

Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forest?

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Abstract

As a result of extensive deforestation, the survival of many tropical forest species may depend on disturbed forests. However, recent studies demonstrate that tree regeneration following logging can be slow, decreasing the conservation value of disturbed forests. Here we test whether the dominating herb, *Acanthus pubescens*, in the understory of logged forest, suppresses tree regeneration in Kibale National Park, Uganda. We compare the establishment, growth, and survival of tree seedlings over 2.5 years between sites cleared of *A. pubescens* and controls. We also consider the role of elephants (*Loxodonta africana*) in inhibiting tree regeneration. Seedling abundance and species richness was greater in cleared than control plots at the start of the study. Seedling abundance decreased over the study, but remained greater in cleared than control plots. Species richness did not vary over the study. However, species composition of the cleared plots was marginally different from control plots at the start, but converged on the composition of control plots by the end of the study. This suggests a common regeneration assemblage derived from reorganisation of species, rather than recruitment of new species. There was no difference in recruitment rates between cleared and control plots. These findings suggest no strong direct effects of the herb on tree regeneration in this disturbed forest. However, when we modelled (i.e., removed) the effect of elephants on regeneration, the abundance of seedlings increased in both plot types and remained reasonably constant over time. The decline in density of regenerating stems over the study was most likely caused by elephants visiting the plots. We conclude that elephants have a far greater effect in suppressing tree regeneration at Kibale than the herb stratum and are ultimately responsible for arresting succession in disturbed forest. However, as intensive logging creates conditions favourable for *A. pubescens*, which is eaten by elephants, the best management intervention is to constrain logging intensities to below levels above which widespread establishment of *A. pubescens* is promoted, thus limiting elephant activity in regenerating areas.

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1. Introduction

Forest area decreased in tropical Africa by approximately 10%, or 0.7% per annum, between 1980 and 1995 (FAO, 1997, p. 139). Faced by this rapid rate of conversion to agricultural and pasture lands, it is increasingly clear that the survival of many forest species will depend on the capacity of disturbed forests to support their populations (Putz et al., 2000; Fimbel et al., 2001). The most prevalent form of disturbed forest habitat with conservation potential is

selectively logged forest (Frumhoff, 1995; Struhsaker, 1997). However, recent studies demonstrate that tree regeneration following logging can be slow or possibly arrested. In Kibale National Park, Uganda, many abandoned logging gaps showed little forest recovery 30 years after selective logging was concluded (Chapman and Chapman, 2004; Paul et al., 2004). In Budongo Forest Reserve, Uganda, Plumptre (1996) found that 50 years of regeneration was insufficient for forest structure to recover to unlogged levels for all variables measured, including basal area and crown height. Slow rates of recovery reduce the conservation value of some disturbed forests. Understanding the mechanisms responsible for arresting succession is necessary to establish the conservation and biodiversity importance of disturbed forests and to design management plans to avoid pathways

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leading to arrested succession, or to facilitate recovery of areas not regenerating at the desired rate.

In Kibale forest, where this study was conducted, the large size of canopy gaps created during logging, the lack of aggressive colonizing tree species, the concentration of elephant (*Loxodonta africana*) activity in logged areas, and an aggressive herb community, are all thought to combine to delay vegetation recovery (Struhsaker et al., 1996; Chapman and Chapman, 1997). Of these factors, the extensive establishment in the understory of shrubs and herbs, in particular the woody herb *Acanthus pubescens* (Acanthaceae), is purported to be the most important factor responsible for the limited tree regeneration and/or arrested succession in areas logged-over 30 years ago (Chapman and Chapman, 1997; Struhsaker, 1997; Chapman et al., 1999; Paul et al., 2004). Subcanopy shrubs, ferns, herbs, and grasses inhibit canopy tree recruitment in many temperate and tropical forests worldwide (Veblen, 1982; Denslow et al., 1991; George and Bazzaz, 1999a,b; González et al., 2002; Slocum et al., 2004). However, elephants (*Loxodonta africana*) frequently use areas of secondary growth (Laws, 1970) and have also been suggested to inhibit regeneration through their browsing and trampling (Eggeling, 1947; Struhsaker et al., 1996). The relative importance of the different factors to inhibiting regeneration is unknown.

