

## Shrub Cover Influence on Seedling Growth and Survival Following Logging of a Tropical Forest

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### ABSTRACT

Logging in tropical forests may create large canopy openings. These gaps provide suitable conditions for some opportunistic shrubs and herbs to take advantage of the surge in resources and rapidly colonize disturbed sites. This dense plant cover may limit forest regeneration by interfering with tree seedling establishment, growth, and survival by altering the light and nutrients available to seedlings, modifying herbivore behavior, or a number of other factors. In Kibale National Park (Uganda), old logging sites are mainly covered by dense stands of *Acanthus pubescens* Engl., which appear to inhibit tree regeneration. We wanted to identify the ecological processes underlying this regeneration collapse. To do so, we designed a factorial experiment to evaluate the influences of herbivory and vegetation cover on the growth and survival of tree seedlings. We compared the survival and growth of transplanted tree seedlings in *A. pubescens* stands and logged forests, in the presence or absence of the understory vegetation layer (logged forest) or vegetation cover (*A. pubescens*), and with or without herbivory. We found no evidence to support the hypothesis that herbivory is significantly higher under dense *A. pubescens* cover. Seedling survival was not influenced by the environment. Seedling growth, however, was positively influenced by the removal of *A. pubescens*, suggesting that changes in resource availability associated with the presence of *A. pubescens*, may be important for regeneration. Our results suggest that sustained cutting of *A. pubescens* cover could foster the growth of established seedlings and could lead to tree regeneration and habitat restoration.

Abstract in French is available in the online version of this article.

*Key words:* *Acanthus pubescens*; Kibale National Park; light; regeneration.

IN TROPICAL FORESTS, DISTURBANCES THAT RESULT IN CANOPY GAP FORMATION ARE IMPORTANT FOR TREE REGENERATION and therefore, contribute significantly to the maintenance of the structure and diversity of the ecosystem (Brokaw 1985). Under natural disturbance regimes, canopy gaps vary in size, causing spatial variation in resources, which might benefit different species (Denslow *et al.* 1998). Anthropogenic activities, mainly logging, in tropical regions over the last century, have altered the natural dynamic of tropical forest ecosystems (Phillips 1997) by creating large gaps where tree regeneration is often inhibited (Royo & Carson 2006). Nowadays, nearly half of all pantropical forests are degraded and fragmented, raising worldwide concerns about the conservation of this diverse biome (Wright 2005). Although pressure from logging is declining in some tropical regions (FAO 2010), many disturbed areas show few or no sign of forest recovery (Goldsmith *et al.* 2011). The lack of tree regeneration in large canopy gaps may partially be caused by aggressive plant species which rapidly colonize disturbed areas.

Disturbed tropical forests are more prone to aggressive colonization by opportunistic exotic or indigenous plant species than undisturbed forests (Fine 2002, Royo & Carson 2006). In fact, the increasing number of empirical studies relating plant invasions

in tropical forests calls into question the apparent resistance of tropical forest to invasion (Martin *et al.* 2009). Large canopy openings caused by logging create a surge in resources, providing suitable conditions for some shrub and herb species to aggressively colonize disturbed areas. The resulting dense plant cover might directly or indirectly interfere with tree seedling establishment, growth, and survival (Chapman *et al.* 1999, Hooper *et al.* 2005, Lawes & Chapman 2006, Chen *et al.* 2008) and might ultimately lead to changes in plant community composition and structure (de Rouw 1991, Brown *et al.* 2006, Minden *et al.* 2010). It can alter both abiotic and biotic conditions: modifying light regime and nutrient supply, impeding seedling growth and survival by exploitative competition (Denslow *et al.* 1998, Holl 1998), or changing herbivore behavior (Braithwaite *et al.* 1989, Reinhart *et al.* 2006, Dutra *et al.* 2011). Indeed, dense herbaceous or shrub cover can benefit herbivores like rodents, which often rely on vegetation as protection against predators (Mattos & Orrock 2010). These indirect consequences of vegetative cover, termed apparent competition, can inhibit forest regeneration (Orrock & Witter 2010).

To reactivate ecological processes essential to the restoration of disturbed tropical forests, researchers and managers need to understand the impacts of such established shrub or herb cover on tree regeneration dynamics. In this study, we conducted an experiment in old logging sites in Kibale National Park (Uganda),

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where the dense cover of the shrub species *Acanthus pubescens* Engl. appears to inhibit the regeneration of tree species (Chapman *et al.* 1999). Our objective was to identify the effects of a dense cover of *A. pubescens* on the regeneration of three common tree species found at Kibale National Park. We hypothesized that tree regeneration failure under dense *A. pubescens* patches is associated with low resources (light, nutrients) and higher herbivory, both associated with the presence of *A. pubescens*. We predicted that seedling survival and growth would be higher (1) in logged-over forest compared with *A. pubescens* patches; (2) in plots in which the *A. pubescens* cover was removed; and (3) in herbivore exclosures.

