Arrested succession in logging gaps: is tree seedling growth and survival limiting?

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Abstract

Thirty years after selective timber harvest in the Kibale National Park, Uganda, many abandoned logging gaps are dominated by *Acanthus pubescens*, and show little forest recovery. To examine if this arrested successional state was caused by limited tree seedling growth and survival, we planted seedlings of four forest tree species (*Albizia grandibracteata, Mimusops bagshawei, Prunus africana* and *Uvariopsis congensis*) in *A. pubescens*-dominated logging gaps and in control areas of adjacent forest. To assess if clearing *A. pubescens* facilitates forest regeneration, we planted seedlings of two species (*A. grandibracteata* and *U. congensis*) in small clearings cut within the logging gaps. We examined mortality, growth, herbivory and site characteristics among the treatments. Finally, we described the physical attributes of the *A. pubescens*-dominated gaps. Seedlings of all the four species survived and grew equally well in *A. pubescens* and forest treatments, and most site characteristics were also similar. Seedlings planted in clearings grew more than in either forest or *A. pubescens* sites. Very few established trees were found in *A. pubescens* sites, and most of these were near the forest edges. We also discussed the role of elephants (*Loxodonta africana*) and collapsing *A. pubescens* canopies in the maintenance of an arrested successional state in these logging gaps.

Key words: Acanthus, Kibale, regeneration, succession, tropical forest

Résumé

Trente ans après qu'on a procédé à des coupes de bois sélectives dans le Parc National de Kibale, en Ouganda, de nombreuses trouées abandonnées sont dominées par *Acanthus pubescens* et présentent peu de régénération forestière. Pour voir si cet état évolutif figé est causé par la croissance et la survie limitées de jeunes plants d'arbres, nous avons replanté des jeunes de quatre espèces d'arbres de forêt (*Albizia grandibracteata, Mimusops bagshawei, Prunus africana* et *Uvariopsis congensis*) dans une ancienne trouée dominée par *A. pubescens* et dans des aires de contrôle de la forêt voisine. Afin d'évaluer si l'enlèvement des *A. pubescens* facilite la régénération de la forêt, nous avons planté des jeunes de deux espèces (*A. grandibracteata* et *U. congensis*) dans de petites clairières dégagées au sein des trouées. Nous avons examiné la mortalité, la croissance, le taux de prélèvement par les herbivores et les caractéristiques des sites selon le traitement appliqué. Enfin, nous avons décrit les caractères physiques des trouées dominées par *A. pubescens*. Les plants des quatre espèces ont survécu et ont poussé tous aussi bien dans le traitement *A. pubescens* et dans le traitement forestier, et la plupart des caractéristiques des sites étaient aussi semblables. Les jeunes arbres plantés dans les clairières dégagées poussaient mieux que dans les deux autres traitements ci-dessus. On n'a trouvé que très peu d'arbres installés dans les sites à *A. pubescens*, et la plupart d'entre eux se trouvaient près de la lisière des forêts. Nous discutons le rôle des éléphants (*Loxodonta africana*) et de la disparition des canopées de *A. pubescens* dans la persistance d'un stade évolutif figé dans ces trouées.

Introduction

Canopy openings associated with selective logging or other major disturbances of tropical forests increase light reaching the forest floor, and may benefit the growth of the

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established saplings and seedlings (Cannon *et al.*, 1994; Chazdon, 1998). However, in some cases, such gaps become infested with aggressive pioneering herbs, vines and shrubs (Osmaston, 1959; Pinard, Howlett & Davidson, 1996; Ashton *et al.*, 1997; Chapman & Chapman, 1997) that appear to repress tree regeneration, and halt succession towards a mature forest community (Sarmiento, 1997; Chapman *et al.*, 1999). In some cases, pioneer trees are still absent from these sites decades after disturbance (Pinard *et al.*, 1996; Chapman & Chapman, 1997).

The forest in some parts of the Kibale National Park, Uganda, has large gaps created by mechanized logging 30 years ago, when the area was a forest reserve. Many of these gaps are dominated by *Acanthus pubescens* Engl. (Acanthaceae), and have little or no tree regeneration (Chapman & Chapman, 1997). *Acanthus pubescens* is a sub-woody shrub (Eggeling & Dale, 1951), commonly found in swamp forests as well as in disturbed sites and forest margins throughout East Africa.