Here we test the hypothesis that by dominating the understory of disturbed forest, *A. pubescens* acts as an ecological filter that influences the establishment and survival of tree-seedling species, ultimately suppressing tree regeneration in Kibale National Park, Uganda. We also consider the role that elephant activity plays in inhibiting tree regeneration in this region. By comparing the establishment, growth, and survival of tree seedlings over 2.5 years between sites cleared of *A. pubescens* and adjacent controls (not cleared) in the Kibale forest, we address the following questions: (1) How are tree seedling densities and composition affected by the removal of *A. pubescens*? (2) Is the seedling response to removal of *A. pubescens* a new recruitment or a reorganizational response? (3) Does *A. pubescens* suppress or arrest forest succession by reducing the growth and survival of tree seedlings, as suggested by Paul et al. (2004). (4) What is the relative importance of herb cover and elephants in driving the differences in seedling abundance and richness between *A. pubescens* and *A. pubescens* free sites.

2. Methods

2.1. Study species

A. pubescens (Acanthaceae) is a polycarpic subwoody shrub (Eggeling and Dale, 1951), commonly found in swamp forests, as well as in disturbed sites and forest margins throughout East Africa. It grows in densely packed stands and achieves full height (3–5 m) within a few years (3–4 years) and has a substantial woody stem (5–10 cm DBH) and dense crown of large leaves (Paul et al., 2004). The growth of forest tree seedlings appears to be suppressed beneath *A. pubescens* (Paul et al., 2004). In addition, seedlings beneath *A. pubescens* may

be smothered when large networks of *A. pubescens* stems periodically collapse, either as a consequence of natural senescence or elephant damage (Chapman and Chapman, 1997; Struhsaker, 1997; Paul et al., 2004).

Elephants (*Loxodonta africana*) are known to be significant agents of habitat change in both forest and woodland systems (Laws, 1970; Dublin et al., 1990). In forest systems they have a propensity to use forest clearings and to feed on secondary growth (Laws, 1970; Kasenene, 1987; Struhsaker et al., 1996), and at Kibale, in previously logged areas dominated by herbaceous vegetation, particularly *A. pubescens* (Wing and Buss, 1970; Nummelin, 1990; Struhsaker et al., 1996).

2.2. Study area

This study was conducted from October 2001 to May 2004 in the Kibale National Park, Uganda. The park (795 km²; 0°13′–0°41′N and 30°19′–30°32′E) is a moist, mid-altitude (920–1590 m) evergreen forest intermixed with swamps, secondary forests, and grasslands. The area was a forest reserve until 1993, and certain parts were selectively logged. Our study was conducted in forestry compartment K-15, which was selectively logged in 1968 and 1969 with an average of 21 m³ ha⁻¹ or approximately 7.4 stems ha⁻¹ being harvested (Skorupa, 1988; Chapman and Chapman, 1997). The logging intensity was spatially heterogeneous, and there are now large tree-less gaps dominated by *A. pubescens* adjacent to relatively undisturbed areas.

2.3. Plot layout and sampling of regeneration

In October 2001, we established 20 sites, each with a matched cleared sample plot (*A. pubescens* cleared) and a control plot (not cleared), in large *A. pubescens*-dominated gaps (*Brillantaisia* sp. and *Mimulopsis* sp. were also present) that were adjacent (within 20 m) to closed-canopy forest. Sites were inventoried at 5-month intervals from October 2001 to May 2004, giving six sample periods. Seedlings and saplings of woody species that were ≥10 cm tall were monitored in 10 m × 10 m sample plots at each site. The plots were placed in areas dominated by large *A. pubescens*. To reduce the influence of edge effects by *A. pubescens* on woody seedlings in cleared plots, we removed *A. pubescens* from a 13 m × 13 m area and centrally nested the 10 m × 10 m sample plot within this larger cleared area. All *A. pubescens* and other herbs in the family Acanthaceae were cut down at their base and removed from the cleared plot. Care was taken not to trample or destroy seedlings of woody species already established in the plots. Control plots were located 5 m from cleared sample plots on a randomly selected compass bearing and in *A. pubescens* of the same density, cover, and height as found in the matched cleared plot.

