage 1994), so many seeds may end up far into the forest interior. Chimpanzees, as the other large frugivorous ape, are probably even poorer quality dispersers than gorillas, because they have never been known to nest in savanna at Lopé, and tend to nest further in from the forest edge than gorillas, always in trees (C. Tutin, pers. comm.), although there are savanna-dwelling populations of chimpanzees in West Africa (e.g. McGrew *et al* 1988). All the large mammals remove unripe *Antidesma* fruit in quantity, which will contribute to seed waste if the immature seeds are inviable. The viability of immature seeds was not tested, but it is likely to be low.

Over time, there are chances for some seeds to be deposited by all the consumers into microsites favourable for establishment, as they repeatedly forage throughout this particular habitat mosaïc. This reflects what is a generalist dispersal scenario for ostensibly 'bird' type fruit. Generally, sugary fruits with few lipids are thought to be 'non-specialist' fruits, whereas specialist bird fruits tend to be high in fats and/or protein, as they have to satisfy the nutritive demands of a species with a restricted diet (e.g. Janzen 1975, McKey 1975, Stiles 1993). Small, sugary 'generalist' fruit might therefore be expected to be eaten by many consumers, as is the case for these small-seeded species. Larger-bodied frugivores at Lopé find these three study species worthwhile on account of the way in which they are 'packaged', their distributions, and their fruiting patterns. Gorillas are probably poor dispersers for these species, relative to their interaction with some of the larger-seeded species of the forest (including those studied during this research) because of their pattern of habitat use and treatment of seeds. Nonetheless they make a contribution to the dispersal of seeds of these species, along with a large number of other consumers.

Chapter 7

SEED DISPERSAL BY GORILLAS - A CONCLUDING DISCUSSION

7.1 DISPERSAL STRATEGIES: HOW TO ATTRACT GORILLAS

Patterns of fruit production

The fruiting patterns of the two least common trees studied, *Ganophyllum* and *Dialium*, tend to be of a relatively short duration, with a sharp peak of synchronous fruit production in the population (Chapter 3). This strategy, in a species that is of relatively low abundance, probably increases the likelihood that an individual tree is fed in by gorillas. For both these species, gorillas visit a high proportion of the trees with fruit (Chapter 4). *Ganophyllum* trees advertise the ripe fruit crop clearly by means of colour change, but *Dialium* does not. This may be related to the extremely short fruiting period of *Ganophyllum*: trees show a strong 'message' to be certain of attracting appropriate frugivores. *Dialium* trees have to rely on 'sampling' by apes as they test the ripeness of the fruit. If, as seems to be the case for *Dialium*, most of a tree's crop ripens at once, then gorillas need not spend much time selecting fruit when feeding, which could otherwise limit the benefits gained from eating relatively small fruit. It is possible that pre-dispersal seed predation has acted to limit the advertisement of ripe *Dialium* fruit. *Ganophyllum* trees normally fruit every year, but *Dialium* individuals fruit at best every other year, although as a species it usually fruits annually. This may be a natural rhythm, although the resources required to repair structural damage (see below) might limit a tree's capacity for reproductive allocation.

The two abundant trees, *Cola* and *Uapaca*, normally fruit every year (Chapter 3). They bear fruit over a period of several months, and fruit ripen sequentially, which may increase the opportunity for consumption by gorillas (important for the more 'specialist' *Cola*), as well as other consumers (the case for the more 'generalist' *Uapaca*). Ripe fruit of these species is usually abundant enough and offers sufficient nutritive rewards to ensure that gorillas always feed on it, even if not all the fruiting trees are visited by gorillas in any one season (Chapter 4).

Types of fruit

The sweet mesocarp of *Ganophyllum* is firmly attached to the seed, which increases the likelihood that a seed is swallowed by consumers. It also means that more wasteful dispersers such as monkeys have to spend time processing the fruit, which limits the quantity they take. The protective and distasteful (at least to humans) skin is easily removed by primates. Gorillas are able to remove much of a *Ganophyllum* tree's fruit crop in a single feeding bout (Chapter 4). The fruit and seeds of *Dialium* are small relative to an ape, but the large spreading canopy supports a dense array of fruiting panicles that provide sufficient quantities of food to attract gorillas and chimpanzees, even though they have to 'pop' open each small capsule. The bulk of the seed crop is removed by these apes, and the indication is that gorillas are more reliable visitors than chimpanzees (Chapter 4). For a *Dialium* tree to bear fruit when most others do not is disastrous, because the fruit is taken immature and the seed crop is wasted, which was the case in 1993. This might lead to selection for synchronous flowering or fruiting.

The seeds of *Cola* are too large to be swallowed regularly by any consumer other than gorillas, which suggests a close association between the species and its principal disperser. The high sugar content of the mesocarp makes the fruit much sought-after by gorillas. The structure of *Cola* trees may facilitate fruit removal by gorillas with minimal damage; they have small crowns and stout branches, and the fruit is borne relatively close to the trunk. The large, thick-walled *Cola* pod does not exclude monkeys from feeding on the mesocarp, but elephants are excluded, probably because of the chemical composition of the pod, fluid or seeds. Monkeys carry out some scatter-dispersal of seeds, although they drop many, and also waste seeds when they feed on immature fruit.

The fruit of *Uapaca* attracts a wide range of consumers apart from gorillas, many of which disperse its seeds. Gorillas often knock down a lot of immature and ripe fruit, but elephants disperse many of those dropped by feeding on fallen fruit under the canopies of parent trees. The damage to the canopy suffered by fruiting trees, which is often severe for *Dialium* and *Uapaca* trees, may amount to a considerable energetic cost to the tree in return for the services of seed dispersal (Chapter 4).

These different strategies reflect the ecological interactions the species have had with their various dispersers over evolutionary time, as well as interactions with non-dispersers. "Tight" coevolutionary associations between tropical trees and their animal dispersers are thought to be uncommon, for reasons discussed in Chapter 1 (e.g. Wheelwright & Orians 1983, Herrera 1985). It is also apparent that some of the consumers are so similar in size or morphology that it is difficult to imagine how a fruit trait could develop to exclude one and not the other. *Dialium*, *Ganophyllum* and *Uapaca* trees do not exclude chimpanzees, but *Cola* does to some extent (Chapter 3). The apes might also be close in patterns of seed deposition, which would restrict the selection for exclusion.

The strategy found in *Cola* is perhaps a relatively close association between it and the only animal to swallow its seeds regularly (Tutin *et al* 1991b). The characteristics of its fruit might be regarded as an "ape syndrome" as far as dispersal is concerned. They are large, well-protected and indehiscent (like 'ruminant-rodent' fruit) but are brightly coloured (like 'bird-monkey' fruit) (Gautier-Hion *et al* 1985). Nonetheless it still does not exclude other consumers.

The geographical distribution of *Cola lizae* and that of gorillas overlap entirely. The *Dialium* species studied also occurs only where there are gorillas. Although this does not necessarily mean that gorillas are the only important disperser of these species (chimpanzee dung contained more *Dialium* seeds than gorilla dung), it would suggest that there has been a long period of ecological interaction between the tree species and their principal dispersers. The generalist *Uapaca* occurs outwith the range of gorillas and could probably persist in their absence at Lopé, since it has a wider coterie of consumers.

Cola is an example of an abundant tree which has a relatively specialised group of seed dispersers. A rare tree might also benefit from a close association with its dispersers. *Ganophyllum* seems to be able to guarantee removal by gorillas by its sharp peak of fruiting and the effective advertisement of a high-quality reward, although the fruit structure itself is not particularly 'specialised'. That kind of phenological pattern by a tree with a clumped distribution can result in the deposition of its seeds in a similar area to that in which adult trees are found, which might be beneficial if the species is habitat-limited in any way. Gorillas certainly remain and nest within the *Ganophyllum* 'zone' when the species is in fruit, so seeds are deposited by them within a broad habitat that is favourable for adult trees at least.

Most tree species exhibit an array of "covarying complexes" with respect to the dispersal of their seeds (Fischer and Chapman 1993). Fruit are fed upon usually by a coterie of several or many species, not all of which provide dispersal services. This may limit specialisation, but there can still be important dispersers within the coterie of consumers, a kind of non-exclusive specialisation whereby a tree cannot avoid some consumers but 'targets' certain ones anyway. All the four species studied are reliably fed upon and dispersed by gorillas, a result of the combination of fruit quality, design and fruiting pattern.

7.2 DO GORILLAS SATISFY THE CRITERIA FOR HIGH-QUALITY DISPERSAL?

Seed removal

Chapters 4 and 5 covered the two principal components of seed dispersal quality, *i.e.* the removal of seeds from the parent tree, and the fate of deposited seeds. All four species are important and favoured foods for gorillas, which reliably feed on them each fruiting season. The likelihood of visitation to a particular tree was determined by the abundance of the species, crop size and ranging behaviour of the gorillas. The location and quantity of food, and the nutritional requirements of the group (particularly the leading silverback), determine their selection of foods and hence their ranging (Tutin *et al* 1991b).

For the two least common trees, *Ganophyllum* and *Dialium*, a high proportion of known fruiting trees were visited (Chapter 4). In years when there is some competition for the *Ganophyllum* fruit resource, such as more than one group of gorillas using a particular area, then even trees with smaller crops have most of their seeds removed by gorillas, as found in 1992. In other years, gorillas are able to be more selective, and may only feed in those trees with the larger crops (Chapter 4, Figure 4.6b). De Steven (1994) points out the importance of individual fecund trees as sources for recruitment into the population. Trees with consistently small crops might not make a major contribution if they are unable to attract high quality dispersers as a result of their crop size. Gorillas removed the bulk of the seed crops of all the *Dialium* trees monitored (Chapter 4, Figure 4.9). The removal of many seeds is not necessarily always best in dispersal terms (Janzen 1983), if a large proportion are deposited in unfavourable sites, or if a disperser that removes only a few somehow ensures they are deposited in better sites.

Many *Cola* and *Uapaca* trees did not have their fruit removed by gorillas during the study, a result of both the abundance of fruiting trees and the ranging patterns of gorillas during that season. Over the lifetime of an individual tree, however, gorillas are likely to visit it many times. Which tree is favoured by what dispersers varies annually, and the mixed fortunes of the seed source probably contribute to the genetic diversity of the population. Gorillas tended to remove a considerable proportion of the crop of the trees they did feed in (Chapter 4, Figure 4.8B & 4.11), but this was rarely as dramatic as for *Ganophyllum* and *Dialium*. The loss of some seeds may be a relatively small 'cost' to the plant if a large proportion of the crop are removed by a legitimate disperser, something that Howe (1980) suggests after reporting that howler monkeys remove about 70% of *Virola nobilis* seeds.

Ape meals consist of a variety of fruit species (which creates a mix of seeds in the dung), they have relatively large home ranges that cover a variety of different habitats and they deposit seeds in large quantities. These factors led Wrangham *et al* (1994) to suggest that chimpanzees are important dispersers in tropical forests, more so than their densities would suggest. Until now, there have been no data on seed dispersal by gorillas, because the frugivorous nature of the diet of lowland gorillas is a relatively recent finding (Chapter 2). The data reported here provides evidence that gorillas are possibly more important than chimpanzees, in terms of the reliability of visitation and the quantity of seeds removed, and can be seen as important consumers for each of the four study species, including the more generalist *Uapaca*. Their importance is likely to apply to any diverse lowland forest in Central Africa where they occur (see below).

The fate of dispersed seeds

For a plant, true 'dispersal' of seeds is merely their removal away from the parent plant, a service often carried out by animals. Beyond that, other factors come into play that are largely outwith the control of the plant (Estrada & Coates-Estrada 1986). The disperser behaves to a certain extent randomly (from the plant's point of view) over a patchy environment, so chance events feature in the post-dispersal fate of seeds.

