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Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings

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Summary

Recent studies suggest that regeneration following large-scale disturbance in Kibale National Park, Uganda, is slow or possibly arrested. Here, data is provided on the growth and mortality of seedlings in the forest understory, treefall gaps, and in large gaps that suggest that this pattern of arrested succession can be attributed partially to the fact that this East African community lacks aggressive colonizing tree species. Growth and mortality rates were contrasted for seedlings of six tree species planted in the understory, small gaps, and large gaps for 36 months. Data suggest that species are adapted to gaps of particular sizes. For example, *Uvariopsis congensis* grew faster in the understory than in small gaps, whereas *Warburgia ugandensis* had the lowest mortality rate and highest growth rate in large gaps. Seedlings ($n = 170$) of 15 species were transplanted to assess the response of the tree community to large gap conditions. The limited survival of seedlings in large gaps relative to the understory suggests that only a small proportion of the tree community in this forest regenerates best in gaps larger than those created by the collapse of a single tree. These findings differ from a number of studies conducted in other geographical regions, and suggests that tree communities differ with respect to the proportion of tree species adapted to gaps of particular sizes. This may relate to variation among regions in their history of disturbance and thus frequency of gap formation, size of gaps, and the duration of periods of release. Such variation could imply the existence of a corresponding pattern among tropical forests of differential vulnerability to human disturbance, which tends to create many large gaps.

Key words: deforestation, forest dynamics, gaps, strategies, regeneration

Résumé

Des études récentes suggèrent que la régénération qui suit la perturbation importante qu'a connue le Parc National de Kibale, en Ouganda, est lente, voire même stoppée. On trouve ici les données sur la croissance et la mortalité des pousses dans les sous-bois, dans les trous dus aux chutes d'arbres et dans les éclaircies plus grandes, qui suggèrent que ce schéma d'évolution immobilisée peut être dû, en partie, au fait que

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cette communauté est-africaine manque d'espèces d'arbres agressivement colonisantes. On a comparé pendant 36 mois, les taux de croissance et de mortalité des jeunes pousses de six espèces d'arbres plantées dans les sous-bois, les petits trous et les éclaircies plus grandes. Les données laissent entendre que chaque espèce est adaptée à un espace de taille particulière. Par exemple, *Uvariopsis congensis* croît plus vite dans les sous-bois que dans les petits trous, tandis que *Warburgia ugandensis* connaît son taux de mortalité le plus bas et le taux de croissance le plus élevé dans les trous plus grands. Les plants ($n = 170$) de 15 espèces ont été transplantés pour évaluer la réponse de la communauté des arbres aux conditions qui sont celles des clairières plus grandes. La survie limitée des jeunes plantes dans les clairières par rapport au sous-bois suggère que seule une petite proportion de la communauté des arbres de cette forêt se régénère mieux dans des clairières que dans les trous laissés par la chute d'une arbre. Ces observations diffèrent d'un certain nombre d'études menées dans d'autres régions et suggèrent que les communautés d'arbres diffèrent en fonction de la proportion des espèces adaptées aux trous de différentes tailles. Ceci peut être lié aux variations qui existent selon les régions quant à l'historique des perturbations et donc la fréquence de l'apparition des trous, la taille de ceux-ci, et la durée des périodes de calme. De telles variations pourraient impliquer l'existence d'un schéma correspondant parmi les forêts tropicales diversement vulnérables face aux perturbations dues aux hommes, qui tendent à créer de nombreuses éclaircies.

Introduction

Recent studies suggest that regeneration following large-scale disturbance in Kibale National Park, Uganda, is slow or possibly arrested (Chapman & Chapman, 1997). For example, many areas that were logged almost 30 years ago are now dominated by herbaceous growth, primarily *Acanthus pubescens*, and tree regeneration is limited. A number of mechanisms were suggested to account for this, including the idea that the tree community in this part of East Africa lacks aggressive colonizing tree species. Here, preliminary data are provided to address this idea, offer possible evolutionary explanations for the slow post-disturbance recovery, and practical implications are considered.