The species, height, and diameter was recorded for all seedlings and saplings that were in the plots at the start of the study and for all individuals that recruited into the plots over the study once they reached 10 cm tall. Individuals were identified and labeled and their fate followed. Elephant damage (trampling and uprooting) to seedlings was recorded each

time a plot was sampled. We cut back *A. pubescens* and vines in the cleared sample plots typically once a month, but left the grasses and other herbs that established. At the end of the study we recorded the dominant vegetation at 1 m intervals along transects aligned north–south and east–west through the centre of each plot. From the latter we estimated the percent cover by grass, shrubs, and invasive weeds in a plot. We also identified and measured the height of trees > 2 m tall in the plot. This manipulation tested whether clearing *A. pubescens* enhanced tree seedling establishment and accelerated seedling growth and increased survival.

2.4. Statistical analyses

The species richness and abundance data are from 2.5 years of repeated samples of sites. Thus, we analysed the main effect of removing *A. pubescens* cover on the abundance and species richness of woody seedlings using repeated measures ANOVA (subjects by trials design). We added the percent ground cover as a covariate in the analysis, effectively accounting for the influence of ground cover on seedling abundance. To meet the assumption of sphericity of the data, the Greenhouse–Geisser adjustment to the degrees of freedom for the *F*-test was used to interpret within-subject trends (Quinn and Keough, 2002).

Data on recruitment and mortality of seedlings were compiled for each period starting with the second sample. The number of individuals that recruited into or died in plot was counted for each sample. These trends were analysed using a randomized blocked ANOVA design with sample period as a random factor and the *A. pubescens* treatment as the fixed factor. These analyses were conducted using SPSS Version 11.5. Seedling growth was measured as stem elongation (height) over a minimum of four periods and converted to monthly growth rate.

To determine tree seedling species response to removal of *A. pubescens*, we compared plots species composition at the start and the end of the study. Because independence between the first and last sample period for a plot cannot be assumed, we used a Mantel test (Sokal and Rohlf, 1995) to evaluate the null hypothesis of no relationship in assemblage structure for a plot across the sample period. We compared the assemblage composition between paired cleared and control plots at the beginning and end of the sample period using a blocked multi-response permutation procedures (MRBP) test, a non-parametric permutation procedure for testing the hypothesis of no difference between pre-defined groups (McCune et al., 2002). Analyses were conducted using PC-Ord for Windows Version 4 (McCune and Mefford, 1999). Species diversity was compared between the start and end of the study and within treatment levels using Species Diversity and Richness Version 2.65 software (Henderson and Seaby, 2001). Species differences between treatments at a site and between the start and end of the study were identified to demonstrate which species responded to removal of *A. pubescens* as new recruits as opposed to a reorganizational response.

We controlled for the effect of elephants on regeneration in the treatment groups by modelling the abundance of stems in a time step (*t*) in the absence of elephant damage. We did this by

replacing in the next time step (*t* + 1) those stems noted as damaged or eaten by elephant. The number of stems added to a plot was adjusted by the mean survival probability of stems from one sample period to the next. The calculation of mean survival probability used only those stems that experienced natural mortality, but not those stems severely damaged or destroyed by elephants. Because data for survival from one time period to the next follows a binomial distribution (i.e., survive or not), we modelled the survival probability using a generalized linear model with a logit link function. This approach assumes that the probability of survival of reinstated stems was the same for the duration of the study. This process allowed us to compare the influence of seedling mortality caused by elephants on seedling abundance against other causes of mortality. In this way, we address the question of whether elephants are driving the system in disturbed forests (Struhsaker et al., 1996).

3. Results

3.1. Seedling abundance

Seedling abundance decreased significantly over the 2.5 years ($F_{2,1,33,9} = 6.24$, $P = 0.004$). However, there was a significant interaction between sample period and the main effect of clearing *A. pubescens*, so that seedling abundance was greater in cleared (mean \pm 1 S.E. = 31.5 ± 4.1 stems per plot per sample period, $n = 120$) than control plots (21.5 ± 4.7 , $n = 120$; $F_{2,1,33,9} = 4.86$, $P = 0.013$) for most sample periods, particularly the first three sample periods, but declined and was similar between treatment plots in the sample periods thereafter (Fig. 1). This difference was evident when the plots were first sampled and likely reflects some initial condition rather than a treatment effect. There was no effect of ground cover on seedling abundance.