This study was limited in terms of the length of time seedling fate was monitored, but seedlings were followed for longer than any other study of seed dispersal by primates that I am aware of, except perhaps for work in Barro Colorado Island (see Chapter 1). This studyis the first to follow the fate of seeds dispersed by African apes for any length of time. Ideally, seedlings should be followed to the sapling stage and beyond; however, the stage of seed to seedling is critical, so an indication of the effectiveness of a particular disperser can be gained from studies covering this vulnerable period. Most seeds do not survive even to the stage of a large seedling, so it is a rare event that is being studied. Despite the huge mortality, if among the few that survive it can be determined which are more likely to persist, or if the likelihood of survival can be related to disperser behaviour, then some idea can be gained of the importance of different dispersers.

Due to the dormant nature of *Dialium* seeds and a small sample size, nothing could be concluded regarding the effect of gorilla dispersal on the fate of seeds, although initial germination success, and survival, was better at the nest site than elsewhere (Chapter 5, Figure 5.18). In the case of the other species, in spite of small samples and high variation, it was clear that the highest survival and the best performance of seedlings always occurred at a gorilla nest site. Nest sites were not always favourable for seedling growth, but the alternatives to dispersal by gorillas (*i.e.* dropped under the parent, or scatter-dispersed) tended to result in low survival and/or poor performance. The fate of seeds dispersed by chimpanzees (in the case of *Dialium* and *Uapaca*) and elephants (in the case of *Uapaca*) was not investigated. It is likely that chimpanzees are poorer quality dispersers than gorillas for these species, if only because they always nest in trees (Chapter 2). It would be interesting to pursue a community study to compare the effect of dispersal by these three large frugivores on particular species.

This study suggests that gorillas are beneficial to these species because they disperse seeds reliably to sites where seeds and seedlings survive and perform better than those that are dispersed by other means, or are not dispersed at all. De Steven (1994) suggested that the numerical size of a new seed cohort was proportional to its contribution to the seedling population at a later stage. In a similar vein, the large quantity of seeds deposited by gorillas at a nest site often resulted in the site forming a relatively large seedling 'bank' (Chapter 5). There is evidently much variation within a dispersal association, so there is not necessarily a 'typical year' (Jordano 1992), either in fruit production, or the behaviour of a coterie of frugivores. Similarly, there is not really a 'typical' gorilla nest site, since they vary so much as sites favouring regeneration.

The particular site that seeds ended up in was important, at least with regard to the nature of the surrounding vegetation. In this study, the seedlings that were in more open locations, with less vegetation cover, showed better performance than those deposited in more shady sites (Chapter 5), although seeds were vulnerable to desiccation in very open habitats (Chapter 4). This finding has been reported for several species of tropical trees in different regions (Chapter 1). Better growth in gap sites may enable seedlings to reach a more resilient stage quickly, as well as allowing them to divert resources for defences (Folgarait & Davidson 1994). Nonetheless the temperature and humidity in gap sites may return to 'pre-gap' levels within two years (Denslow 1987), although the difference in light quality is likely to persist for longer.

Gorillas appear to select more open conditions for nest building, and possibly play a role in creating or maintaining such environments (see below). Larger-seeded species may be more able to survive in understorey conditions (Sork 1987, De Steven 1994), and most tropical tree seeds end up in a shaded environment, so the regeneration strategy of the species, and the conditions of the site (in particular the light environment) is important with respect to the post-dispersal fate of seeds and performance of seedlings. The regeneration requirements of the different species probably contribute to the diversity of composition of the forest as well as its ability to respond to particular disturbance regimes (Raich & Gong 1990).

It is important to extend the context of survival beyond the seedling stage to be more certain of the effects of disperser behaviour on tree population biology, both in terms of understanding forest dynamics as well as the evolutionary elements of dispersal. There is always a difficulty in trying to investigate aspects that operate at an evolutionary time scale or a long ecological one by studying their short-term ecology, especially in the case of long-lived tropical trees. Nonetheless, ecological processes studied in the short term provide some clues to the longer term dynamics, and possibly the evolutionary aspects of a system, because evolutionary processes operate through persistent ecological interactions. Dispersers play a central role in plant demography and community evolution because they act at the final stages of reproduction and at the most vulnerable part of the plant lifecycle, determine the seed shadow and hence the pattern of possible future populations, and deposition by them affects seed survival and establishment (Jordano 1992). Overlaid on these aspects, however, are the effects of climate, germination requirements, phylogenetic constraints, physiological constraints and post-dispersal hazards that mitigate the direct effect of animals on the actual patterns of abundance of plants.

Deposition patterns and contemporary seedling distributions cannot necessarily be linked, then, to sapling distributions, since there is likely to be a shifting mosaïc of favourable sites and hence densities of seedlings and saplings, although Fleming and Heithaus (1981) suggested some links they identified between the seed shadows they observed arising from the dispersal activity of bats and birds and the distribution of adult trees. The actual densities of species reflect their dispersal and establishment strategies as well as local mortality factors during the years of growth to maturity.

7.3 DISPERSAL AND REGENERATION IN MARANTACEAE FOREST

This study was based in an area of Marantaceae forest (see Chapter 2, Tutin *et al* 1994a, White *et al* 1995 for a description) which was logged selectively for okoumé 30 years ago. This forest type is of recent origin and is regarded as a transitional phase between colonising and closed canopy forest. The major feature of Marantaceae forest that influences seedling establishment is probably the density of herbaceous cover. As such, it provides a particular set of conditions for seedling establishment and growth. Although the upper canopy is broken and there is little cover in the middle storey, the herbaceous vegetation creates considerable shade at ground level. The herbs may reduce the quantity of light reaching the forest floor, but without dense overhead tree cover, the quality of light that reaches seeds and seedlings, particularly in sunflecks, might be similar to the 'gap' conditions referred to in other studies (see Chapter 1), although temperatures and humidity might be less extreme. To the human observer, the open aspect of Marantaceae forest makes it a less shady environment than closed canopy forest, and this may persist at ground level in patches of sparse vegetation.

In the dense shade of herbaceous vegetation, surviving seeds and seedlings should be shade tolerant, be nourished by sunflecks alone, and await the creation of the occasional gap. In this respect, establishment conditions in Marantaceae forest are relatively difficult. The disturbance created by the large animals that use this habitat for food and/or nesting may create the kinds of disturbance some species require for successful establishment. Elephants create gaps in the herbaceous cover as they feed, and gorillas can flatten large areas when they nest, or when feeding and resting in one place (pers. obs.). Both of these animals create 'patches of possibility' for seedling establishment and growth, and gorillas certainly deposit seeds reliably into such sites. Janzen (1983) suggested that the creation of suitable sites by dispersers might ultimately link them more tightly to the species they disperse.

The favourability of a site for seedling establishment is unlikely to be a part of decision making by gorillas when they nest, but they often incidentally select or actively create a favourable site for many of the seeds they deposit, or at least one that is better than the alternative deposition sites. This is important, if it is accepted that a crucial aspect of the quality of dispersal is how seeds are deposited over a varied habitat "template" (Jordano 1992). In Marantaceae forest there probably exists a shifting mosaïc of regeneration probabilities that are related as much to gaps created in the herb layer by large animals as to gaps created by natural treefalls, which are often cited as important features for regeneration (Chapter 1, & Denslow 1987). Marantaceae forest probably persists for a long time, in a dynamic flux of gains by herbaceous vegetation, and the occasional establishment of woody species. As tree numbers increase, so does the shade over the herbs, which consequently thin out (White, 1995).

As a species in Marantaceae forest *Cola* is successful perhaps because it is able to establish successfully from dropped or scatter-dispersed seeds in the shade of herbaceous vegetation (Chapter 5). Large-seeded species with ample cotyledonar reserves for the growing seedling are often shade-tolerant (Sork 1987, De Steven 1994). *Cola* was the most shade-tolerant of the species studied (Chapter 5). Another factor that might contribute to its success is that its huge leaves create shade over seedlings when they fall to the ground. They do not decay particularly rapidly, and fallen *Cola* leaves have been noticed to directly impair the growth of seedlings of other species by shading them out (R. Parnell, pers. comm.).

Avenues for further research

Inevitably, the gaps and questions generated by this study pose tempting possibilities for further investigation. The most important is to continue monitoring of the surviving seedlings; with the recent censuses by SEGC staff, some seedlings have now been followed for over 3 years. A sufficiently large sample size to allow for disruptive sampling of dung piles in order to assess seed losses accurately would be beneficial. Similarly, with sufficient quantity of seedlings, some could be sampled to measure biomass and root/shoot growth, which other studies have shown to be important aspects of seedling performance (*e.g.* Osunkoya *et al* 1993, and see Chapter 1). More rigorous experimental trials of seed germination would provide more precise information on germination strategies. To follow germination and growth in experimentally cleared patches of herbaceous vegetation would provide more information on the role of cover in limiting seedling establishment. Exclosure trials, although hazardous in a forest full of large mammals, would indicate the mortality due to rodents, dung beetles and browsers. The activity of dung beetles warrents further investigation. In terms of light and vegetation, the 'canopy stereogeometry' method of assessing the cover over a particular site (Lieberman *et al* 1989) could be very useful. Hemispherical photography would provide a more sophisticated estimate of cover, and enable the more crude measures used in this study to be assessed. The use of light sensors and data loggers would be constrained by the damage caused by the afore-mentioned large animals. Community-wide studies to include the role played by elephants and chimpanzees would also be rewarding.

7.4 IMPLICATIONS FOR THE USE OF FOREST RESOURCES BY HUMANS

Evidence for the importance of gorillas as seed dispersers of four species of forest tree has been given in this thesis. Gorillas are also dispersers of many more species, for some of which they might provide the best quality dispersal (see Table 2.7) due to the number of seeds they remove or their behaviour and the consequent patterns of seed deposition. At Lopé, some 75% of trees above 10cm dbh rely on animals for the dispersal of their seeds (White 1994a), and the percentage is probably higher if smaller woody plants or all higher plants are included. The logical conclusion, not requiring any further study, is that animals are important for the maintenance of the forest system. The implications of a disruption of seed disperser fauna are thus far-reaching.

A particular animal might be important if it is the only high-quality disperser of one or more plant species, or an assemblage of different species of animal might be important for a certain plant. It is not necessarily the case that an important animal disperser is critical for the persistence of a plant species if seedlings can establish under the parent, or if poor quality dispersers or other means of dispersal remain. This issue has been discussed by Janzen and Martin (1982) and their critics (Howe 1985, Hunter 1989), as well as by Chapman & Chapman (in press). However, the principal dispersers are likely to be critical for the maintenance of the population structure of the plant species. If dispersed seeds are more likely to become adults than undispersed seeds, then a loss of dispersers is likely to alter the plant species' density, distribution, or both. This effect would occur even if only the more "important" dispersers were lost, and dispersers of poorer quality remained.

The ecological links among plant and animal species are numerous, so a loss of dispersers could have related effects on other species not directly involved in the dispersal association. This would be critical if the plant affected by a loss of its disperser provides in any way a 'keystone' resource for another species of animal. A plant can be a keystone resource for one or more animal species, or an animal can be a keystone resource for a plant.

Concern over the loss of dispersers should not be restricted to the effect on the trees they disperse that may or may not have a current, economically recognised human use. A plant species affected by the loss of its disperser may be vital for some other creature, such as a pollinating insect, that is important for a plant species humans do use. Alternatively, species currently deemed not to be economically useful might become so at some stage in the future. It is not only the direct effects of hunting that reduces the disperser fauna. Some species may be more sensitive to disturbance than others (such as chimpanzees at Lopé: White 1994d), and harvesting of certain trees may deplete a critical food resource of certain dispersers. For example, the bast of the commercially important timber tree iroko (*Milicia excelsa* Moraceae) is a keystone food for gorillas at Lopé (Rogers *et al* 1994).