Studies of regeneration in tropical forests have highlighted the importance of canopy gaps, typically resulting from treefalls, in determining forest structure (e.g. Denslow, 1980, 1987; Brown & Whitmore, 1992; Whitmore & Brown, 1996). The concept of gap partitioning rests on the assumption that the ability to take advantage of gaps of different sizes involves sets of characters on which natural selection can operate. Therefore, it seems reasonable to argue that if the frequency of gap formation, size of gaps, and/or the duration of periods of release differs among regions, the benefits of different strategies of gap partitioning will also differ. Thus, tree communities in different regions may differ in the proportion of species adapted to exploit gaps of different sizes. A number of authors have used similar logic to explain the structure of particular communities and have suggested that the disturbance regime over evolutionary time will influence the composition of particular communities [e.g. monsoon forests (Whitmore, 1974, 1990); Amazonian caatinga (Coomes & Grubb, 1996)].

As treefalls are episodic in nature, contrasting the frequency with which treefalls occur among different regions is difficult. However, there is evidence that the frequency of large-scale disturbances (e.g. earthquakes, hurricanes) varies among regions. The most complete evidence for geographical variation in large-scale disturbance relates to seismic activity. Approximately 18% of tropical rain forests lie in zones of high seismic activity. This includes 38% of the Indo-Malayan forests and 14% of the South-central American forests, but less than 1% of the African rain forests (Garwood, Janos & Brokaw, 1979). In American and Indo-Malayan forests, the effect of earthquakes can be dramatic. For example, in 1976 two earthquakes struck off the coast of Panama triggering extensive landslides that affected at least 450 km^2 and denuded $\approx$54 km^2 (Garwood *et al.*, 1979). Similarly, in 1935 two earthquakes hit Papua New Guinea and denuded 130 km^2 of forested land (Garwood *et al.*, 1979; Johns, 1986, 1992).

Hurricane (or cyclone) activity also varies geographically. For example, between 1920 and 1972, 362 hurricanes hit Madagascar (Ganzhorn, 1995). Between 1871 and 1964 an average of 4.6 hurricanes affected the Caribbean each year (Walker *et al.*, 1991). The effect of hurricanes on forest systems can be dramatic. When Hurricane Joan touched land in Nicaragua, 80% of the trees were felled (Boucher, 1990). Mainland African forests do not appear to be influenced similarly by hurricanes.

There has been a great deal of debate over the frequency and extent of large-scale fires before the appearance of humans. Leighton & Wirwan (1986) reported on fires in South-east Asia that damaged 3.7 million ha and suggested that massive dieoffs from drought and fire in East Borneo occur once every several hundred years. Sanford *et al.* (1985) discovered that charcoal was common in the soils of mature Amazonian rain forest and suggested that these forests have experienced fires repeatedly over the last 6000 years. Unlike South America (Bush & Colinvaux, 1994) and South-east Asia (Whitmore, 1984), the authors are unaware of descriptions of large-scale natural fires in moist forest in Africa (Tutin, White & Mackanga-Missamdzou, 1996).

If there is geographical variation in the size or frequency of disturbance, with Africa having fewer and smaller disturbances than elsewhere, then one might expect the tree communities in Africa to include relatively few aggressive colonizing tree species that can invade large gaps. This may help to explain the slow rate of succession seen in some African forests after large-scale disturbance (Dean & Milton, 1995; Richards, 1996; Chapman & Chapman, 1997). In this paper, an initial assessment is provided of the idea that some African tree communities have few aggressive colonizing tree species by assessing the growth and mortality of seedlings growing under different conditions. The growth of seedlings of six tree species planted in the understory and small gaps is first described and then mortality rates of seedlings of these species among the understory, small gaps, and large gaps in Kibale National Park, Uganda, are compared. Second, seedling survival in large gaps is compared to that in the understory for 15 species to determine what proportion of this tree community regenerates best in gaps larger than those created by the collapse of a single tree.

Methods

Seedling growth and mortality in understory, small gaps, and large gaps were studied in Kibale National Park, Uganda (0°13′–0°41′ N 30°19′–30°32′ E). Kibale is a moist, evergreen forest (Struhsaker, 1975, 1997; Chapman & Chapman, 1995, 1996) with a relatively species-poor flora (68 tree species were identified in 4.8 ha of vegetation sampling; Chapman *et al.*, 1997). The study was conducted near the Makerere Biological Field Station situated at an elevation of ≈1500 m [mean annual rainfall is 1700 mm (1990–96), mean daily minimum temperature is 15.5°C, and mean daily maximum temperature is 23.7°C (1990–1996)]. Rainfall is well dispersed throughout the year, falling on an average of 166 days per year (Kingston, 1967); however, it is bimodal in distribution. May to August and December to February tend to be drier than other months. On average, the first rains of the year (March–April) are less severe than the September–November rains. Despite these bimodal trends, there is great year-to-year variation in the magnitude, onset, and duration of wet and dry seasons. Plant species nomenclature follows Hamilton (1991).