3.2. Species richness

There was no effect of clearing *A. pubescens* on seedling species richness. Overall, species richness did not vary

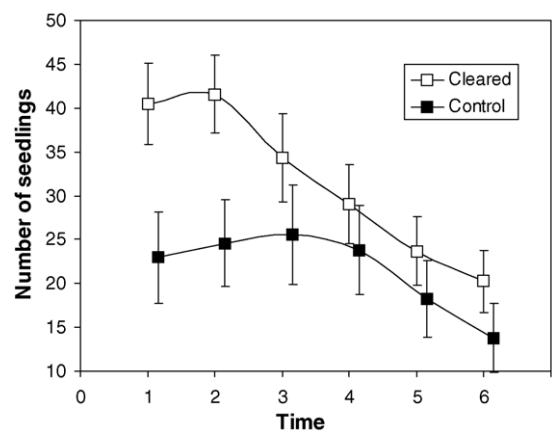


Fig. 1. Mean number of canopy-tree seedlings (\pm 1 S.E.) per plot in each of cleared and control plots over the six sample periods (5-month intervals from October 2001 to May 2004).

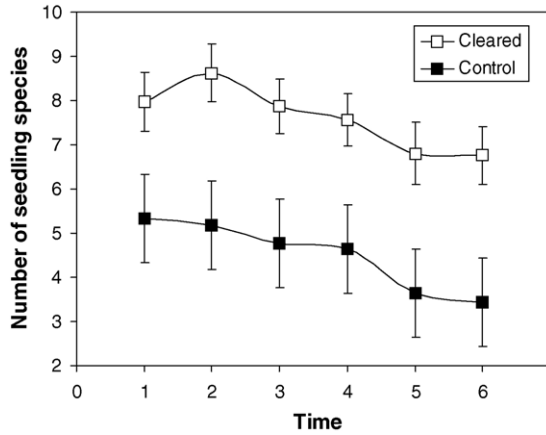


Fig. 2. Mean number of canopy-tree seedling species (± 1 S.E.) per plot in each of cleared and control plots over the six sample periods (5-month intervals from October 2001 to May 2004).

significantly over time ($F_{2,6,97.4} = 1.91, P = 0.16$). There were significantly more species in cleared plots (mean ± 1 S.E. = 7.6 ± 0.6 species per plot per sample period, $n = 120$) than control plots ($4.5 \pm 0.6, n = 120; F_{1,18} = 9.87, P = 0.006$; Fig. 2). This difference was apparent at the start of the study and was not a result of the clearing treatment. Accordingly, there was no interaction between sample period and the main effect of clearing *A. pubescens* ($F_{2,2,40.24} = 0.34, P = 0.735$). Ground cover had a significant effect on species richness ($F_{1,18} = 11.4, P = 0.003$). Initial differences in species richness were maintained throughout, in spite of declining numbers of individuals over the study period.

3.3. Species composition

Species composition of the cleared plots was marginally different from control plots at the start of the study ($P = 0.06$), but approached a common composition in control and cleared plots by the end of the study (Table 1). The composition of control plots (*A. pubescens* intact) did not differ between the start and finish, while species composition in cleared plots at

the end was significantly different from the composition at the start (Table 1). However, species assemblages were not more diverse in cleared plots at the end (Fishers $\alpha = 7.17$) than at the beginning ($\alpha = 7.10$) of the experiment ($P = 0.88$). These findings describe greater species turnover in cleared plots than control plots. Clearly, changes to species composition and the reorganisation of assemblage structure took place mainly in cleared plots. The following species were present in cleared plots at the start of the experiment but not at the end: *Blighia micrantha*, *Dasyalepis eggelini*, *Euadenia eminens*, *Funtumia africana*, *Myrianthus arboreus*, and *Prunus africana*. Only *Erythrina abyssinica* was present in cleared plots at the end, but not at the start.