It is crucial to maintain parts of the forest as an intact ecosystem, with its full complement of biodiversity. Apart from the importance of maintaining biodiveristy in its own right, such refuges can act as sources of plant and animal species to rehabilitate disturbed areas. Just as timber harvesting should leave seed trees to promote regeneration, within all areas used by humans there should be zones that are left intact. This should be organised at the scale of each logging concession as well as regionally within the country.

The principal use of forests in Gabon is for the national and export timber markets and for animal protein. In the past, the selective logging was of low intensity, and most hunting was at a subsistence or village level, so disruption of fauna was more likely to be small in scale and/or temporary (C.E.G.Tutin, pers. comm.). Current forestry practices generally involve a greater number of timber species and a higher level of extraction and therefore damage. Associated with most logging concessions is the hunting of animals not only for local consumption but increasingly for the bushmeat trade. There is also organised hunting for the trade that operates independently of logging activity. As a result, some areas suffer a considerable loss of seed dispersers over and above the physical and other ecological disruption caused by careless forestry. Losses depend in part on which species are hunted, but also on the degree of vulnerability of an animal species.

Hunting can also reduce the diversity of the seedling flora of a forest through the loss of herbivores, something that has been demonstrated in Panama (Dirzo & Miranda 1991, Wright *et al* 1994). Conversely, if large seed predators are hunted, then seedling densities may respond positively to reduced predation (De Steven & Putz 1984, Sork 1987).

For the long-term use of forest resources for benefits including timber and protein, the maintenance of a seed dispersal fauna (and thus the habitats required by such fauna) is critical (see Pannell 1989). This implies dispersers of all kinds; as much of the intact system as possible should persist, such that the regeneration of currently and potentially useful species can be guaranteed. This is as important as the more immediate need for careful forestry practices that minimise disturbance and ensure the continued existence of a valuable forest resource. Particularly important is the attention paid to juveniles of exploited species, adults as seed sources, and those that provide food resources for animals.

The dispersal mode of the trees harvested might not always involve animals, but it is not sufficient to assume (in Gabon) that natural regeneration of wind-dispersed okoumé is all that is required. Hunting on logging concessions must be strictly controlled, as should be the bushmeat trade at a national level. After harvesting, access by road into a concession must be prevented. The return time for subsequent harvesting should be long enough not only to allow sufficient growth of the smaller trees but also to allow the re-establishment of the wildlife that carry out the vital roles involved in plant reproduction and regeneration. The SEGC study site was logged some time in the past, but currently supports a high diversity of fauna and flora at high densities, so selective logging need not be disastrous. To be sustainable, however, it requires large animals.

Gabon is fortunate to have what some have described as an "opportunity before the crisis" (McShane 1990), but the situation in many areas is already critical. The natural resource wealth of the country was mentioned in Chapter 1, but most of it is based on non-renewable resources. Timber is Gabon's most important renewable natural resource, so the careful management and conservation of its forests, as suggested in Wilks (1990), is crucial.

The implications from the study presented here can be extended to other areas in Gabon, and to other countries in the region, or even further afield. Gorillas eat a certain amount of different fruit in different places, depending on the forest composition. In the Ndoki Forest site (in Congo) the *Ganophyllum*, *Cola* and *Dialium* species studied here have not been recorded (Moutsamboté *et al* 1994), although there are other congeners of *Cola* and *Dialium* listed, for which gorillas might be important dispersers. The importance of certain species as foods may vary between locations, as might alternative foods and what other sympatric vertebrates make up the frugivore community. These could all influence the role of gorillas as dispersers for a particular suite of plant species, but it is likely that they are important for some, if not many, species wherever they occur, particularly if the best performance of seedlings is consistently at gorilla nest sites, as shown here in a small-scale study.

The disperser community elsewhere may contain a different array of species. Chimpanzees have been suggested as important dispersers in Ugandan forests where gorillas do not occur (Wrangham *et al* 1994), and the loss of elephants in west Africa may already be affecting the regeneration potential of that region's forests. Cassowaries could be seen as the apes or elephants of Australian rain forests, and in some south-east Asian forests orang-utans or hornbills might be critical large frugivores. The precise dynamics and particular dispersal associations are important to identify, but the essential situation is the same. That is, we can be certain that the forest will lose its integrity and value if we unduly disrupt the plant - animal interactions that are so crucial for its regeneration.

REFERENCES

Alexandre, D.Y. 1978. Le rôle disséminateur des éléphants en forêt de Tai, Côte-d'Ivoire. *La Terre et la Vie* 32: 47-72

Alvarez-Bullya, E. & Martinéz-Ramos, M. 1990. ? *Oecologia* 84: 314-325

Anderson, A.N. 1989. How important is seed predation to recruitment in a stable population of long-lived perennials? *Oecologia* 81: 310-315

Augspurger, C.K. 1983a. Seed dispersal of the tropical tree *Platypodium elegans* and the escape of its seedlings from fungal pathogens. *J. Ecology* 71: 759-771

Augspurger, C.K. 1983b. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189-196

Augspurger, C.K. 1984. Seedling survival among tropical tree species: interactions of dispersal distance, light gaps and pathogens. *Ecology* 65: 1705-1712

Augspurger, C.K. & Kelly, C.A. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density and light conditions. *Oecologia* 61: 211-217

Bawa, K.S. & Hadley, M. (eds) 1990. *Reproductive ecology of tropical forest plants.* UNESCO/Parthenon

Bazzaz, F.A. & Ackerly, D.D. 1992. Reproductive allocation and reproductive effort in plants. Pp 157-192 *in* Fenner, M. (ed.) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford.

Becker, P. 1983. Effects of insect herbivory and artificaial defoliation on the survival of *Shorea* seedlings. Pp 241-252 *in* Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (eds) *Tropical rainforest: ecology and management.* Blackwell Scientific, Oxford.

Blain, D. & Kellman, M. 1991. The effect of water supply on tree seed germination and seedling survival in a tropical seasonal forest in Veracruz, Mexico. *J. Trop. Ecol.* 7: 69-83

Bodmer, R. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23: 255-261

Brandani, A., Hartshorn, G.S. & Orians, G.H. 1988. Internal heterogeneity of gaps and richness in Costa Rican tropical wet forest. *J. Trop. Ecol* 4: 99-119

Breteler, F.J. 19--. Caesalpiniacées. *Flore du Gabon*

Breteler, F.J. 1994. Novitates Gabonensis 16: *Dialium lopense*, a new *Leguminoseae-Caesalpinoideae* from central Gabon. *Bull. Jard. Bot. Nat. Belg* 63: 201-204

Brokaw, N.V.L. 1985. Gap phase regeneration in a tropical forest. *Ecology* 66: 682-687

Brokaw, N.V.L. & Scheiner, S.M. 1989. Species composition in gaps and the structure of a tropical forest. *Ecology* 70: 538-541

Burkey, T.V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* 97: 533-540

Caballé, G. 1983. *Vegetation.* Pp 34-37 *in* J. Barret (ed) *Geographie et Cartographie du Gabon.* EDICEF, Paris

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548-550

Chapman, C.A. 1989. Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 21: 148-154

Chapman, C.A., Chapman, L.J. (in press). Survival without dispersers?: seedling recruitment without dispersers. *Cons. Biol.*

Chapman, C.A., Chapman, L.J. & Wrangham, R.A. 1993. *Ballanites wilsoniana:* elephant dependent dispersal? *J. Trop. Ecol* 8: 275-283

Chapman, C.A., Wrangham, R.A., Chapman, L.J., Gebo, D. & Gardner, L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527-531

Chapman, C.A., Wrangham, R.A. & Chapman, L.J. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160-171

Chazdon, R.L. 1988. Sunflecks and their importance to forest understorey plants. *Adv. Ecol. Res.* 18: 1-13

Chazdon, R.L. & Fetcher, N. 1984. Photosynthetic light environment in a lowland tropical rain forest in Costa Rica. *J. Ecol.* 72:553-564

Chivers, D.J. 1989. Adaptations of digestive systems in non-ruminant herbivores. *Proc. Nut. Soc.* 48: 59-69

Chivers, D.J. & Hladik, C.M. 1984. Diet and morphology in primates. Pp 213-230 *in* D.J. Chivers, B.A. Wood & A. Bilsborough (eds)*Food Aquisition and processing in Primates.* Plenum Press, London

Christy, P. & Clarke, W. 1994. Guide des Oiseaux de la Réserve de la Lopé. ECOFAC/Multipress, Libreville, Gabon.

Clark, D.A. & Clark, D.B. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island Galapagos. *Oecologia* 49: 73-75

Clark, D.A. & Clark, D.B. 1984. Spacing dynamics of a tropical rainforest tree: evaluation of the Janzen-Connell model. *Amer. Nat.* 124: 769-788

Clark, D.B. 1990. The role of disturbance in the regeneration of tropical moist forest. Pp 291-316 *in* Bawa, K.S. & Hadley, M. (eds) *Reproductive ecology of tropical forest plants.* UNESCO/Parthenon

Collet, J-Y., Bourreau, E., Cooper, R.W., Tutin, C.E.G. & Fernandez, M. 1984. Experimental demonstration of cellulose digestion by *Troglodytella gorillae*, an intestinal ciliate of lowland gorillas. *Int. J. Primatol.* 5: 328

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. Pp 298-312 *in* den Boer, P.J. & Gradwell, P.R. (eds) *Dynamics of Populations.* PUDOC, Wageningen.

Corlett, R.T. & Lucas, P.W. 1990. Alternative seed handling strategies in primates: seed spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* 82: 166-171

Crawley, M.J. 1983. *Herbivory: the Dynamics of Animal-Plant Interactions.* Blackwell Scientific,Oxford.

Crawley, M.J. 1992. Seed predators and plant population dynamics. Pp 157-192 *in* Fenner, M. (Ed.) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford.

De Steven, D. 1988. Light gaps and long-term seedling performance of a neotropical canopy tree (*Dipteryx panamensis*, Leg.). *J. Trop. Ecol.* 4: 457-411

De Steven, D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *J. Trop. Ecol.* 10: 369-383

De Steven, D. & Putz, F.E. 1984. The impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis* in Panama. *Oikos* 43: 207-216.

Denslow, J.S. 1980. Notes on the seedling ecology of a large-seeded species of Bombacaceae. *Biotropica* 12: 220-222

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* 18: 431-51

Denslow, J.S., Newell, E. & Ellison, A.M. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23: 225-234

Dinerstein, E. and Wemmer, C.M. 1988. Fruits *Rhinoceros* eat: megafaunal seed dispersal on a South Asian flood plain. *Ecology* 69: 1768-1775

Dirzo, R. & Domínguez, C.A. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp 237-50 *in* A. Estrada and T.H. Fleming (eds) *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht

Dirzo, R. & Miranda, A. 1990. Contemporary neotropical defaunation and forest structure, function and diversity - a sequel to John Terborgh. *Cons. Biol.* 4: 444-447

Dirzo, R. & Miranda, A. 1991. Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. Pp 273-287 in P.W. Price, P.W. Lewinsohn, G.W. Fernandes & W.W. Benson (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions.* Wiley, N.Y.

Dixson, A.F. 1981. *Natural History of the Gorilla.* Weidenfeld & Nicolson, London.