For six tree species (*Uvariopsis congensis, Mimusops bagshawei*, *Pseudospondias microcarpa, Monodora myristica, Cordia millenii* and *Warburgia stuhlmanni*) seeds were germinated, seedlings were grown in a greenhouse, and seedlings were transplanted into three different conditions. These species were chosen based on their availability and on the ease with which they germinated. Seeds were obtained from frugivore dung and germinated in cloth towelling in individually labelled Petri dishes that were watered daily (Chapman, 1989; Wrangham *et al.*, 1994). After the seeds germinated, they were planted into individual cups that had been filled with topsoil collected from the forest (Chapman & Chapman, 1996).

To ensure that the small gaps monitored were approximately the same age, monitoring of an area of forest for newly formed single treefall gaps was started in August 1990. Brokaw (1982, 1985) was followed to define a gap. Treefall gaps in Kibale are typically not dominated by large-leafed herbs or ferns, rather they are slowly filled by advanced growth of tree species. By August 1993, 11 gaps had been located that averaged 81 m^2 (SD = 50.5, range 45–155 m^2). At this time seedlings that had reached a height of ≈11 cm were transplanted from the greenhouse into randomly-assigned positions in the gaps. Bare-rooted seedlings were planted into slits or holes in the soil and were watered on the day of planting only. To minimize variation caused by within-gap spatial heterogeneity (Brandani, Hartshorn & Orians, 1988), areas within 1 m of the defined edge or where there was freshly exposed soil were excluded. Growth (height) and mortality of seedlings were monitored every 3 months until July 1996 (≈36 months).

To imitate the conditions experienced by a seedling growing in a large gap, such as those created by landslips or hurricanes, an area in which trees had been felled for additions to the field station (≈1 ha), but where construction had been postponed, was selected. In July 1992, 26 seedlings of the focal species were planted into this clearing, spaced 1 m apart. Survival and growth were monitored until July 1995 (≈36 months). Mortality in the large gap was very high for most species, thus, analysis of growth rates was limited to comparisons of understory and small gaps.

To quantify the growth and mortality rate of seedlings in the understory transects were established, and 237 seedlings of the six focal species were planted at 5-m intervals, 1 m from the transect edge. These transects were established between October 1990 and December 1993 as greenhouse-grown seedlings became available, and their survival and growth were monitored every 3 months until June 1996 (a maximum of 45 months). Although the starting date was not the same for each seedling, the growth and mortality is reported for 36 months.

The six focal species are non-pioneer trees (Swaine & Whitmore, 1988) that have large seeds and are capable of germinating in the understory. *Mimusops bagshawei* is a canopy-level to emergent tree with an orange drupe averaging 1.7 cm in length (SD = 1.7, *n* = 25 fruits from six trees). The seeds are oval, with the longest axis averaging 1.1 cm (SD = 1.8, *n* = 25). *Uvariopsis congensis* is a common understory tree that can reach up to 20 m in height. It has a simple red fruit that averages 3 cm in length (range 1.5–5.0 mm, SD = 4.2, *n* = 30 from six trees) and contains between two and seven seeds (mean = 4.5, SD = 1.36, *n* = 30). The seeds average 1.3 cm along their longest axis (SD = 1.2, *n* = 30). *Pseudospondias microcarpa* produces a purple drupe averaging 1.9 cm long (SD = 0.17, *n* = 30 from six trees) with a single spherical seed that averages 1.6 mm in length (SD = 1.1, *n* = 30). *Monodora myristica* is a canopy-level tree that produces large green spherical fruit (16 cm in diameter) which contain many seeds averaging 1.8 cm in length (SD = 1.8, *n* = 30 from six trees). *Warburgia ugandensis* is an abundant canopy-level tree in some areas of Kibale, however, it is rare or absent in other areas of the park. This tree produces abundant ovoid green 3–5 cm long fruit, that contain many flat seeds that average 0.68 mm in diameter (SD = 0.31, *n* = 30 from six trees). *Cordia millenii* is a canopy-level tree that produces a spherical yellow-brown fruit that averages 4 cm long and contains a single 1.9 cm seed (SD = 0.71, *n* = 16 from six trees).