We investigated whether *A. pubescens*-dominated logging gaps suppress forest succession by reducing the growth and survival of the tree seedlings. We followed the fate of 160 planted tree seedlings of four species for 11 months to assess if seedling mortality was greater in *A. pubescens*-dominated areas than in the adjacent forest. We also planted an additional 40 seedlings of two of these species in parts of the gaps cleared of *A. pubescens* to see if removal of *A. pubescens* enhanced forest regeneration. We examined differences in growth rate and herbivory among the seedlings in each habitat, and compared site characteristics between *A. pubescens*-dominated areas and the adjacent forest.

Materials and methods

This study was conducted from August 1995 through November 1996 in the Kibale National Park, Uganda. The park (766 km^2), located in western Uganda, near the base of the Ruwenzori Mountains (0°13′–0°41′N and 30°19′–30°32′E), is a moist, mid-altitude (920–1590 m) evergreen forest intermixed with swamps, successional forests, grasslands and pine plantations (Chapman & Lambert, 2000). The park was a forest reserve until 1993, and certain areas were selectively logged.

Our study was conducted in two forestry compartments. Compartment K-14 was selectively logged in 1969, with relatively light harvesting, averaging 14 m^3 ha^{-1} or approximately 5.1 stems ha^{-1} (Skorupa, 1988). Compartment K-15 was logged in 1968 and 1969; here, the harvest averaged 21 m^3 ha^{-1} or approximately 7.4 stems ha^{-1} (Skorupa, 1988; Chapman & Chapman, 1997). Within both compartments, logging intensity was spatially heterogeneous, and there are now large tree-less gaps dominated by *A. pubescens*, where logging was presumably intense.

In August 1995, we established 20 sites (nine in K-15 and 11 in K-14) using a stratified-random design, where large *A. pubescens*-dominated gaps were adjacent to the closed-canopy forest. Usually, only a single site was placed in each gap, but three sites were situated in one large gap, and two sites were located within each of the two large gaps. We measured the gap size (canopy edge boundary) and recorded any emergent trees. These gaps were typically dominated by *A. pubescens*, with *Brillantaisia* sp. and *Mimulopsis* sp. also abundant. At each site, we planted one seedling of each test species (described below) under *A. pubescens*-dominated vegetation and another under adjacent closed-canopy forest. Planting sites were chosen haphazardly, and seedlings of each species were chosen at random. The two treatments (*A. pubescens*-dominated gap and forest) were always located within approximately 50 m of one another. At each *A. pubescens* site, we also cleared a small area (≈10 m^2) of all vegetation and planted seedlings of two of the four test species in the clearing (*Albizia grandibracteata* and *Uvariopsis congensis*). Over the course of the study, we cut back *A. pubescens* and vines at these cleared sites monthly, but let the grasses and herbs that established remain. This manipulation tested whether clearing *A. pubescens* accelerated seedling growth and increased survival.

Our experiment used seedlings of four tree species common in Kibale (nomenclature follows Howard, Davenport & Matthews, 1996). Seedlings were either germinated from seed in a shade house or collected from the forest; the origins of the seedlings were randomized for the experiment. All seedlings had cotyledons, and usually a few had true leaves. Seedling heights at the start of the experiment were similar among the treatments.

Albizia grandibracteata Taub. (Leguminosae, Mimosoideae) is a deciduous tree that reaches up to 30 m and is common in secondary forest and edges (Hamilton, 1991). In some areas of Kibale, it forms fairly monospecific stands of even-aged successional forest. Hawthorne & Abu-Juam (1995) reported West African *Albizia* spp. as wind-dispersed, but there is also evidence suggesting animal dispersal (Zanne & Chapman, 2001) and vegetative reproduction (J. Paul & A. Randle, personal observation). *Mimusops bagshawei* S. Moore (Sapotaceae) is a canopy level to emergent trees found most abundantly in unlogged forests. The orange drupes are dispersed by primates (Wrangham, Chapman & Chapman, 1994; Lambert, 1997) and black-and-white-casqued hornbills (*Ceratogymna subcylindricus*; Kalina, 1988). *Prunus africana* (Hook. f.) Kalkman (Rosaceae) is a medium-stature species usually found along the forest edges in Kibale (Hamilton, 1991). The fruits are eaten by *Cercopithecus* monkeys (Lambert, 1997) and medium-sized birds (e.g. barbets, Capitonidae; J. Paul, personal observation). *Uvariopsis congensis* Robyns & Ghesquiere (Annonaceae) is an under- to mid-storey tree, common in both unlogged and selectively logged forests (Chapman & Chapman, 1997). *Uvariopsis congensis* fruits fairly synchronously, producing many red drupes that are eaten and dispersed primarily by primates (Lambert, 1997).