Dubost, G. 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. *J. Mammal.* 65: 298-316

EDICEF 1983. *Geographie et Cartographie du Gabon.* J. Barret (ed) EDICEF, Paris

Estrada, A. & Coates-Estrada, R. 1984. Fruit-eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rainforest of Los Tuxtlas, Mexico. *Am. J. Primat.* 6: 77-91

Estrada, A. & Coates-Estrada, R. 1986. Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. Pp 93-104 *in* A. Estrada and T.H. Fleming (eds)

Frugivores and seed dispersal. Dr. W. Junk, Dordrecht

Estrada, A. & Coates-Estrada, R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabideae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol* 7: 459-474

Estrada, A. and Fleming, T.H. (eds) 1986. *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht

Estrada, A., Halfter, G., Coates-Estrada, R., & Merritt Jr, D.A. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol* 9: 45-54

Failho, R.F. 1990. Effect of dispersal site on seed survivorship. *Biotropica* 22:423-424

Fenner, M. 1985. *Seed ecology.* Chapman and Hall.

Fenner, M. 1992. *Seeds: the ecology of regeneration in plant communities.* CAB International

Fischer, K. & Chapman, C.A. 1993. Frugivores and fruit syndromes: differences in patterns at the genus and species levels. *Oikos* 66:472-482

Fisher, B.L., Howe, H.F. & Wright, S.J. 1991. Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understorey. *Oecologia* 86: 292-297

Fleming, T.H. & Estrada, A. (eds) 1993. *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Fleming, T.H. & Heithaus, E.R. 1981. Frugivorous bats, seed shadows and the structure of tropical forest. *Biotropica* 13(suppl): 45-53

Fleming, T.H. & Williams, C.F. 1990. Phenology, seed dispersal and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *J. Trop. Ecol.* 6: 163-178

Fleming, T.H., Williams, C.F., Bonaccorso, F.J. & Herbst, L.H. 1985. Phenology, seed dispersal and colonisation in *Muntingia calabura*, a neotropical pioneer tree *Amer. J. Bot.* 72: 383-391

Fleming, T.H., Venable, D.L. & Herrera, M. 1993. Opportunism vs. specialisation: the evolution of dispersal strategies in fleshy-fruited plants. Pp107-120 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Flores, S. 1992. Growth and seasonality of seedlings and juveniles of primary species of a cloud forest in northern Venezuela. *J.Trop. Ecol.* 8: 299-305

Folgarait, P.J. & Davidson, D.W. 1994. Antiherbivore defenses of myrmecophytic Cecropia under different light regimes. *Oikos* 71: 305-320

Forget, P-M. 1990. Seed dispersal of *Vouacapoua americana* (Caesalpiniaceae) by cavimorph rodents in French Guiana. *J. Trop. Ecol.* 6: 459-468

Fouilloy, R. & Hallé, N. 1973. Sapindacées. *Flore du Gabon* 23: 190-192

Fowler, J. & Cohen, L. 1992. *Practical Statistics for Field Biology.* John Wiley & Sons, Chichester

Garber, P.A. 1986. The ecology of seed dispersal in two species of Callitrichid primates (*Sanguinus mystax* and *Sanguinus fuscicollis*). *Am. J. Primat.* 10: 155-170

Garber, P.A. 1987. Foraging strategies among living primates. *Ann. Rev. Anthropol.* 16: 339-364

Garwood, N.C. 1983. Seed germination in tropical trees: a community study. *Ecol. Monog.* 53:159-181

Garwood, N.C. 1986. Constraints on the timing of seed germination in a tropical forest. Pp 347-55 *in* A. Estrada and T.H. Fleming (eds) *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht.

Gautier-Hion, A. 1990. Interactions among fruit and vertebrate fruit-eaters in an African tropical rain forest. Pp219-230 *in* K.S. Bawa and M. Hadley (eds) *Reproductive ecology of tropical forest plants.* UNESCO/ Parthenon

Gautier-Hion, A. & Michaloud, G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70: 1826-1833

Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J-P., Dubost, G., Emmons, L.H., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J-M. 1985 Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337

Gentry, A.W. (Ed.) 1990. *Four Neotropical Rainforests.* Yale University Press, New Haven/London

Gilbert, L.E. & Raven, P. 1975. *Coevolution of Animals and Plants* U. Texas Press, Austin.

Greig-Smith, P. 1983. *Quantitative plant ecology.* Studies in ecology volume 9. Blackwell Scientiifc, Oxford

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145

Gutterman, Y. 1992. Maternal effects on seeds during development. Pp 27-60 in M. Fenner (ed) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford

Hallé, N. 1961. Sterculiacées. *Flore du Gabon* 2: 38-78

Hallé, N. 1987. *Cola lizae* N. Hallé (*Sterculiaceae*), nouvelle espèce du Moyen Ogooué (Gabon). *Bull. Mus. Natn. Hist. Nat., Paris* 4e sér, 9, *Adansonia* 3: 229-237.

Ham, R. 1994. *The ecology of the grey-cheeked mangabey* (Cercocebus albigena) *in the Lopé Reserve, Gabon.* PhD Thesis, University of Stirling

Harcourt, A.H., Stewart, K.J. & Hauser, M. 1993. Functions of wild gorilla 'close' calls I: Repetoire, context and interspecific comparison. *Behaviour* 124: 89-122

Harper, J. L. 1977. *The population biology of plants.* Academic Press, London.

Harrison, M.J.S. & Hladik, A. 1986. Une primate granivore: le colobe noir dans la forêt du Gabon; potentialité d'évolution du compartement alimentaire. *Rev. Ecol (Terre et Vie)* 41: 281-298

Hartshorn, G.S. 1980. Neotropical forest dynamics. *Biotropica* 12(Suppl.): 23-30

Herrera, C.M. 1985. Determinants of plant-animal coevolution: the case for mutualisic dispersal of seeds by vertebrates. *Oikos* 44: 132-141

Herrera, C.M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pp 1-16 *in* A. Estrada and T.H. Fleming (eds) *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht.

Herrera, C.M., Jordano, P., Lopéz-Soria, L. & Amat, J.A 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monog.* 64: 315-344

Hladik, A. & Blanc, P. 1987. Croissance des plantes en sous-bois de forêt dense humide africaine (Makokou, Gabon) *Revue d'Ecologie (Terre et Vie)* 42: 209-234

Hladik, A. and Miquel, S. 1990. Seedling types and plant establishment in an African rain forest. Pp 261-82 *in* K.S. Bawa & M. Hadley (eds) 1990. *Reproductive ecology of tropical forest plants.* UNESCO/ Parthenon

Horvitz, C.C. & Schemske, D.W. 1986. Seed dispersal of a neotropical Myrmechochore: variation in removal rates and dispersal distance. *Biotropica* 18: 319-323

Howe, H.F. 1980. Monkey dispersal and waste of a neo-tropical fruit. *Ecology* 61: 944-959

Howe, H.F. 1984. Constraints on the coevolution of mutualisms. *Am. Nat.* 123: 764-777

Howe, H.F. 1985. Gomphothere fruits: a critique. *Am. Nat.* 125: 853-865

Howe, H.F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417-426

Howe, H.F. 1990a. Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. *J. Trop. Ecol.* 6: 259-280

Howe, H.F. 1990b. Seed dispersal by birds and mammals: implications for seedling demography. Pp 191-218 *in* K.S. Bawa & M. Hadley (eds) *Reproductive ecology of tropical forest plants.* UNESCO/ Parthenon.

Howe, H.F. 1993a. Specialized and generalised dispersal systems: where does 'the paradigm' stand? *Vegetatio* 107-108: 3-14 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Howe, H.F. 1993b. Aspects of variation in a neotropical seed dispersal system.*Vegetatio* 107-108: 149-162 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Howe, H.F. & Richter, W. 1982. The effect of seed size on seedling size in a neotropical nutmeg (*Virola surinamensis*): a within and between crop analysis. *Oecologia* 53: 347-351

Howe, H.F. & Smallwood, J. 1982. The ecology of seed dispersal *Ann. Rev. Ecol. Syst.* 13: 201-223

Howe, H.F. & Vande Kerckhove, G.A. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093-1106

Howe, H.F., Schupp, E.W. & Westley, L.C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781-791

Hubbell, S.P. & Foster, R.B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. Pp 317-339 *in* K.S. Bawa & M. Hadley (eds) *Reproductive ecology of tropical forest plants.* UNESCO/ Parthenon.

Hunter, J.R. 1989. Seed dispersal and germination of *Enereolobium cyclocarpum* (Jacq.) Griseb. (Leg: Mimosaceae): are megafauna necessary? *J. Biogeog.* 16: 369-378

Idani, G. 1986. Seed dispersal by pygmy chimps (*Pan paniscus*): a preliminary report. *Primates* 27: 441-

447.

Janson, C.H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219: 187-189

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Am Nat.* 104: 501-528

Janzen, D.H. 1975. *Ecology of plants in the tropics.* Edward arnold, London

Janzen, D.H. 1981c. Guanacaste tree seed-swallowing by Costa-Rican range horses. *Ecology* 62: 587-592

Janzen, D.H. 1982a. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. *Oikos* 38: 150-156

Janzen, D.H. 1982b. *Ecology* 63: 1889-1900

Janzen, D.H. 1983a. Seed and pollen dispersal by animals: convergence in the ecology of contamination and sloppy harvest. *Biol. J. Linn. Soc.* 20: 103-113

Janzen, D.H. 1983b. Dispersal of seeds by vertebrate guts. Pp: 232-262 *in* D.J. Futuyma and M. Slatkin (eds) *Coevolution.* Sinauer Ass., Inc., Sutherland.

Janzen, D.H. 1986. Mice, big mammals and seeds: it matters who defaecates what where. Pp 251-272 *in* A. Estrada and T.H. Fleming (eds) *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht

Janzen, D.H. & Martin, P. 1982 Neotropical anachronisms: what the gomphotheres ate. *Science* 215: 19-27

Jordano, P. 1992. Fruits and frugivory. Pp105-156 *in* M. Fenner (ed) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford.

Julliot, C. 1992. *Utilisation des ressources alimentaires par le singe hurleur roux,* Alouatta seniculus *(Atelidae, Primates), en Guyane: impact de la dissemination des graines sur la regeneration forestière.* Thèse de Doctorat, Univ. de Tours.

Kwesiga, F. & Grace, J. 1985. The role of the red/far-red ratio in the response of tropical tree seedlings to shade. *Ann. Bot. (London)* 57: 283-290

Larson, D. & Howe, H.F. 1987. Dispersal and destruction of*Virola surinamensis* seeds by agoutis: appearance and reality. *J. Mammol.* 68: 859-860

Leighton, M. 1990. Seed dispersal syndromes of Bornean fruits: the dependancy of plants on birds and mammals for seed dispersal and forest regeneration. Report to LIPI/PHPA/Ministry of Forestry.

Leighton, M. 1993. Modeling diet selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14: 257-314

Leighton, M. & Leighton, D.R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rainforest. Pp 181-196 in S.L. Sutton, T.C. Whitmore & A.C. Chadwick (eds) *Tropical rainforest: ecology and management.* Blackwell Scientific, Oxford.