Finally, it is described how a segment of the Kibale tree community responds to large gaps. Given the difficulties of germinating seeds and growing seedlings, seedlings were transplanted in mid-March 1996 from the forest into randomly-selected 1 × 1 m grid cells in a new plot. The plot was located in an area near the field station where trees had been recently felled. In mid-May, new seedlings were planted into grid cells to replace seedlings that had died. To evaluate the effect of transplantation, seedlings were also transplanted back into the forest along transect lines. Seedlings were watered on the day of transplant, but not subsequently. In total, 170 seedlings of 15 species were transplanted (mean of 12 seedlings/species, SD = 3.15). Ninety-one seedlings were planted in the large, gap and 79 seedlings were planted back into the forest as controls (Table 1). Species were selected based on their availability in the forest.

Results

Four different growth and mortality responses were evident among seedlings transplanted into the understory, small gaps, and large gaps (Fig. 1a,b): (1) The growth rate of *Uvariopsis* (Mann–Whitney $P = 0.560$) and *Mimusops* ($P = 0.167$) did not differ between the small gaps and understory. Both species had 100% mortality in large gaps. (2) *Pseudospondias* ($P = 0.06$) and *Monodora* ($P = 0.07$) grew marginally more quickly in small gaps than in the understory. Mortality rates in the understory and small gaps were similar, whereas all seedlings transplanted into the large gap died. (3) *Cordia* exhibited higher growth rates in small gaps ($P = 0.05$) than in the understory. Mortality was highest in the understory, followed by large gaps, and it was lowest in the small gaps. (4) Finally, for *Warburgia,* growth in small gaps and understory conditions did not differ ($P = 0.459$). Unlike the other species, mortality of *Warburgia* in the large gaps was relatively low, and growth was high (four-fold that of small gaps).

In the examination of the community-wide response to large gaps it was found that 81% (42) of the seedlings transplanted into the large gap in mid-March had

Table 1. Characteristics of the tree species planted in the large gap and in the understory. Information on seed size comes from measurements made of 25–30 seeds collected from six trees (mean length and SD are presented) or from Hamilton (1991), height and leaf/leaflet size data are from Hamilton (1991), and dispersal mode is based on personal observations

Family/species	Height (m)	Dispersal mode	Seed size (cm)	Leaf type	Leaf/leaflet size (cm)
Anacardiaceae *Pseudospondias microcarpa*	30	Animal	1.6 (1.1)	Imparipinnate	13 Leaflet
Annonaceae *Uvariopsis congensis*	15	Animal	1.3 (1.2)	Simple	14
Monodora myristica	30	Animal	1.8 (1.8)	Simple	12
Apocynaceae *Funtumia latifolia*	30	Wind	< 0.5	Simple	20
Bignoniaceae *Markhamia platycalyx*	25	Wind	< 2.5 (flat)	Imparipinate	15 Leaflet
Boraginaceae *Cordia millenii*	35	Animal	3.5	Simple	16
Ebenaceae *Diospyros abyssinica*	30	Animal	0.9	Simple	11
Euphorbiaceae *Neoboutonia macrocalyx*	20	Animal	1	Simple	30
Leguminosae *Albizzia grandibracteata*	30	Legume	0.5	Bipinnate	3 Leaflet
Craibia brownii	10	Legume	5	Imparipinnate	13 Leaflet
Cynometra alexandri	50	Legume	5 (flat)	Paripinnate	7 Leaflet
Rosaceae *Parinari excelsa*	45	Animal	3.5	Simple	7
Pygeum africanum	35	Animal	1.3	Simple	15
Warburgia stuhlmanni	40	Animal	0.7 (0.3)	Simple	9
Rutaceae *Teclea nobilis*	25	Animal	0.5	Foliate	14 Leaflet
Sapotaceae *Bequartiodendron oblanceolatum*	15	Animal	1.5	Simple	14
Mimusops bagshawei	40	Animal	1.1 (1.8)	Simple	10
Sterculiaceae *Cola gigantea*	35	Animal	2.5	Simple	30
Ulmaceae *Celtis durandii*	25	Animal	0.5	Simple	9

died by the end of the study ($\approx$140 days, Fig. 2). Of the seedlings that died, survival under large gap conditions averaged 60 days (range 5–140 days). Of the 50 seedlings transplanted back into the forest, only nine died (11%) in the same period of time.