We measured seedling growth and degree of herbivory monthly. The height of each seedling was measured twice with a ruler from the base of the stem to the apical meristem, and the average value was recorded. We used net growth (initial seedling height subtracted from final seedling height) for all analyses. Height measurements made 2 weeks after planting were used as our initial height estimates to allow the seedlings and the surrounding soil to settle. For herbivory, any leaves with missing tissues were counted as damaged. We counted the number of leaves with any herbivore damage and divided them by the total number of leaves for a percent-damaged estimate. Leaflets of *A. grandibracteata* were counted as leaves. Seedling survival at the end of the study was contrasted among treatments with a χ^2-test of independence. Growth and herbivory were compared pair-wise among treatments with paired *t*-tests (paired by site).

To compare seedling abundance between habitats, we examined how many naturally occurring seedlings were found under *A. pubescens* and under forest cover. We sampled a 0.5 m radius around each of our planted seedlings at each site (thus, four plots per site per treatment), and averaged the four plot measurements for analysis. We considered any stem <1 m tall as a seedling. Woody plants were not differentiated from the other plants because the young seedlings of some woody species can appear herbaceous. We compared the number of seedlings between the forest and the *A. pubescens* sites with paired *t*-tests.

We also compared general site characteristics between *A. pubescens*-dominated gaps and the adjacent forest. We measured soil moisture and pH with a hand-held meter. We took one reading in the approximate centre of each site at the end of the dry season (March 1996). We used a densiometer to measure percent canopy cover at the height of each planted seedling. Over the course of the study, this was performed once for each seedling. Contrasts were made with paired *t*-tests. To get a general description of the physical structure of the *A. pubescens*-dominated gaps, we measured the mean canopy height of 14 gaps, as well as the minimum distance from the top of the 60 planted seedlings to the first vegetative stems. All statistical analyses used $\alpha = 0.05$.

Results

After 11 months, survival of the planted seedlings did not differ between forest and *A. pubescens* sites ($\chi^2 = 0.32$; df = 3; $P > 0.90$; Table 1) or between the forest or the *A. pubescens* and the cleared sites ($\chi^2 = 0.17$; df = 2; $P > 0.90$; Table 1). *Prunus africana* had the greatest mortality, while *U. congensis* had the greatest overall survival (Table 1). Seedling net growth differed among treatments for two species. *Albizia grandibracteata* grew taller in the cleared sites than in either the forest or the *A. pubescens* sites (Table 2). Growth of *U. congensis* was significantly less in the *A. pubescens* sites than in either the forest or the cleared sites (Table 2). Herbivory differed between treatments for only one species, *A. grandibracteata*, for which damage was greater in the cleared sites than in either the *A. pubescens* or the forest sites (Table 3). Percent herbivory of *M. bagshawei*

Table 1 Percent of seedlings surviving after 11 month for four tree species ($N = 20$ for each spp.), and total percent surviving for each species and treatment

	Percent survival			
Species	Forest	*Acanthus pubescens*	Cleared	Total
Mimusops bagshawei	75	75	–	75
Prunus africana	40	55	–	48
Uvariopsis congensis	90	95	90	92
Albizia grandibracteata	80	85	95	87
Total	71	78	93	–

Seedlings were planted in forest sites, *Acanthus pubescens*-dominated sites and cleared *A. pubescens* sites.

approached significance for greater damage in the forest sites than in the *A. pubescens* sites (Table 3).

The *A. pubescens* sites had greater percent cover than the forest sites, and the cleared sites had less percent cover than either the forest or the *A. pubescens* sites (Table 4). The cleared sites had greater soil moisture than both the *A. pubescens* and the forest sites (Table 4). None of the sites differed significantly in soil pH, although the cleared sites

Table 2 Mean (±SD) seedling net growth (cm; final height–initial height) of the four focal tree species in each treatment ($N = 20$)

	Net growth (cm)				
Species	Forest	*Acanthus pubescens*	Cleared	*t*-value	*P*-value
Mimusops bagshawei	0.945 ± 2.76	1.193 ± 2.46	–	−0.297	0.770
Prunus africana	1.593 ± 2.32	3.022 ± 5.81	–	−0.964	0.347
Albizia grandibracteata	1.473 ± 4.30	2.088 ± 3.17	–	−0.497	0.625
	1.473 ± 4.30	–	15.718 ± 13.6	−4.417	<0.001
	–	2.088 ± 3.17	15.718 ± 13.6	−4.352	<0.001
Uvariopsis congensis	1.596 ± 1.96	0.310 ± 1.23	–	2.197	0.041
	1.596 ± 1.96	–	1.973 ± 2.30	−0.485	0.633
	–	0.310 ± 1.23	1.973 ± 2.30	−2.980	0.008

The *t*- and *P*-values refer to paired *t*-tests of the two treatments in a given row.