## METHODS

**STUDY SITE.**—Our study took place at the Makerere University Biological Field Station (MUBFS) in Kibale National Park (KNP; 795 km<sup>2</sup>) in western Uganda (0°13'–0°41' N and 30°19'–30°32' E; Fig. S1) at the foot of the Rwenzori Mountains at 1500 m asl (Chapman & Chapman 1997). The tropical climate of KNP is characterized by mean annual precipitation of 1707 mm (1990–2010 or 1547 mm/yr from 1903 to 2001) falling mainly from March to May and from October to December (C. A. Chapman and L. Chapman, unpubl. data) with the northern section of the park receiving greater precipitation than the south (Chapman *et al.* 2005).

**FOREST COMMUNITY.**—In 2008, it was estimated that 61 percent of the park's area was covered by 30 m-high canopy of intact evergreen rain forest, which represents a transitional state between the lowland and the mountain forests (Chapman & Chapman 1997, Hartter *et al.* 2011). Throughout the park, the canopy is primarily dominated by *Parinari excelsa*, *Aningeria altissima*, *Olea welwitschii*, and *Newtonia buchananii* (Chapman & Chapman 1997). The remaining area of KNP is covered by a mosaic of forests logged *ca* 40 yr ago (Omeja *et al.* 2009), former pine (*Pinus elliottii* var. *elliottii* *Pinus patula*) and cypress (*Cupressus lusitanica*) plantations that were harvested *ca* 15 yr ago, abandoned agricultural lands and marshes.

Before acquiring National Park status in 1993, the KNP area was logged at various intensities. In the northern section of the park, commercial timber extraction resulted in logged forest where the degree of canopy opening is function of the intensity of selective logging (Struhsaker 1997). Some sections were heavily logged (K15, 347 ha logged in 1968–1969 at 21 m<sup>3</sup>/ha, which represents 47% of the total basal area) while others underwent only light to moderate selective logging (K14, 390 ha in 1969 at 14 m<sup>3</sup>/ha; 25% of the total basal area) or were left unexploited commercially (K30, 300 ha) (Chapman & Chapman 1997). Some sections were also logged and spread with herbicide (K13, 622 ha logged in 1968 at 17 m<sup>3</sup>/ha; 50% of the total basal area; Struhsaker 1997).

Nowadays, many disturbed areas created by logging have a dense cover of grasses (*e.g.*, *Pennisetum pupureum*), and shrubs (*e.g.*, *Acanthus pubescens*, *Mimulopsis* sp.), which could reproduce via clonal

growth (Paul *et al.* 2004, Lawes & Chapman 2006). This phenomenon might be associated with the lack of aggressive native pioneer species which should thrive in such sites (Chapman *et al.* 2003). Of these herb and shrub species, *A. pubescens* is the dominant species. Although not an invasive species *sensu stricto* (as it does not expand into the adjacent forests), *A. pubescens* might act as one in this particular environment and inhibit tree regeneration.

**EXPERIMENTAL DESIGN AND SITE SELECTION.**—A split-block experimental design was used to evaluate the influence of mammal herbivores, low vegetation cover (<3 m) and any synergistic interaction between these two factors on the growth and survival of tree seedlings in two environments (logged forests and *A. pubescens* patches). Main plots were selected in the K14 section: seven sites dominated by *A. pubescens* based on patch size and accessibility and seven sites in the adjacent logged forest. Each site dominated by *A. pubescens* is thus paired with one site in the adjacent logged forest, and each pair is considered as a block in the experimental setup. Within each site of any block, we randomly placed four sub-plots of 16 m<sup>2</sup> (4 m × 4 m) and assigned each to one of the following treatments: (1) control; (2) low vegetation cover removal; (3) herbivore exclusion; and (4) low vegetation cover removal and herbivore exclusion. For treatments 2 and 4, we initially removed herbs, shrubs, seedlings and saplings, and regrowth was cut on a weekly basis. In other words, the *A. pubescens* cover was removed in the open patches whereas the understory vegetation was removed in the logged forest. For treatments 3 and 4, we excluded mammal herbivores by protecting seedlings with exclosures fixed to the ground with bendable metal wire. Exclosures were made of thin metal wire (0.05 cm, mesh size: 0.5 cm × 0.5 cm) and measured 45 cm (ht) × 15 cm × 22.5 cm.

**TREE SPECIES SELECTION AND SEEDLING HARVEST.**—We chose tree species according to seedling availability on the forest floor when the experiment began, taking dispersal mode and successional stage into consideration. We selected three species; *Diospyros abyssinica*, *Uvariopsis congensis* and *Tealea nobilis*. For these old growth and animal-dispersed species, seedlings were abundant on the forest floor (Lwanga 2003).

We collected seedlings close to the different study sites to minimize the time between the harvest and the transplantation. Not more than two seedlings were collected under the same parental tree to avoid genetic bias. Seedlings were identified by a local botanist using leaf and cotyledon morphologies and stem color. They were collected by lifting the soil carefully with a machete to prevent root damage. Only *D. abyssinica* and *U. congensis* seedlings with cotyledons were collected for transplanting. As the identification of *T. nobilis* cotyledons is difficult, we collected seedlings with up to eight leaves. All seedlings were transplanted within two hours.