Letouzey, R. 1968. *Étude Phytogéographique du Cameroun.* Encyclopédie Biologique no. 69. Editions Paul Lechevalier, Paris

Levey, D.J. 1987. Seed size and fruit handling techniques of avian frugivores*Am. Nat.* 129:471-485

Levey, D.J. 1990. Habitat-dependent fruiting behaviour of an understorey tree, *Miconia centrodesma,* and tropical treefall gaps as keystone habitats in Costa Rica. *J.Trop. Ecol.* 6: 409-420

Lieberman, M. & Lieberman, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *J. Trop. Ecol.* 2: 113-126

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not Swiss cheeses: canopy stereogeometry of non-gaps in tropical rainforest. *Ecology* 70: 550-55

Lieberman, D., Hall, J.B, Swaine, M.D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana *Ecology* 60: 65-75

Loiselle, B.A. 1990. Seeds in droppings of tropical fruit-eating birds: the importance of considering seed composition. *Oecologia* 82: 494-500

Loiselle, B.A. & Blake, J.G. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. Pp177-190 *in* A. Estrada and T.H. Fleming (eds) *Frugivores and seed dispersal.* Dr. W. Junk, Dordrecht (*Vegetatio* 107/108)

Longman, K.A. 1985. *Tropical forest trees.* Pp 33-39 *in* A. H. Halevy (ed.) *Handbook of Flowering.* CRC Press, Boca Raton, USA

Longman, K.A. & Jenik, J. 1987. *Tropical Forest and its Environment.* Longman Scientific, Harlow

Mabberley, D.J. 1987. *The Plant Book: a portable dictionary of the higher plants.* Cambridge Uni. Press

Mabberley, D.J. 1992. *Tropical rainforest ecology.* Blackie/Chapman and Hall

Macedo, D.S. & Anderson, A.B. 1993. Early ecological changes associated with logging in an Amazon floodplain. *Biotropica* 25: 151-163

Maisels, F. & Gautier-Hion, A. 1994. Why are Caesalpinioidae so important for monkeys in hydromorphic rainforests of the Zaire basin? Pp 189-204 *in* J.I.Sprent & D. McKey (eds) *Advances in Legume Systematics 5: the Nitrogen Factor.* Royal Botanic Gardens, Kew.

Manasse, R.S. & Howe, H.F. 1983. Competition for dispersal agents among tropical trees: influence of neighbours *Oecologia* 59: 185-190

Marquis, R.J., Young, H.J. & Braker, M.E. 1986. The influence of understory vegetation cover on germination and seedling establishment in tropical lowland wet forest. *Biotropica* 18: 273-278

Martínez-Ramos, M. & Soto-Castro, A. 1993. Seed rain and advanced regeneration in a tropical rain forest. Pp299-318 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht (*Vegetatio* 107/108)

McGrew, W.C., Baldwin, P.J. & Tutin, C.E.G. 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *Am. J. Primatol.* 16: 213-226

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp 159-191 *in* L.E. Gilbert and P. Raven (eds), *Coevolution of animals and plants.* U. Texas Press, Austin.

McShane, T.O. 1990. Conservation before the crisis-an opportunity in Gabon. *Oryx* 24(1): 9-14

Milton, K. 1984. The role of food-processing factors in primate food choice. Pp 250-279 in P.S Rodman & J.G.H. Cant (eds) *Adaptations for foraging in non-human primates.* Columbia University Press, New York.

Miquel, S. 1987. Morphologie fonctionnelle de plantules d'espèces forestières du Gabon *Bulletin du Muséum Nationa d'Histoire Naturelle, Paris, 4eme série, section B, Adansonia* 9: 101-121

Molofsky, J. & Augspurger, C.K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68-77

Mori, A. 1988. Utilisation of fruiting trees by monkeys as analysed from feeding traces under fruiting trees in tropical rainforest of Cameroun. *Primates* 29: 21-40

Moutsambote, J-M., Yumoto, T., Mitani, M., Nishihara, N., Suzuki, S. & Kuroda, S. 1994. Vegetation and list of plant species identified in the Nouabalé-Ndoki Forest, Congo. *Tropics* 3: 277-294

Murdoch, A.J. & Ellis, R.H. 1992. Longevity, viability and dormancy. Pp 193-230 *in* M. Fenner (ed) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford

Murray, D.R. (ed.) 1986. *Seed dispersal.* Academic Press, Sydney

Murray, D.R. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. *Am. Nat.* 129: 18-31

Myers, N. 1991. Tropical forests: present status and future outlook. *Climate Change* 19: 3-33

Ng, F.S.P. 1978. Strategies of establishment in Malayan forest trees. Pp 129-162 *in* P.B. Tomlinson & H. Zimmerman (eds) *Tropical Trees as Living Systems.* Cambridge Univ. Press, Cambridge, USA

Ng, F.S.P. 1981. Vegetative and reproductive phenology of dipterocarps. *Malaysian Forester* 44: 197-221

Nishihara, T. 1992. A preliminary report on the feeding habits of western lowland gorillas (*Gorilla gorilla gorilla*) in the Ndoki Forest, northern Congo. Pp 225-240 *in* N. Itoigawa, Y. Sugiyama, G.P. Sackett & R.K.R. Thompson (eds) *Topics in Primatology Vol. 2.* Univ. of Tokyo Press.

Nuñez-Fárfán, J. & Dirzo, R. 1988. Within-gap spatial heterogeneity and seedling performance in a Mexican tropical rain forest. *Oikos* 51: 274-284

Oldeman, R.A.A. 1983. Tropical rainforest architecture, sylvigenesis and diversity. Pp 139-150 *in* S.L. Sutton, T.C. Whitmore and A.C. Chadwick (eds) *Tropical rainforest: ecology and management.* Blackwell Scientific.

Orians, G.H. 1983. The influence of treefalls in tropical forest on tree species richness. *Tropical Ecology* 23: 255-279

Oslisly, R. 1995. The middle Ogooué valley, Gabon, from 3500 years BP: cultural changes and paleoclimatic implications. *Azania* (in press)

Osunkoya, O.O., Ash, J.E., Graham, A.W. & Hopkins, M.S. 1992. Factors affecting survival of tree seedlings in North Queensland rainforests. *Oecologia.* 91: 569-578

Osunkoya, O.O., Ash, J.E., Graham, A.W. & Hopkins, M.S. 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *J. Trop.Ecol.* 9: 1-18

Pannell, C.M. 1989. The role of animals in natural regeneration and the management of equatorial rain forest for conservation and timber production. *Comm. For. Rev.* 68: 309-314

Pannell, C.M. & Koziol, M.J. 1987. Ecological and phytochemical diversity of arillate seeds in *Aglaia*

(Meliaceae): a study of vertebrate dispersal in tropical trees. *Phil. Trans. R. Soc. Lond.* B136: 303-333

Peres, C.A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazônia. *Biotropica* 23: 262-270

Peters, C.M, Gentry A.H. & Mendelsohn, R.O. 1989. Valuation of an Amazonian rainforest. *Nature (Lond.)* 339: 655-656

Pratt, T.K. & Stiles, E.W. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *Am. Nat.* 122: 797-805

Price, M.V. & Jenkins, S.H. 1986. Rodents as seed consumers and dispersers. Pp 191-235 *in* D.R. Murray (ed.) *Seed dispersal.* Academic Press, Sydney

Primack, R.B. 1990. Seed physiology, seed germination and seedling ecology-commentary. Pp 233-36 *in* K.S Bawa & M. Hadley (eds) *Reproductive ecology of tropical forest plants.* UNESCO/ Parthenon.

Popma, J. & Bongers, F. 1988. The effects of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625-632

Pourtier, R. 1989. *Le Gabon: Etat et Developpement..* L'Harmattan, Paris

Publicover, D.A. & Vogt, K.A. 1991. Canopy stereogeometry of non-gaps in a tropical forest-a comment. *Ecology* 72: 1507 1510

Raich, J.W. & Gong, W.K. 1990. Effects of canopy openings on tree seed germination in a Malaysian Dipterocarp forest. *J. Trop. Ecol.* 6: 203-217

Redford, K.H., Bouchardet da Fonseca, G.A. & Lacher, T.E. 1984. The relationship between frugivory and insectivory in primates. *Primates* 25: 433-440

Reid, N. 1989. Dispersal of a mistletoe by a honeyeater and a flowerpecker: Components of seed dispersal quality. *Ecology* 70: 137-145.

Rogers, M.E. & Williamson, E.A. 1987. Density of herbaceous plants eaten by gorillas in Gabon: some preliminary data. *Biotropica* 19: 278-281

Rogers, M.E., Williamson, E.A.W., Tutin, C.E.G. & Fernandez, M. 1988. Effects of the dry season on gorilla diet in Gabon. *Primate Report* 22: 25-33

Rogers, M.E., Maisels, F., Williamson, E.A., Fernández, M. & Tutin, C.E.G. 1990. Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia* 84: 326-339

Rogers, M.E. & Parnell, R.J. 1991. *The role of gorillas as frugivores in Gabonese rain forest.* Unpublished Report to the National Geographic Society

Rogers, M.E., Maisels, F., Williamson, E.A., Tutin, C.E.G. & Fernandez, M. 1992. Nutritional aspects of gorilla food choice in the Lopé Reserve, Gabon. Pp 255-266 *in* N. Itoigawa, Y. Sugiyama, G.P. Sackett & R.K.R. Thompson*Topics in Primatology Vol. 2.* Univ. of Tokyo Press.

Rogers, M.E., Tutin, C.E.G., Williamson, E.A., Parnell, R.J., Voysey, B.C. & Fernandez, M. 1994. Seasonal feeding on bark by gorillas: An unexpected keystone food? Pp 37-44 *in* B. Thierry, J.R Anderson, J.J Roeder & N. Herrenschmidt (eds) *Current Primatology* U. Louis Pasteur, Strasbourg

Rowell, T.E. & Mitchell, B.J. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *J. Trop. Ecol* 7: 269-274

Ruvolo, M., Pan, D., Zehr, S., Goldberd, T., Disotell, T.R. & van Dornum, M. 1993. Gene trees and Hominid phylogeny. *Proc. Nat. Acad. Sci.*

Sasaki, S. & Mori, T. 1981. Growth responses of Dipterocarp seedlings to light. *Malaysian Forester* 44: 319-344

Schemske, D.W. 1983 Limits to specialisation and coevolution in plant-animal mutualisms. Pp. 67-111 *in* M.H. Nitecki (ed.) *Coevolution.* Univ. of Chicago Press, Chicago.

Schupp, E.W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest *Oecologia* 76: 525-530

Schupp, E.W. 1988b. Predation on seeds and early seedlings in the forest understorey and in treefall gaps. *Oikos* 51: 71-78.

Schupp, E.W. 1990. Annual variation in seedfall, postdispersal predation and recruitment of a neotropical tree *Ecology* 71: 504 415

Schupp, E.W. 1992. The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. *Am. Nat.* 140: 526-530

Schupp, E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals.*Vegetatio*

107/108: 15-30 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Schupp, E.W. & Frost, E.J. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. *Biotropica* 21: 200-203

Siegel, S. & Castellan, N.J. 1988. *Nonparametric Statistics for the Behavioural Sciences.* McGraw-Hill International

Snow, B & Snow, D. 1988. *Birds and Berries.* T & AD Poyser, London

Sork, V.L. 1985. Germination response in a large-seeded neotropical tree species, *Gustavia superba* (Lecythidaceae). *Biotropica* 17: 130-136

Sork, V.L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba. Ecology* 68: 1341-1350

Spinage, C. 1994. *Elephants.* T & AD Poyser, London

Steege, H.T., Bokdam, C., Boland, M., Dobbelsteen, J. & Verburg, I. 1994. The effects of man-made gaps on germination, early survival and morphology of *Chlorocardium rodiei* seedlings in Guyana. *J. Trop. Ecol.* 10: 245-260

Stiles, E.W. 1992. Animals as seed dispersers. Pp 87-102 *in* M. Fenner (ed) *Seeds: the Ecology of Regeneration in Plant Communities.* CABI, Wallingford.