Table 3 Mean (±SD) percent herbivory of the four focal tree species in each treatment ($N = 20$)

	Herbivory (%)				
Species	Forest	*Acanthus pubescens*	Cleared	*t*-value	*P*-value
Mimusops bagshawei	78.5 ± 19.8	71.0 ± 24.9	–	1.963	0.064
Prunus africana	70.1 ± 26.2	76.7 ± 16.2	–	−0.922	0.368
Albizia grandibracteata	54.2 ± 12.5	50.4 ± 13.2	–	1.022	0.319
	54.2 ± 12.5	–	68.6 ± 9.2	−3.947	0.001
	–	50.4 ± 13.2	68.6 ± 9.2	−5.654	<0.001
Uvariopsis congensis	77.0 ± 12.8	77.1 ± 11.3	–	−0.027	0.979
	77.0 ± 12.8	–	80.5 ± 10.2	−1.270	0.219
	–	77.1 ± 11.3	80.5 ± 10.2	−1.096	0.287

The *t*- and *P*-values refer to paired *t*-tests of the two treatments in a given row.

Table 4 Mean (±SD) percent canopy-cover, litter depth, soil moisture, and soil pH of each treatment ($N = 20$)

Species	Forest	*Acanthus pubescens*	Cleared	*t*-value	*P*-value
Canopy cover (%)	97.7 ± 1.37	98.6 ± 1.02	–	−3.851	0.001
	97.7 ± 1.37	–	76.7 ± 11.4	8.006	<0.001
	–	98.6 ± 1.02	76.7 ± 11.4	8.489	<0.001
Litter depth (cm)	4.47 ± 0.95	4.29 ± 1.30	–	0.451	0.657
Soil moisture (%)	66.8 ± 6.45	68.6 ± 7.19	–	−0.789	0.440
	66.8 ± 6.45	–	72.7 ± 8.56	−2.108	0.049
	–	68.6 ± 7.19	72.7 ± 8.56	−2.591	0.018
Soil pH	6.52 ± 0.29	6.51 ± 0.30	–	0.066	0.948
	6.52 ± 0.29	–	6.36 ± 0.36	1.780	0.091
	–	6.51 ± 0.30	6.36 ± 0.36	1.976	0.063

The *t*- and *P*-values refer to paired *t*-tests of the two treatments in a given row.

appeared slightly more acidic (Table 4). The forest sites had more naturally occurring seedlings (mean ± SD = 22.8 ± 10.8) than the *A. pubescens* sites had (5.90 ± 2.5; $t = 6.784$, df = 19; $P < 0.001$). Mean (±SD) canopy height of the *A. pubescens* sites was 4.3 ± 0.6 m, and the minimum height of the *A. pubescens* stems above the planted seedlings was 1.02 ± 0.5 m.

Gap size ranged from approximately 300 m^2 to over 6500 m^2 (mean ± SD = 1363 ± 1463 m^2). In these gaps, 60 trees were found emergent from the vegetation. Of these, 85% (51) were within 5 m of the edge. Excluding trees >20.0 cm DBH, because they were likely taller than *A. pubescens* canopy height at the time of logging, only 35 emergent trees (average 9.8 ± 5.6 cm DBH) were found in an area of over 2.38 ha (or ≈14.7 stems ha^{-1}). Of these 35 trees, the most common species was *A. grandibracteata*, which made up 46% of the emergent trees. Other species included *Celtis africana* Burm.f. (9%), *Erythrina* spp. (3%), *Markhamia platycalyx* Sprague (3%), *Milletia dura* Dunn (9%), *Neoboutonia* spp. (3%), *Newtonia buchananii* Gilbert & Boutique (3%), *Ritchiea* spp. (11%), *Tabernaemontana* spp. (3%) and *Teclea nobilis* Delile (3%).