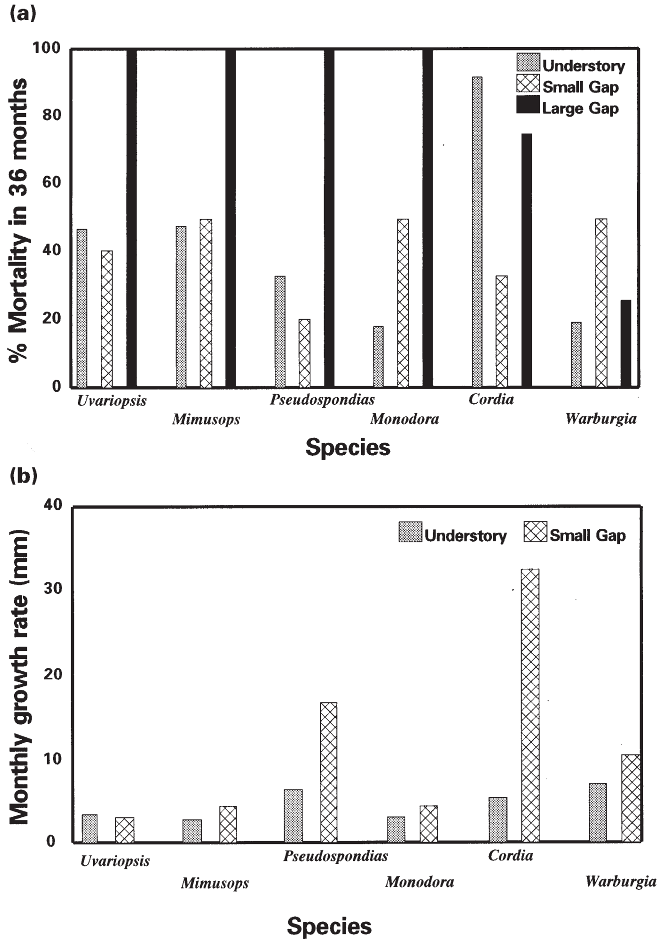

Fig. 1. (a) The percentage of seedlings that were planted in three conditions (understory, small gap, large gap) that died in 36 months (*Uvariopsis congensis* understory $n=65$, small gap $n=5$, large gap $n=4$; *Mimusops bagshawei* $n=5,57,4$; *Pseudospondias microcarpa* $n=5,64,5$; *Monodora myristica* $n=5,22,4$; *Cordia millenii* $n=4,13,4$; *Warburgia stuhlmanni* $n=5,16,4$). (b) The growth rate of seedlings during 36 months of growth under small gap and understory conditions.

Of the 43 seedlings transplanted into the large gap in mid-May, 33 had died (77%) by the end of the study ($\approx$70 days) with an average life span of 33 days (range = 22–64 days).

Discussion

Data on the growth and survival of seedlings in the understory, small gaps, and large gaps suggest that species are adapted differentially to gaps of different sizes. For example, the growth rate of *Uvariopsis* and *Mimusops* did not differ between understory and small gap conditions, whereas *Cordia* grew faster in the small gaps than in the understory, and *Warburgia* had a low mortality and high growth rate in large gaps. The survival of seedlings in large gaps relative to the understory was