3.4. Recruitment, mortality, and growth

There was no difference in recruitment rates between cleared (mean ± 1 S.E. = 2.15 ± 0.41 individuals per plot every 5 months, $n = 100$) and control plots ($2.01 \pm 0.47, n = 100; F_{1,194} = 0.065, P = 0.79$). Seedlings were no more or less likely to establish in either treatment group. On the other hand, there was more mortality among seedlings in cleared plots (mean ± 1 S.D. = 6.01 ± 0.52 individuals per plot every 5 months, $n = 100$) than in control plots ($4.75 \pm 0.55, n = 100$). Although this difference was not statistically significant ($F_{1,194} = 2.85, P = 0.09$) we suspect it is an important ecological trend and examine mortality more closely in the next section.

As expected, on average seedlings grew faster in cleared plots (mean ± 1 S.D. = 16.9 ± 27.9 mm month⁻¹, $n = 480$) than in control plots (13.5 ± 33.6 mm month⁻¹, $n = 460$), but this difference was not significant ($F_{1,938} = 3.03, P = 0.082$).

3.5. Are elephants maintaining this system?

All plots experienced some damage over the study (range = 1–37 stems per plot damaged over the study). Damage was greatest in the last four sample periods. Elephant damage was significantly greater in cleared plots (mean ± 1 S.D. = 2.0 ± 2.7 stems per plot, $n = 120$) than control plots (1.1 ± 1.8

Table 1

Results of blocked multi-response permutation procedures (MRBP) and the Mantel test, of the comparison of plot seedling species composition between *A. pubescens* clearing treatment at the start and the end of the study

Data	Groups	Block	T	A	P
Blocked multi-response permutation procedure					
Start	Cleared vs. control	Plot	-1.818	0.037	0.06
End	Cleared vs. control	Plot	0.186	-0.003	0.457
Data	Groups		Standardized Mantel statistic, r		P
Mantel test					
Control	Start vs. end		0.193		0.145
Cleared	Start vs. end		0.855		0.001

The test statistic, *T*, describes the separation between groups. The more negative *T* is, the stronger the separation. The effect size is provided by the chance-corrected within-group agreement (*A*). *A* describes within-group homogeneity, compared to the random expectation. *A* = 1 when all items are identical within groups ($\delta = 0$); *A* = 0 when heterogeneity within groups equals expectation by chance; *A* < 0 with more heterogeneity within groups than expected by chance. *P* = probability of smaller or equal delta. The standardized Mantel statistic ranges from -1 to 1 and measures the degree of association between groups. *P* = proportion of randomized runs with *Z* more extreme or equal to the observed *Z*.

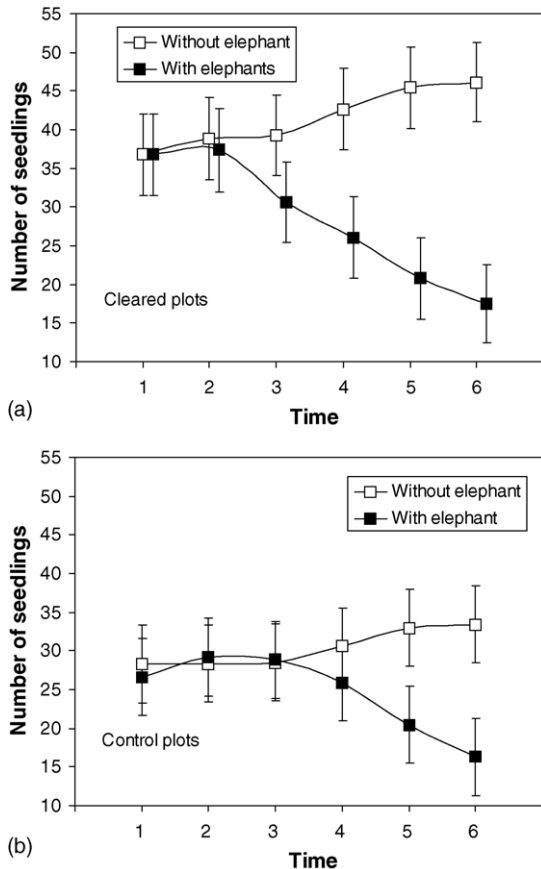


Fig. 3. Mean number of canopy-tree seedlings (± 1 S.E.) per plot with and without the effect of mortality caused by elephant damage for (a) cleared plots and (b) control plots. See Section 2 for an explanation of how elephant damage was controlled for in these analyses.

stems per plot, $n = 120$; $F_{1,219} = 10.88$, $P = 0.001$). The probability of survival of a stem from one time step to the next was lower in cleared plots (0.82) than in controls (0.85).