Stiles, E.W. 1993. The influence of pulp lipids on fruit preference by birds. *Vegetatio* 107/108: 227-235 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Stocker, G.C. & Irvine, A.K. 1983. Seed dispersal by Cassowaries (*Casuaris casuaris*) in North Queensland's rain forest. *Biotropica* 15: 170-176

Sussman, R.W. 1991. Primate origins and the evolution of angiosperms. *Am. J. Primatol.* 23: 209-223

Terborgh, J. 1990. Seed and fruit dispersal-commentary. Pp 181-90 *in* K.S. Bawa & M. Hadley (eds) *Reproductive ecology of tropical forest plants.* UNESCO/Parthenon

Terborgh, J., Losos, E., Riley, M. P. & Bolaños-Riley, M. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. *Vegetatio* 107/108:375-386 *in* T.H. Fleming & A. Estrada (eds) *Frugivory and seed dispersal: ecological and evolutionary aspects.* Dr. W. Junk, Dordrecht

Thomas, W.W., Cloutier, D., Provencher, M. & Houle, C. 1988. The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. *Biotropica* 20: 347-348

Thompson, K. 1992. The functional ecology of seed banks. Pp 231-258 *in* M.Fenner (ed) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford

Turner, I.M. 1990. The seedling survivorship and growth of three *Shorea* species in a Mlaysian tropical rain forest. *J. Trop. Ecol.* 6: 469-478

Tutin, C.E.G. & Fernandez, M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am. J. Primatol.* 6: 313-336

Tutin, C.E.G. & Fernandez, M. 1985. Food consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. *Int. J. Primatol* 6: 27-44

Tutin, C.E.G. & Fernandez, M. 1993a. Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. *J. Trop. Ecol.* 9: 241-248

Tutin, C.E.G. & Fernandez, M. 1993b. Composition of the diet of chimpanzees and comparisons with that of lowland gorillas in the Lopé Reserve, Gabon. *Am. J. Primatol.* 30: 195-211

Tutin, C.E.G. & Fernandez, M. 1994. Comparison of food processing by sympatric apes in the Lopé Reserve, Gabon. Pp 29-36 *in* B. Thierry, J.R Anderson, J.J Roeder & N. Herrenschmidt (eds) *Current Primatology* U. Louis Pasteur, Strasbourg

Tutin, C.E.G. & Oslisley, R. 1995. *Homo, Pan* and *Gorilla*: coexistence over 60 000 years at Lopé in central Gabon. *J. Human. Evol.* (in press)

Tutin, C.E.G., Williamson, E.A., Rogers, M.E. & Fernandez, M. 1991a. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *J. Trop. Ecol.* 7: 181-199

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A., McGrew, W.C. 1991b. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Phil. Trans. R. Soc. Lond. B* 334: 179-186

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A. 1992. A preliminary analysis of the social structure of lowland gorillas in the Lopé Reserve, Gabon. Pp 245-253 *in* N. Itoigawa, Y.

Sugiyama, G.P. Sackett & R.K.R. Thompson (eds) *Topics in Primatology Vol. 2.* Univ. of Tokyo Press.

Tutin, C.E.G., White, L.J.T., Williamson, E.A., Fernandez, M. & McPherson, G. 1994. List of plant species identified in the northern part of the Lopé Reserve, Gabon. *Tropics* 3: 249-276

Tutin, C.E.G., Parnell, R.J., White, L.J.T. & Fernandez, M. 1995. Nest building by lowland gorillas in the Lopé reserve, Gabon: environmental influences and implications for censusing. *Int. J. Primatol.* (in press)

van Schaik, C.P., Terborgh; J. & Wright, S.J. 1993. The phenology of tropical trees: adaptive significance and consequence for primary consumers. *Ann. Rev. Ecol. Syst.* 24: 353-377

Vázquez-Yanes, C. & Orozco-Segovia, A. 1990. Ecological significance of light controlled seed germination in two contrasting tropical habitats. *Oecologia* 83: 171-175

Vázquez-Yanes, C. & Orozco-Segovia, A. 1992. Effects of litter from a tropical rain forest on tree seed germination and establishment under controlled conditions. *Tree Physiology* 11: 391-410

Vázquez-Yanes, C. & Orozco-Segovia, A. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Ann. Rev. Ecol. Syst.* 24: 69-87

Vázquez-Yanes, C., Orozco-Segovia, A., Rincón, E., Sánchez-Coronado, M.E., Huante, P.,Toledo, J.R. & Barradas, V.L.D. 1990. Light beneath the litter in a tropical forest: effect on seed germination *Ecology* 71: 1952-1958

Webb, S.L. & Willson, M.F. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 83: 171-175.

Wheelwright, N.T. 1985a. Competition for dispersers and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44: 564-477

Wheelwright, N.T. 1985b. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818

Wheelwright, N.T. 1991. Frugivory and seed dispersal: 'La coevolución ha muerto-¡Viva la coevolución!' *TREE* 6:312-313

Wheelwright, N.T. & Orians, G. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology and constraints on coevolution. *Am Nat.* 119: 402-413

Whelan, C.J., Willson, M.F., Tuma, C.A. & Souza-Pinta, I. 1991. Spatial and temporal patterns of postdispersal seed predation. *Can. J. Bot.* 69: 428-436.

White, F. 1983. *The vegetation of Africa.* UNESCO, Paris

White, L.J.T. 1993. *Vegetation history and logging disturbance: effects on rainforest mammals in the Lopé Reserve, Gabon.* PhD Thesis, University of Edinburgh.

White, L.J.T. 1994a. *Saccoglottis gabonensis* fruiting and the seasonal movements of elephants in the Lopé Reserve, Gabon. *J. Trop. Ecol.* 10: 121-125

White, L.J.T. 1994b. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *J. Trop. Ecol.* 10: 289-312

White, L.J.T. 1994c. The effects of commercial mechanised selective logging on a transect in lowland rain forest in the Lopé Reserve, Gabon *J. Trop. Ecol.* 10: 313-328

White, L.J.T. 1994d. Biomass of rain forest mammals in the Lopé Reserve, Gabon. *J. Animal. Ecol.* 63: 499-512

White, L.J.T. 1994e. Forest-savanna dynamics and the origins of Marantaceae forest in the Lopé reserve, Gabon. *In* W. Weber, A. Vedder & H. Simmons-Morland (eds) *African Rain Forest Ecology and Conservation.* Yale Univ. Press

White, L.J.T., Tutin, C.E.G. & Fernandez, M. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *Af. J. Ecol.* 31: 181-189.

White, L.J.T., Tutin, C.E.G. & Fernandez, M. 1994. Behavioural and dietry similarities of elephants and apes in the Lopé Reserve, Gabon: Should forest elephants be re-classified as apes? Pp19-28 *in* B. Thierry, J.R Anderson, J.J Roeder & N. Herrenschmidt (eds) *Current Primatology* U. Louis Pasteur, Strasbourg

White, L.J.T., Rogers, M.E., Tutin, C.E.G., Williamson, E.A. & Fernandez, M. 1995. Herbaceous vegetation in different forest types in the Lopé Reserve, Gabon: implications for keystone food availability. *African J. Ecol.* 33:

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70: 536-538

Wilks, C. 1990. *La Conservation des Ecosystèmes Forestiers du Gabon.* IUCN/UICN, Cambridge

Williamson, E.A. 1988. *Behavioural ecology of western lowland gorillas* (Gorilla g. gorilla) *in Gabon.*

PhD thesis, University of Stirling.

Williamson, E.A. 1993. Methods used in the evaluation of lowland gorilla habitat in the Lopé Reserve, Gabon. *Tropics* 2: 199-208

Williamson, E.A., Tutin, C.E.G. & Fernandez, M.. 1988. Western lowland gorillas feeding in streams and on savannas. *Primate Report* 19: 29-34

Williamson, E.A., Tutin, C.E.G., Rogers, M.E., Fernandez, M. 1990. Composition of the diet of lowland gorillas at Lopé in Gabon. *Am. J. Primatol.* 21: 265-277.

Willson, M.F. 1992. The ecology of seed dispersal. Pp 61-86 *in* M. Fenner (ed) *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford.

Willson, M.F. & Whelan, C.J. 1990. Variation in post-dispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. *Oikos* 57: 191-198.

Wrangham, R.W., Chapman, C.A. & Chapman, L.J. 1994. Seed dispersal by forest chimpanzees in Uganda. *J. Trop. Ecol.* 10: 355-368

Wright, S.J., Gompper, M.E. & DeLeon, B. 1994. Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71: 279-294

Yamagiwa, J., Mwanza, N., Yumoto, T. & Maruhashi, T. 1992. Travel distances and food habits of eastern lowland gorillas. Pp 267-282 *in* N. Itoigawa, Y. Sugiyama, G.P. Sackett & R.K.R. Thompson (eds)*Topics in Primatology Vol. 2.* Univ. of Tokyo Press.

Yumoto, T., Yamagiwa, J., Mwanza, M. & Maruhashi, T. 1993. List of plant species identified in the Kahuzi-Biega National Park, Zaire. *Tropics* 3: 295-308.

Appendix A

List of mammals known to occur in the SEGC study site, Lopé Reserve, Gabon (incomplete)

Order/family	Subfamily	Genus/species	
Even-toed ungulates, Artiodactyla			
Suidae		*Potamochoerus porcus*	P
Tragulidae		*Hyemoschus aquaticus*	
Bovidae	Cephalophinae	*Cephalophus monticola*	F
		Cephalophus dorsalis	F
		Cephalophus ogilbyi	F
		Cephalophus callipygus	F
		Cephalophus leucogaster	F
		Cephalophus sylvicultor	F
	Neotraginae	*Neotragus batesi*	
	Tragelaphinae	*Tragelaphus scriptus*	
		Tragelaphus spekii	
	Bovinae	*Syncerus caffer*	
Hyraxes, Hyracoidea		*Dendrohyrax dorsalis*	
Elephants, Proboscidea		*Loxodonta africana*	F
Scaly anteaters, Pholidota			
Manidae		*Manis tricuspis*	
		Manis gigantea	
Rodents, Rodentia			
Sciuridae		*Protoxerus spp*	P
		Myosciurus spp	P
		Heliosciurus spp	P
		Funisciurus spp	P
Anomaluridae		*Anomalurops beecrofti*	P
Hystricidae		*Atherurus africanus*	P
Thryonomyidae		*Thryonomis swinderianis*	P
Carnivores, Carnivora			
Mustelidae		*Mellivora capensis*	
		Aonyx congica	
Viverridae		*Genetta tigrina*	F
		Viverra civetta	F
		Nandinia binotata	F
		Herpestes spp	
Felidae		*Panthera pardus*	
		Profelis aurata	
Primates, Primata			
Lorisidae		*Galago senegalensis*	
		Galago demidovii	
		Perodicticus potto	
Cercopithecidae	Papiinae	*Mandrillus sphinx*	P/F
		Cercocebus albigena	P/F
	Cercopithecinae	*Cercopithecus nictitans*	F
		Cercopithecus pogonias	F
		Cercopithecus cephus	F
	Colobinae	*Colobus satanus*	P
Pongidae		*Gorilla gorilla*	F
		Pan troglodytes	F

F: fruit pulp a component of the diet; P: eats seeds

Appendix B Details of the individual dimensions of the focal trees of the four study species and their estimated crop sizes