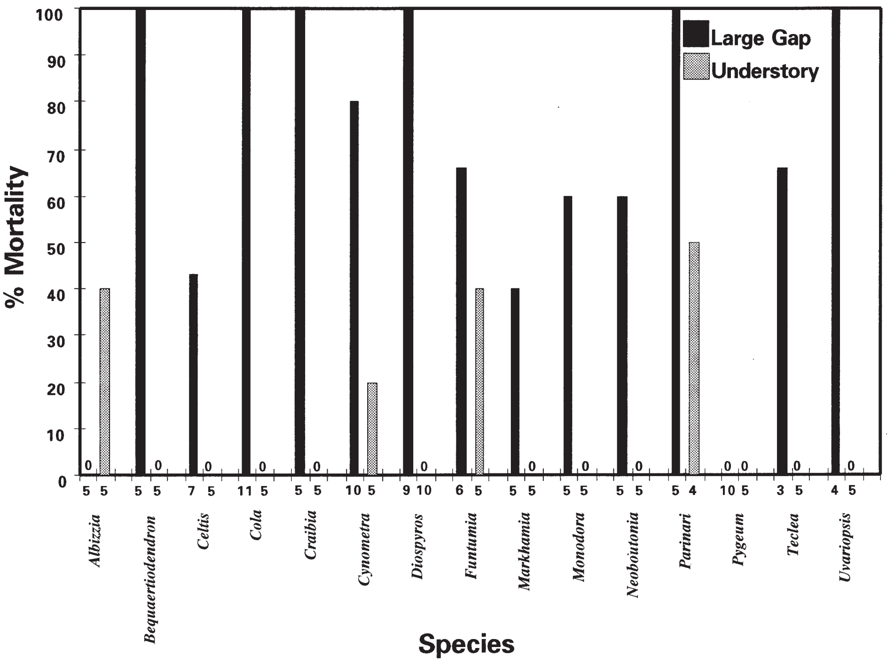

Fig. 2. The mortality of seedlings of a variety of species planted in a large gap (solid bars) and in the understory (hatched bars); 0 indicates that no seedling died in that condition. The number of each species planted in the different conditions is presented below the bar. Species names in full are: *Albizzia grandibracteata*, *Bequartiodendron oblanceolatum*, *Celtis durandii*, *Cola gigantea*, *Craibia brownii*, *Cynometra alexandri*, *Diospyros abyssinica*, *Funtumia latifolia*, *Markhamia platycalyx*, *Monodora myristica*, *Neoboutonia macrocalyx*, *Parinari excelsa*, *Pygeum africanum*, *Teclea nobilis*, *Uvariopsis congensis*.

assessed for 19 species. Kibale has a relatively species-poor flora [68 tree species (> 10 cm d.b.h.) identified in 4.8 ha], thus a fairly large proportion of the flora was evaluated (those not evaluated were typically rare). These data suggest that only a small proportion of the tree community in this forest regenerates best in gaps larger than those created by the collapse of a single tree.

The data on the growth and survival of seedlings in gaps of different sizes in Kibale differ from a number of studies conducted in other regions. This lends support to the idea that tree communities vary among regions in the relative importance of different gap partitioning strategies. Augspurger (1984) and Brokaw (1985) examined recruitment of several tree species in different conditions on Barro Colorado Island, Panama, and found that all of the species exhibited higher growth and survival in the sun than in the shade. Similarly, Pompa & Bongers (1988) documented that in Los Tuxtlas, Mexico, the growth of all species examined was enhanced in large (500 m^2) and small (50 m^2) gaps, and in large gaps the growth was more rapid than in small gaps. In Madagascar, an area that is affected frequently by hurricanes, Ganzhorn (1995) reports that almost all overstory tree species regenerated best in gaps larger than those created by the collapse of a single tree. In contrast, this study in Kibale demonstrated that, for some species, growth in small gaps was not faster than growth in the understory, and for most species there was higher mortality for seedlings grown in large gaps relative to the understory.

If the frequency of disturbance, size of gaps, and/or duration of periods of release associated with gap openings differ between regions, it seems reasonable to expect the benefits of different strategies of gap partitioning to vary. As reviewed in the Introduction, there is evidence to suggest that African forests may experience fewer and less intense scale disturbances than other tropical rain forest regions (e.g. disturbance from seismic activity, hurricanes, and, potentially, from large-scale fires). These patterns of disturbance suggest that the frequency of disturbance and the size distribution of gaps created may differ among regions.