The abundance of regenerating stems in plots over time was significantly greater when we controlled for elephant damage (cleared plots: $F_{1,6, 60.0} = 70.9$, $P < 0.0001$; control plots: $F_{1,8, 61.4} = 25.4$, $P < 0.0001$; Fig. 3). Elephant damage appears to account for the decline in individuals over the study period, particularly in the later stages of the study.

4. Discussion

Understorey plants, including herbs, have previously been found to suppress or arrest tree species succession in forests (Denslow et al., 1991; Struhsaker, 1997; George and Bazzaz, 1999a,b; Reed and Clokie, 2000; González et al., 2002; Slocum et al., 2004). While we demonstrated that there were more seedling species in the cleared plots than the controls, this was the case before the clearing was carried out and persisted over the study. Seedling abundance, on the other hand, decreased significantly in cleared plots and particularly during the periods of most elephant damage (i.e., the last four sample periods). Thus, in contrast to the findings of other studies of the general effect of the understorey herb layer on tree regeneration, we

conclude that there was no strong direct effect of the herb on either seedling abundance or richness. In addition, the herb stratum per se had no obvious effect on seedling mortality or survival and our findings accord with those of Paul et al. (2004) from the same study area.

However, the direct (herbivory) and indirect (trampling) effects of herbivores, particularly elephant, did reduce regeneration rates beneath *A. pubescens*. When we removed the effect of elephants on regeneration, the abundance of seedlings increased and remained reasonably constant over time. Our data suggest that elephants (and possibly other large herbivores, such as chimpanzees) have a greater effect in suppressing tree regeneration in disturbed forest at Kibale than the herb stratum.

The relative importance of the effect of elephants arises because elephants eat *A. pubescens* and these large and destructive herbivores are attracted to disturbed forests (Wing and Buss, 1970; Nummelin, 1990; Struhsaker et al., 1995). In contrast, at locations where the herb layer is not also a food source, or densities of large herbivores are low, the herb layer per se may have a relatively greater negative effect than herbivory and trampling on tree regeneration. For example, Reed and Clokie (2000) found that in Afromontane forests on Mount Elgon, the dense stands of *Mimulopsis alpina* (Acanthaceae), rather than herbivory by cattle, were responsible for suppressing tree regeneration.

We did not compare tree regeneration in disturbed compartments to regeneration in intact compartments. However, Paul et al. (2004) found lower densities of tree seedlings in *A. pubescens*-dominated areas (including K-15) than the adjacent forest where *A. pubescens* was absent. In addition, regeneration rates of tree species and the recovery of disturbed compartments was much reduced by comparison with unlogged compartments over the longer-term (Chapman and Chapman, 2004). Chapman and Chapman (1997) found abundant viable seeds in the soil beneath *A. pubescens* stands at Kibale, but few seedlings. Together with our results, the above findings suggest no dispersal limitation on tree regeneration in *A. pubescens* stands, but possible recruitment limitation (*sensu* Clark et al., 1999). In other words, while seed supply appears substantial, the recruitment of tree species is suppressed in disturbed forest that is dominated by *A. pubescens*. The conclusion that the direct effect of the herb layer on tree-seedling emergence and establishment is greater than the effect of the herb on growth and survival of established seedlings, is supported by other studies of the effect of understorey herbs or ferns on forest regeneration (George and Bazzaz, 1999a,b; Reed and Clokie, 2000; Standish et al., 2001; Slocum et al., 2004). For example, George and Bazzaz (1999a,b) found that fern cover differentially decreased the emergence of tree seedlings species, as well as their growth and survival, but that mortality of some species below the fern understorey was balanced by mortality resulting from insect herbivory in fern-free areas.