Tree #	dbh	ht	LB	crown diameters (m)		FFA (m2)	crown shape	canopy depth (m)	crown surface area (m2)	crown vol (m3)	estimated seed crop		no. of confirmed gorilla visits	
				1st	2nd						1992	1993	1992	1993
Ganophyllum														
G 7	51	26	12	17	9	120.17	1/3 hemisp	9	177.0	384	5725	2609	0	(brief)
G 15	66	25	11	20	7	110	1/2 ellipsoid	4	220.0	147	4400	830	2	0
G 1	74	29	14	18	16	113.9	1/4 sphere	11	227.0	643	14860	16578	1	2
G 4	56	23	10	18	17	120.4	1/4 sphere	9	240.6	702	3835	2559	2	(brief)
G 6	77	27	11	19	16	255.8	95/360 hemisp	12	254.1	741	7765	33800	1	2
G 17	62	28	14	19	11	162.42	1/2 ellipsoid	10	328.4	547	15575	ND	3	
G18	47	17	4	16	15	188.9	hemisphere	ND	377.5	975	ND	7617		
G 16	50	17	7	19	14.5	225.5	hemisphere	7	440.8	1230	2048	30399	0	2
G 9	58	21	7	18.5	16	233.7	1/2 ellipsoid	5	465.1	388	5249	ND	(brief)	
G19	73	27	5	20	15	235.6	1/2 ellipsoid	ND	471.4	628	ND	9812		1
G 2	116	28	7	20	11	204.6	2/3 sphere	11	503.6	1301	8005	ND	1	
G 5	136	32	8	28	24	267	1/4 sphere	14	531.1	2301	17933	ND	1	
G 3	65	26	15	20.5	16.5	274.9	hemisphere	10	537.8	1658	3554	ND	1	
G 11	92	29	12	23	15	271 •	1/2 ellipsoid	9	542.1	813	24197	5612	2	0
G 8	77	25	12	24	21	395.8	1/2 ellipsoid	9	791.9	1188	19237	50034	1	1
mean	75.62	25.3	9.69	20.23	16.00	226.89		9.73	439.3	1008.8	11114.36	19551.38		
SD	25.86	4.61	3.61	3.13.	3.48	73.91		2.41	156.5	527.6	7517.91	16814.35		
median	73	27	10	19	16	233.70		10.00	465.1	813.0	8005.00	13195.00		
Cola														
C7	48	30		9	8.5	30	1/2 ellipsoid		120	160	2596		0	
C5d	39	27	22	8	6.5	42	sphere		165	200	466		0	
C4b	39.5	21	9	9	6.5	46	ellipsoid		184	245	1273		0	
C2e	36	23	18	9	7	51	sphere		201	268	4036		0	
C2a	39	21	17											
C2b	89	26	15											
C2c	57	24	18											
C2d	53	22	17	10	7.5	118	ellipsoid		236	314	11779		0	
C4c	34	22	11	9	8.5	60	sphere		241	351	341		0	
C4a	34	18	10	14	12.5	69	sphere		276	609	4332		1	
C4d	30	19	14	12	8	75	ellipsoid		302	503	838		0	
C6b		26	9											
C6c		23	11	11.5	9	81	ellipsoid		325	434	8726		1	
C9a	44	26	16	12.5	10	101	sphere		398	746	11340		1	
C6a		25	21	11.5	11	99	sphere		398	746	1426		0	
C5e	52	30	12	13	10	106	sphere		416	796	2394		0	
C1	83	26	14	15	10	128	sphere		491	1023	21488		0	
C3a	55	27	16	12	10	94	ellipsoid							
C3b	38	24	15	10	6.5	51	ellipsoid		581	963	3085		0	
C3c	58	26	15	15	12.5	150	sphere		594	1361	1773		0	
C5a	46	23	11	10	8.5	68	sphere							
C5b	29	16	20	9	9	64	sphere							
C5c	26	21	14	6	5	24	sphere		619	840	3276		0	
C8	55	27	20	16	15	189	sphere		755	1950	19755		1	
mean	48.35	23.6	14.8	11.66	9.56	92.3			433.2	818.2	6965.6			
SD	17.65	3.44	3.44	2.63	2.44	40.6			163.6	448.4	7161.6			
median	46	24	15	11.75	9.5	87.5			398.0	746.0	3276			
Dialium														
D1	39.5	22	12	14	13	107	x0.75 hemisph	9	215	483	89649		3	
D7	54	28	15	19	11	164	1/2 ellipsoid	9	328	493	50819		2	
D6	40	26	17	16	14	176	1/2 ellipsoid	7	352	411	57561		2	
D3	44	25	14	15	15	177	hemisph	8	354	884	5841		1	
D2	59	29	20	17	15	202	hemisph	8	402	1072	68803		2	
D8	67	31	11	16.5	16.5	181	1/2 ellipsoid	11	428	784	20636		2	
D4	57	26	10	19.5	13.5	221	hemisph	7	428	1176	4594		1	
D10	49.5	29	18	19	15	230	hemisph	9	454	1286	46255		1	
D9	65	30	15	21	16	274	hemisph	12	538	1658	25229		3	
D5	52.5	26	15	23	16	289	1/2 ellipsoid	8	578	771	94125		2	
mean	52.75	27.20	14.70	18.00	14.50	202.10		8.80	407.7	901.7	46351.2			
SD	9.64	2.70	3.13	2.80	1.67	53.86		1.62	104.6	399.9	32143.6			

median	53.25	27.00	15.00	18.00	15.00	191.50		8.50	415.0	833.9	48537.0			
Uapaca														
U10	39	24	10	12	10	96	hemisph	ND	190	348	5210		0	
U55	49			11	11	95	hemisph	ND	190	348	25885		0	
U51	70	20	7	16.5	14.5	189	hemisph	ND	377	975	21984		1	
U53	60	15	4	16	16	201	hemisph	ND	402	1072	29428		1	
U8	62	18	6	20	18	284	hemisph	ND	567	1796	37060		0	
U9	58	28	9	22	20	347	hemisph	ND	693	2425	61703		0	
U56	80		5	23	21	381	hemisph	ND	760	2788	103305		0	
mean	66.67	23.00	6.67	21.67	19.67	337.33			673.33	2336.33	67356.00			
SD	11.72	7.07	2.08	1.53	1.53	49.22			97.99	501.91	33482.34			
median	62	23	6	22	20	347			693	2425	61703			
1993														
U5	47	17	9	12	8	75	1/2 ellipsoid	5	157	262		13813		3
U33	39	21	4	11	9.5	87	hemisph	9	165	282		13931		2
U8	51	17	4	12.5	11	120	hemisph	9	217	425		30256		1
U9	51	22	9	18	7	99	1/2 ellipsoid	6	246	511		17119		1
U4	57	19	7	13	12	123	hemisph	8	246	511		24231		1
U7	89	23	9	14	12	134	hemisph	9	266	585		20464		1
U6	65+34	14	2	14	13	143	hemisph	8	286	644		33546		0
U1	54	19	7	16	15	189	hemisph	8	377	975		42865		1
U32	57	25	5	18	14.5	211	hemisph	10	415	1123		15570		2
U2	81	26	3	18.5	15	223	hemisph	9	441	1230		31992		1
U34	52	18	4	13	13	133		7						
U35	32	15	5	12	9.5	93		5						
U36	36	19	8	9	8	57	hemisph	6	572	1061		92919		4
U3	90	20	4											
U3a	90	21	4	23	21	381	hemisph	7	760	2788		80700		1
mean	61.00	22.00	4.75	16.38	14.38	189.00		8.50	411.00	1109.33		30142.33		
SD	13.49	4.08	1.71	2.50	0.95	39.90		1.29	32.19	128.05		13741.19		
median	55.5	22	4.5	17	14.75	200		8.5	415	1123		31992		

Appendix C Percentage of the total estimated seed crop handled by different consumers at *Cola* and *Uapaca* trees.

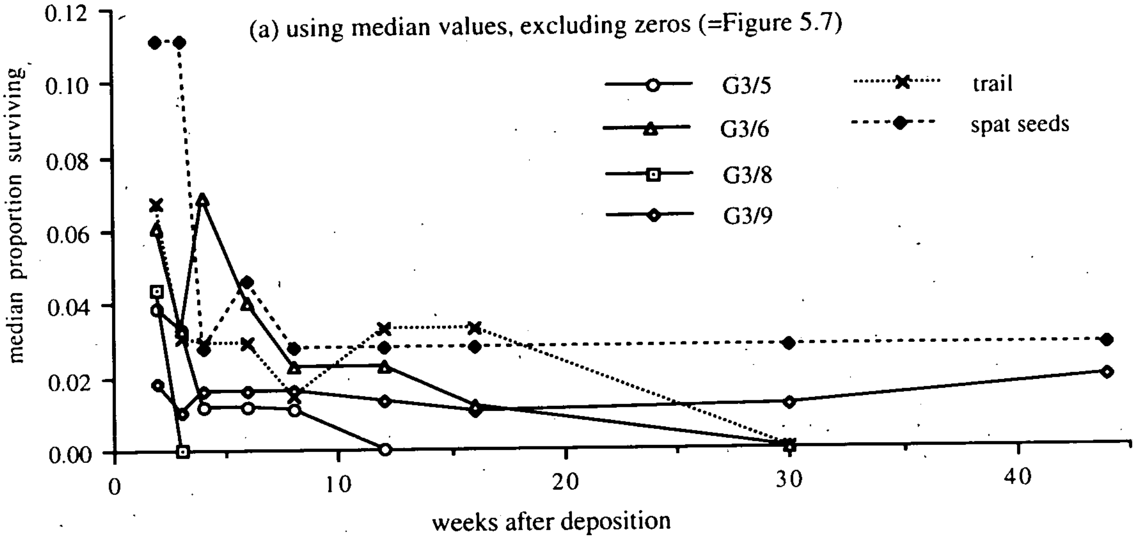
COLA

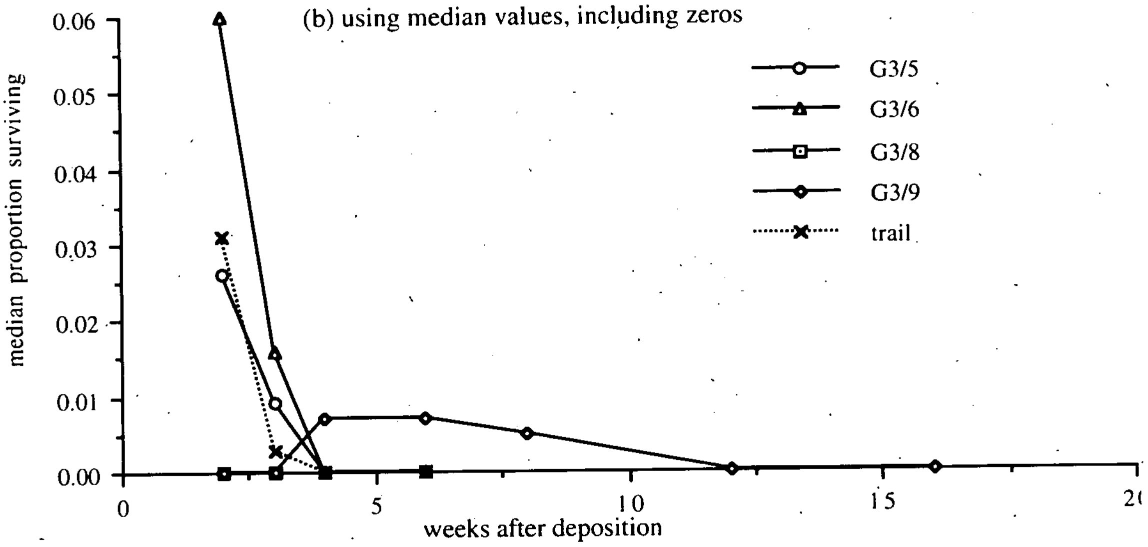
tree	consumer	wasted immature	removed ripe	dropped ripe	wasted ripe	total	damaged
1992							
C1	monkey	46.0	6.2	11.9	4.3	68.4	
	mandrill	27.3				27.3	
	total	73.3	6.2	11.9	4.3		4.3
C2a-d	monkey	15.2	17.2	10.4	21.4	64.2	
	mandrill	13.2	6.4	1.3	1.7	22.6	
	total	28.4	23.6	11.7	23.1		13.4
C2e	monkey	29.5	7.3	14.2	9.8	60.8	
	mandrill	22.2	9.2	1.9	1.7	35.0	
	total	51.7	16.5	16.1	11.5		4.4
C3a-b	monkey	10.5	17.4	3.5	44.3	75.7	24.2
C3c	monkey	3.8	7.3	3.5	49.0	63.6	36.4
C4a	monkey	33.3	40.7	8.9	6.2	89.1	
	gorilla	0.0	10.1	0.7	0.0	10.8	
	total	33.3	50.8	9.6	6.2		0.0
C4b	monkey	1.7	63.2	4.1	12.0	81.0	19.0
C4c	monkey	13.1	30.3	5.1	18.2	66.7	33.3
C4d	monkey	39.5	35.3	1.8	14.2	90.8	9.2
C5a-c	monkey	4.0	40.9	6.8	23.2	74.9	25.0
C5d	monkey	0.0	50.0	17.4	18.5	85.9	14.0
C5e	monkey	1.9	28.9	9.8	28.9	69.5	30.5
C6a	monkey	8.0	41.0	9.2	28.7	86.9	13.2
C6b-e	monkey	2.9	23.1	2.0	25.5	53.5	
	gorilla	0.0	23.1	1.5	4.4	29.0	
	total	2.9	46.2	3.5	29.9		17.6
C7	monkey	8.2	41.2	32.9	12.5	94.8	5.2
C8	monkey	4.5	34.1	2.3	18.0	58.9	
	gorilla	0.0	14.1	0.5	0.0	14.6	
	total	4.5	48.2	2.8	18.0		26.5
C9a	monkey	4.3	54.9	8.2	8.1	75.5	
	gorilla	0.0	15.8	1.7	0.5	18.0	
	total	4.3	70.7	9.9	8.6		6.5
C9b	monkey	4.4	38.3	2.3	21.3	66.3	
	gorilla	0.0	21.6	0.8	6.8	29.2	
	total	4.4	59.9	3.1	28.1		4.4
C10	monkey	ND	12.3	2.4	0.7	15.4	
	gorilla	ND	62.7	5.0	6.8	74.5	
	total		75.0	7.4	7.5		10.2