Discussion

Two lines of evidence suggest that regeneration in the *A. pubescens*-dominated logging gaps is suppressed compared to regeneration in the adjacent forest. First, the *A. pubescens* gaps have lower densities of natural seedlings than the adjacent forest. Secondly, very few small trees emerge from the vegetation within the *A. pubescens* gaps. Of the 35 such trees <20 cm DBH, 40% were covered by vine-tangles, which may further impede their growth. In addition, many trees in the highly disturbed areas of our study site were killed by tree falls (Chapman & Chapman, 1997). Most emergent trees were close to the gap edges, suggesting that these large gaps are filling in from the edges where seed input may be greater and *A. pubescens* may be partially shaded-out by the adjacent forest trees. Chapman & Chapman (1997) found many viable seeds in the soil of the non-gap areas in this logged forest. These seeds either do not reach far into the *A. pubescens* gaps or are unable to germinate and persist in the *A. pubescens*-dominated areas.

Contrary to our expectations, seedling mortality does not appear to be limiting forest regeneration at these sites. *Mimusops bagshawei*, *A. grandibracteata* and *U. congensis* seedlings survived well in all the treatments. In contrast, *P. africana* survived poorly, showing 60% mortality in the forest and almost 45% mortality in the *A. pubescens* sites (Table 1). The absolute difference in canopy cover in the forest and in the *A. pubescens* gaps was small, but still, almost twice as much light could reach the seedlings in the forest as in the gaps. Under-story conditions below *A. pubescens* appear similar to closed forest in regard to soil moisture and pH. The two mature-phase, shade-tolerant species in this study, *U. congensis* and *M. bagshawei*, survived well in both the forest and the gap sites. However, *U. congensis* seedlings did have lower net growth in the *A. pubescens* sites than either in the forest or in the cleared sites. Both these species are dispersed by chimpanzees, which frequent logging gaps to feed on *A. pubescens* pith, and may deposit seeds of these species in the gaps. We noted some natural seedlings of *U. congensis* and a few of *M. bagshawei* in our *A. pubescens* sites. These species may not be particularly hindered by the environmental conditions of the *A. pubescens* gaps, but they also do not appear to flourish.

An important factor preventing tree regeneration in these gaps may be the periodic collapse of *A. pubescens*. Collapses are enhanced by the arching, vine-like growth form of *A. pubescens*, which results in large networks of stems collapsing, often during the rainy season, and sometimes over an area of several square meters. This can smother seedlings. These collapses are compounded by frequent visits by elephants (*Loxodonta africana*; Struhsaker, Lwanga & Kasenene, 1996; Chapman & Chapman, 1997). Osmaston (1959) suggested that the *A. pubescens*-dominated areas were maintained by elephants. During our 14 mo study, over 50% of our plots were visited by elephants. The elephant population size in Kibale has been recently estimated to be *c.* 300 (Chapman *et al.* 1992). *Acanthus pubescens* is a food source for elephants, and open, disturbed sites are the favoured pathways (Struhsaker *et al*., 1996; Vanleeuwe & Gautier-Hion, 1998). Elephants had passed through both our *A. pubescens* and forest sites, but damage was much more perceptible in the *A. pubescens* sites. Elephants killed no experimental seedlings directly, but at least three seedlings in the gaps were smothered by vegetation (and later died) when an elephant knocked a standing dead tree on to a large patch of intertwining *A. pubescens*. The loss of *A. pubescens* stems and additional light provided by the collapses (and elephant trails) may be expected to promote pioneer tree establishment. However, *A. pubescens* quickly re-sprouts and re-invades any open space, initiating another cycle of rapid growth and eventual collapse.

In areas cleared of *A. pubescens*, *A. grandibracteata* seedlings grew more in comparison to the forest or the *A. pubescens* sites, and *U. congensis* grew more than in the *A. pubescens* sites. Thus, clearing areas within the *A. pubescens* gaps and planting appropriate seedlings may be an effective management strategy. In addition, harvesting *A. pubescens* may be a viable multiple-use management option because *A. pubescens* is a common fuel source for cooking stoves in the region (Wallmo & Jacobson, 1998). Also, if these seedlings survive and emerge above the *A. pubescens* canopy, they may attract seed dispersers (Duncan & Chapman, 1999) and create more favourable site conditions for forest succession (McClanahan & Wolfe, 1993).

We suggest that low-seedling recruitment and survival, as a result of high rates of periodic disturbance in *A. pubescens* patches, may result in a steady-state *A. pubescens*-dominated environment. While seedling mortality is not greater in the *A. pubescens* gaps than in the logged forest over a short period, mortality in the *A. pubescens* gaps may be higher because of periodic canopy collapse. If a pioneer sapling does become established, it faces the challenges of strangling by vines, and browsing and crushing by elephants. If the unusual pioneer can escape above the *A. pubescens* and vines, it stands a chance of liberating the gap from its arrested state. Removal of *A. pubescens* may increase the probability of seedling survival.