There is evidence from Kibale that the duration of periods of release in large gaps may be relatively short. There are limited comparative data on the period of release associated with disturbance, but in Kibale, large canopy gaps are quickly colonized by an aggressive and persistent herb layer (primarily *Acanthus pubescens*, Kasenene, 1987; Chapman & Chapman, 1997). A handful of studies from different geographical regions has reported similarly that when mature tropical forest is cut and light availability at ground level is increased, colonizing woody and herbaceous species quickly invade and suppress tree regeneration (Fitzgerald & Seldon, 1975; Brokaw, 1983; Kasenene, 1987; Walker, 1994; Walker *et al.*, 1996). The literature on logging of tropical forests also provides a rich source of anecdotal descriptions that suggest that tree regeneration following logging can be retarded by establishment of an aggressive herb or vine layer (Fox, 1976; Yap *et al.*, 1995; Pinnard, Howlett & Davidson, 1996). Based on these descriptions, it seems likely that there are regional differences in whether or not an aggressive herb layer influences the period of release associated with large gap creation.

Most puzzling is the variation among pioneer species from different regions. Although the structure of trees that establish after disturbance can be variable (Grubb & Metcalfe, 1996), Richards (1996) and others have noted the existence of a guild of large-leafed, fast-growing, widely-dispersed pioneer species typically with umbrella-like crowns [e.g. *Cecropia* (Neotropics), *Musanga* (Africa), and some *Macaranga* (Africa, Asia, and Australia)]. In the course of succession, these pioneers establish a canopy beneath which less light-tolerant species can establish and prosper. Such taxa do occur in Kibale (e.g. *Macaranga*, *Polyscias*, and *Neoboutonia*), but they are either primarily limited to swampy and riverine habitats, or else appear chiefly as medium-gap specialists in mature forest (e.g. *Polyscias fulva* in south Kibale, personal observation). In Kibale, large gaps are colonized quickly by aggressive herbs and shrubs that suppresses subsequent regeneration (Kasenene, 1987; Chapman & Chapman, 1997). Of the six species studied in detail, *Warburgia* most closely approximates a tree species that could be classed as an aggressive pioneer, in that it showed a marked growth increase in gap vs. understory conditions. However, the seeds of *Warburgia* are relatively large. Seeds of this size are typically not as widely dispersed as smaller seeds, and thus, they are unlikely to be deposited in large gaps. Therefore they do not recruit aggressively into large gaps in Kibale and are not significant as large gap successional species in a broad functional sense. In the survey of 15 species in the large gap and understory, only *Albizzia* and *Pygeum* had high survival probabilities in the large gap. *Pygeum* is common along forest edges and regenerating areas after a canopy cover is established, but it does not seem to establish in freshly-disturbed areas or in areas dominated by the grasses or herbs that establish soon after disturbance. It may be that it is not successful at competing with the grasses and herbs that are often associated with disturbance.

Albizzia is often found regenerating in some types of disturbed areas, but not in others. For example, it is commonly found emerging from the tall grasses that are associated with abandoned cropland, but it does not establish in logged areas. Its wide distribution throughout abandoned cropland would suggest that its seeds are widely distributed. Thus, unlike *Warburgia,* its failure to act as an aggressive colonizer is not related to its dispersal abilities. However, it had a relatively high mortality level in the understory, suggesting that it may not be able to germinate and survive as a seedling in forest conditions. This suggests that this species grows best along forest edges or in grasslands. In many areas of the world, plants that occupy large gaps created by human disturbance are not treefall gap plants, but rather they are plants that occupy other types of open areas such as forest edges, savannas, or swampy sites (Grubb, 1976; Marks, 1983; Grubb & Stevens, 1996). *Albizzia* appears to be such a plant. *Neoboutonia* also tends to be found in open areas associated with swamps and valley bottoms, but it is not an aggressive colonizer of large disturbances.

In summary, there is evidence that only a small proportion of the Kibale tree community regenerates best in gaps larger than those created by the collapse of a single tree, and even those that do are not aggressive and do not become abundant in disturbed areas. The forest as a whole appears not to be geared toward recovery from large disturbances, and it is suggested that this may relate to this region's history of disturbance. Thus, within this region, the very large disturbances that result typically from human activity may be unusual over recent evolutionary time, and hence may represent a type of disturbance that the native forest is not prepared to deal with effectively. It may be necessary to take into account the existence of this 'functional deficit' in conservation plans for the remnant rain forests in East Africa. These forests, or what little remains of them, may prove particularly vulnerable to encroachment and edge effects, due to their limited capacity to regenerate after large-scale disturbances such as those inevitably caused by human activity.

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