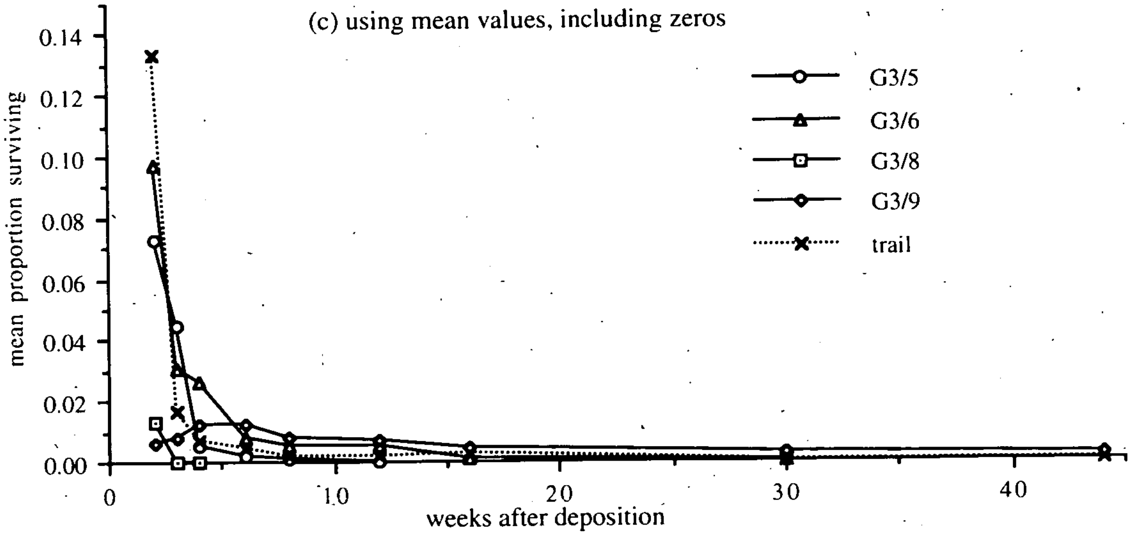
UAPACA

tree	consumer	removed ripe	seeds in dropped fruit.		wasted ripe	total
			Imm	Ripe		
1992						
U51	monkey	25.0	0.4	7.8	14.4	47.6
	gorilla	30.3	12.3	5.3	4.6	52.5
	total	55.3	12.7	13.1	19.0	
U53	monkey	25.7	0.8	18.9	9.9	55.3
	gorilla	7.9	3.5	1.6	1.2	14.2
	chimp	22.3	0.5	4.5	3.4	30.7
	total	55.9	4.8	25.0	14.5	
U55	monkey	39.7	2.7	29.9	27.6	99.9
U56	monkey	47.4	6.3	20.7	25.7	100.1
U8	monkey	52.3	7.5	17.0	15.9	92.7
	gorilla	3.4	0.5	2.0	1.4	7.3
	total	55.7	8.0	19.0	17.3	
U9	monkey	47.0	3.9	14.8	10.3	76.0
	gorilla	7.4	5.2	9.4	2.3	24.3
	total	54.4	9.1	24.2	12.6	
U10	monkey	7.6	32.1	48.1	12.2	100.0
1993						
U1	monkey	31.2	5.6	9.9	14.4	61.1
	gorilla (SB)	2.5	1.5	0.5	0.7	5.2
	chimp	22.2	2.0	2.2	7.3	33.7
	total	55.9	9.1	12.6	22.4	
U2	other monkey	16.8	1.2	29.5	15.5	63.0
	mandrill	10.1	0.7	6.2	4.1	21.1
	gorilla (SB)	8.9	0.0	4.4	2.6	15.9
	total	35.8	1.9	40.1	22.2	
U3	other monkey	29.1	2.2	10.6	10.0	51.9
	mandrill	13.8	2.5	1.8	7.2	25.3
	gorilla (SB)	7.5	1.4	5.3	2.7	16.9
	chimp	4.6	0.2	0.7	0.6	6.1
	total	55.0	6.3	18.4	20.5	
U4	monkey	19.3	12.7	17.1	7.7	56.8
	gorilla (SB)	1.9	1.3	4.3	0.4	7.9
	chimp	14.9	6.1	10.2	4.1	35.3
	total	36.1	20.1	31.6	12.2	
U5	monkey	12.9	1.1	3.1	4.0	21.1
	gorilla (group)	48.6	13.4	10.4	6.6	79.0
	total	61.5	14.5	13.5	10.6	
U6	monkey	7.2	0.0	37.7	8.5	53.4
	chimp	17.7	0.8	7.2	2.4	28.1
	overripe			18.5		18.5
	total	24.9	0.8	63.4	10.9	
U7	monkey	4.8	0.0	10.7	2.2	17.7
	chimp	38.0	0.8	16.4	10.4	65.6
	ape	7.0	3.0	3.8	2.9	16.7
	total	49.8	3.8	30.9	15.5	
U8	monkey	22.7	2.7	28.4	7.8	61.6
	chimp	11.1	0.4	6.4	3.5	21.4
	ape	7.6	0.2	3.0	6.2	17.0
	total	41.4	3.3	37.8	17.5	
U9	monkey	26.4	1.1	62.7	9.8	100.0
U32	monkey	28.9	20.0	4.0	10.4	63.3
	gorilla	17.6	9.6	7.2	2.4	36.8
	total	46.5	29.6	11.2	12.8	
U33	monkey	31.2	1.8	3.4	8.8	45.2
	gorilla	32.2	7.1	9.5	6.0	54.8
	total	63.4	8.9	12.9	14.8	
U34/6	monkey	10.8	4.1	8.3	3.2	26.4
	gorilla	22.0	32.1	16.2	3.2	73.5
	total	32.8	36.2	24.5	6.4	

Appendix D An example of three possible ways of presenting the data on seedling survival: *Ganophyllum*, 1993 (see Chapter 5 for explanation).


(a) using median values, excluding zeros (=Figure 5.7)


(b) using median values, including zeros


(c) using mean values, including zeros

Appendix E Details of the survival and performance of seedlings in gorilla nest sites at the end of the study and since then. Additional data from C.E.G.Tutin & R.J. Parnell.

Ganophyllum		nest site G2/5		
months after deposition		*21.5*	*29*	*35*
no. of seedlings		59	25	18
no. of clumps		7	5	3
median proportion surviving		0.2	0.084	0.063
height of tallest in clump	median	17.5	16.5	24
	range	12-34	15-36	14.5-25
longest leaf in clump	median	66	80	65
	range	31-120	62-138	60-90
max no. of leaves	median	7	7	9
	range	3-13	5-18	7-9

Cola		nest site G2/19			nest site G2/26		
months after deposition		*19.6*	*26.6*	*33*	*19.6*	*26.6*	*33*
no. of seedlings		30	24	22	22	18	17
no. of clumps		7	7	7	9	9	8
median proportion surviving		0.125	0.123	0.113	0.054	0.04	0.037
height of tallest seedling (cm)	median	24.5	26	27	23.5	21	25
	range	12-27	11.5-30	12.5-31	9.5-27	17-31.5	17-31
longest leaf (mm)	median	110	90	95	108	95	90
	range	80-134	65-130	70-140	23-134	60-125	60-125
max no. of leaves	median	5	4	4	3	5	5
	range	3-6	3-6	3-7	1-7	3-8	3-6

Uapaca		nest site G2/81			nest site G2/84			nest site G2/90		
months after deposition		*12.6*	*19.6*	*26*	*12.4*	*19.4*	*26*	*11*	*18*	*24.5*
no. of seedlings		45	15	9	16	nd	9	363	117	68
no. of clumps		6	4	4	8	nd	5	6	5	4
median proportion surviving		0.071	0.043	0.028	0.177	nd	0.1	0.132	0.042	0.028
height of tallest seedling (cm)	median	20.8	40	51	12	nd	18.5	28.5	47	73
	range	12-24.5	13-40	14-54	10-15	nd	12-21	16-34	39-68	47-107
longest leaf (mm)	median	116	130	180	66	nd	120	170	180	195
	range	62-144	85-150	80-190	48-108	nd	70-150	58-222	155-240	170-260
max no. of leaves	median	9.5	15	9	4	nd	9	7.5	10	13
	range	5-11	12-22	6-35	2-7	nd	6-16	3-9	7-28	7-21

		nest site G3/91			nest site G3/95		
months after deposition		*1.6*	*8.6*	*15*	*1.4*	*8.4*	*15*
no. of seedlings		98	26	12	92	20	0
no. of clumps		9	5	4	12	6	
median proportion surviving		0.338	0.233	0.11	0.114	0.034	
height of tallest seedling (cm)	median	9	16	19	9.5	21	
	range	6-13.5	13-30	12-33	6-11	10-24	
longest leaf (mm)	median	na	75	62	na	60	
	range	na	40-130	45-145	na	40-135	
max no. of leaves	median	na	5	9	na	4	
	range	na	4-8	6-16	na	1-7	

		nest site G3/97			nest site G3/103		
months after deposition		*1.4*	*8.4*	*15*	*1*	*8*	*14.5*
no. of seedlings		39	52	30	30	nd	5
no. of clumps		5	7	6	5	nd	2
median proportion surviving		0.817	0.546	0.439	0.216	nd	0.168
height of tallest seedling (cm)	median	6.8	13	17	6.8	nd	43
	range	4.5-11	12.5-18	12-21	5-8.5	nd	23-62
longest leaf (mm)	median	na	75	93	na	nd	22
	range	na	55-105	73-110	na	nd	20-23
max no. of leaves	median	na	5	7	na	nd	15
	range	na	4-7	5-10	na	nd	11-18

NB: G3/93: none left (flooded); G2/89: none left