The herb layer and other agents of mortality appear to influence different regeneration life-history stages of canopy-tree species in disturbed forests. Several studies have identified the importance of the interaction of herb cover and elephant

damage on tree regeneration at Kibale (Osmaston, 1959; Struhsaker et al., 1996; Chapman and Chapman, 1997, 2004; Paul et al., 2004). By feeding on *A. pubescens* and favouring disturbed forest for this purpose, elephants ensure that disturbed forest remains disturbed. Because *A. pubescens* quickly resprouts and reinvasades any open space (Paul et al., 2004), elephants create a disturbance cycle that results in the persistence of *A. pubescens* in disturbed forest areas (Wing and Buss, 1970; Laws, 1970; Struhsaker et al., 1996; Paul et al., 2004). Without this elephant disturbance, advanced regeneration by tree species would likely penetrate the herb canopy and eventually recover disturbed forest, albeit at a much slower rate than if *A. pubescens* were not present (Chapman and Chapman, 2004; Paul et al., 2004). Thus, when the effect of the herb stratum is combined with the effect of elephants and other large herbivores (e.g., chimpanzees) on the system, regeneration beneath the herb stratum becomes effectively arrested (Chapman and Chapman, 1997, 2004). The potentially severe effect of elephants on tree regeneration supports the assertion that elephants are primarily responsible for maintaining *A. pubescens*-dominated areas in disturbed forest (Osmaston, 1959; Struhsaker et al., 1996; Chapman and Chapman, 2004) and for the very slow rate of recovery of heavily logged forest at Kibale (Chapman and Chapman, 1997).

We have demonstrated the potential effect of elephants on seedling mortality and tree regeneration. However, the question of whether the mechanism of elephant interference gives rise to a species-specific regeneration assemblage remains to be answered. Because elephant damage to tree seedlings in a plot was incidental to feeding on *A. pubescens* we predicted it would not be related to the species identity of the tree seedling. We further expected that if select species were affected that this would be due to microclimate conditions created by the herb cover and not elephant damage. Comparison of species composition in cleared plots at the start and end of the study showed some convergence in community composition over time on the composition typically found in control plots, implying the non-random loss and replacement of species from cleared sites. The extirpated species *Blighia micrantha*, *Dasylepis eggelinii*, *Euadenia eminens*, *Funtumia africana*, *Myrianthus arboreus*, and *Prunus africana* were replaced by *Bridelia micrantha*, *Erythrina abyssinica*, and *Uvariopsis congensis* in the cleared plots. In the case of *B. micrantha* and *U. congensis*, they doubled in abundance by the end of the study. Indeed, species compositions of cleared and control plots were not significantly different at the end of the study and all plots comprised a similar mix of species suggestive of a regeneration assemblage derived from reorganisation of species rather than recruitment of new species. These data support the hypothesis that only a small proportion of the tree community regenerates best in large gaps (Chapman et al., 1999), and also that a large proportion of species can regenerate equally well in small gaps or under cover (Obiri and Lawes, 2004).

Our data suggest that the removal of the herb *A. pubescens* is desirable for rapid forest recovery as it will likely reduce feeding visits by elephants to disturbed sites (Struhsaker et al., 1996) and promote tree sapling growth. However, the

herb would have to be removed over large areas, so that elephants are not attracted to the vicinity. Further management interventions to aid forest recovery such as enrichment plantings are probably not necessary. As intensive logging creates conditions favourable for *A. pubescens* (Kasenene, 1987; Paul et al., 2004), and there are considerable logistic constraints to the physical removal of *A. pubescens*, perhaps in the future, the best management intervention would be to constrain logging intensities to below a threshold above which widespread establishment of *A. pubescens* is promoted.

5. Conclusion

While the results of this study are generally consistent with earlier studies that examined forest recovery after logging in this region, they are the first long-term investigation of seedling regeneration that allows us to examine the relative impact of suppression by *A. pubescens* and trampling by elephants. The decline in density of regenerating stems over the study was most likely caused by elephants visiting the plots. However, it is the herbaceous understory that attracts elephants to the logged areas in the first place. Thus, the management of areas currently regenerating from logging and dominated by *A. pubescens*, entails the removal of the herbaceous layer over large areas to eliminate or greatly reduce the areas attractiveness to elephants and allow a tree canopy layer to establish.

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