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References

Ashton, P.M.S., Samarasinghe, S.J., Gunatilleke, I.A.U.N. & Gunatilleke, C.V.S. (1997) Role of legumes in release of successionally arrested grasslands in the central hills of Sri Lanka. *Restor. Ecol.* **5,** 36–43.

Cannon, C.H., Peart, D.R., Leighton, M. & Kartawinata, K. (1994) The structure of lowland rain forest after selective logging in West Kalimantan, Indonesia. *For. Ecol. Manage.* **67,** 49–68.

Chapman, C.A. & Chapman, L.J. (1997) Forest regeneration in logged and unlogged areas of Kibale National Park, Uganda. *Biotropica* **29,** 396–412.

Chapman, C.A., Chapman, L.J., Kaufman, L. & Zanne, A.E. (1999) Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. *Afr. J. Ecol.* **37,** 81–92.

Chapman, L.J., Chapman, C.A. & Wrangham, R.W. (1992) *Balanites wilsoniana*: elephant-dependent dispersal. *J. Trop. Ecol.* **8,** 275–283.

Chapman, C.A. & Lambert, J.E. (2000) Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *Am. J. Primatol.* **50,** 169–186.

Chazdon, R.L. (1998) Tropical forests – Log ''em or leave ''em? *Science* **281,** 1295–1296.

Duncan, R.S. & Chapman, C.A. (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecol. Appl.* **9,** 998–1008.

Eggeling, W.J. & Dale, I.R. (1951) *The Indigenous Trees of the Uganda Protectorate*. Government Printer, Entebbe, Uganda.

Hamilton, A. (1991) *A Field Guide to Ugandan Forest Trees.* Makerere University Printery, Kampala, Uganda.

Hawthorne, W.D. & Abu-Juam, M. (1995) *Forest Protection in Ghana: with Particular Reference to Vegetation and Plant Species*. Forest Department, Republic of Ghana.

Howard, P., Davenport, T. & Matthews, R., Eds (1996) *Kibale National Park Biodiversity Report*. Forest Department, Kampala, Uganda.

Kalina, J. (1988) Ecology and Behavior of the Black-and-White-Casqued Hornbill (Bycanistes Subcylindricus Subquadratus) in Kibale Forest, Uganda. PhD Dissertation. Michigan State University, Michigan, U.S.A.

Lambert, J.E. (1997) Digestive Strategies, Fruit Processing, and Seed Dispersal in the Chimpanzees (Pan Troglodytes) and Redtail Monkeys (Cercopithecus Ascanius) of Kibale National Park, Uganda. PhD Dissertation. University of Illinois, Urbana-Champaign.

McClanahan, T.R. & Wolfe, R.W. (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Cons. Bio.* **7,** 279–288.

Osmaston, H.A. (1959) *Working Plan for the Kibale and Itwara Forests. First revision. Period 1959– 1965.* Uganda Forest Department, Entebbe.

Pinard, M., Howlett, B. & Davidson, D. (1996) Site conditions limit pioneer tree recruitment after logging of a dipterocarp forest in Sabah, Malaysia. *Biotropica* **28,** 2–12.

Sarmiento, F.O. (1997) Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes. *Environ. Conserv.* **24,** 14–23.

Skorupa, J.P. (1988) The Effect of Selective Timber Harvesting on Rain-Forest Primates in Kibale Forest, Uganda. PhD Dissertation. University of California, Davis, CA, U.S.A.

Struhsaker, T.T., Lwanga, J.S. & Kasenene, J.M. (1996) Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *J. Trop. Ecol.* **12,** 45–64.

Vanleeuwe, H. & Gautier-Hion, A. (1998) Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forests. *Afr. J. Ecol.* **36,** 174–182.

Wallmo, K. & Jacobson, S.K. (1998) A social and environmental evaluation of fuel-efficient cook-stoves and conservation in Uganda. *Environ. Conserv.* **25,** 99–108.

Wrangham, R.W., Chapman, C.A. & Chapman, L.J. (1994) Seed dispersal by forest chimpanzees in Uganda. *J. Trop. Ecol.* **10,** 355–368.

Zanne, A.E. & Chapman, C.A. (2001) Expediting reforestation in tropical grasslands: distance and isolation from seed sources in plantations. *Ecol. Appl.* **11,** 1610–1621.

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