**EXPERIMENTAL SET UP AND INITIAL MEASUREMENTS.**—In July 2010, we transplanted nine seedlings (three of each species) in a central area of 2 m<sup>2</sup> (1 m × 2 m) in each 16 m<sup>2</sup> plot, for a total of 504

seedlings. Seedlings were arranged in three rows of three. Holes in which seedlings were transplanted were deep enough to ensure that the seedling's taproot was not bent. Seedlings in the same row were spaced 15 cm from each other, and each row was 30 cm away from the other. After transplanting seedlings, we took the following initial measurements: seedling height (from ground level to upper leaf stalks), number of leaves and cotyledons, signs of herbivory or disease (both qualitative measurements). To prevent seedling herbivory, the exclosures were set in place immediately after measurement. We repeated monitoring on a monthly basis for 12 mo. In July 2011, seedlings were harvested to measure aboveground biomass (stem and leaves). Seedlings were cut at the root junction and dried in a drying cabinet for 48 h. In the hour following the drying period, seedlings were weighed to obtain the dry aboveground biomass.

**ABIOTIC DATA.**—To evaluate the impact of the environment type (logged forest and *A. pubescens* patches) and the presence of low vegetation cover on resources, we measured irradiance (photon flux density) and nutrient availability. Irradiance was measured in each plot with a LI-COR 189 between 11 am and 1 pm on cloudless days. Ten random measurements were taken above seedlings (1 m × 2 m) in each plot at a height of 20 cm. Within a four-week period, we repeated these measurements three times. Sunflecks were avoided in logged forest plots. To quantify nutrient availability for seedling growth, we used PRS<sup>TM</sup>-probes (Plant Root Simulator-Western Ag Innovations Inc., Saskatoon, Canada). This technology is an alternative to conventional soil analysis. Each pair of probes consists in an anion probe and a cation probe designed to simulate root surface. The resin membrane of the probe is able to exchange ions with soil and provides the potential nutrient supply rate to a plant in micrograms of nutrient absorbed per 10 cm<sup>2</sup> of membrane surface over the burial time. Because seedling root system is mainly found in the superficial soil layers, probes were buried 15 cm into the ground for 4 weeks in two sub-plots within each site; one plot where the low vegetation cover was removed and one plot where the low vegetation cover was left intact. The following nutrients were analyzed: total N, Ca, Mg, K, P, Fe, Mn, Cu, Zn, B, S, Pb and Al.

**STATISTICAL ANALYSIS.**—Of the initial 504 seedlings, we removed from the statistical analyzes the 116 seedlings that died of dryness during the first week following transplantation (23.61% of all seedlings). Of these 116 seedlings, 25 percent were *U. congensis*, 34.5 percent were *T. nobilis* and 40.5 percent were *D. abyssinica*. Overall, seedling mortality occurred mainly in the low vegetation removal plots in *A. pubescens* stands (61.2% of the mortality). For the remaining 388 seedlings, we analyzed the final results for each species separately (*i.e.*, at the end of the 12 mo study period).

Statistical analyzes were conducted as a split-block design to take into account the spatial association between *A. pubescens* and logged forest sites. For each response variable, we defined three factors (environment, low vegetation cover and predation) and their interactions as fixed effects whereas sites and the interaction between sites and the other factors were defined as random

effects. For final survival, we used a split-block logit model to take into account the fact that the observations come from a binomial distribution (dead or alive). This model was fitted to data using the GLIMMIX procedure of SAS (SAS 9.2). To analyze height growth and the number of leaves at the end of the experiment, a split-block ANCOVA model was fitted to data with initial measurements as covariate, using the MIXED procedure of SAS. We used the mean height and the mean number of leaves of the three seedlings in each plot to avoid pseudo replication. We applied a square root transformation to the raw number of leaves to obtain a normal distribution (Sokal & Rohlf 1999). Final mean aboveground biomass, soil nutrient availability and irradiance were analyzed in the same way but without covariates. We applied a log transformation to the raw seedlings biomass to obtain a normal distribution. When significant interactions were observed, post-hoc tests (Waller-Duncan) were conducted to identify which treatment combination was significantly different from the other ones.

## RESULTS

**SURVIVAL.**—After 12 mo, seedling survival averaged  $74.4 \pm 4.9$  percent for *T. nobilis*;  $89.6 \pm 2.6$  percent for *D. abyssinica* and  $79.4 \pm 4.6$  percent for *U. congensis*. Only *U. congensis* had a higher survival in plots where the low vegetation cover was left intact (Fig. 1A, B and C; Table S1). Site, environment and herbivore exclusion did not influence the survival of any of the species.

**HEIGHT GROWTH.**—At the time of inception, seedling height averaged  $6.0 \pm 2.2$  cm for *T. nobilis*,  $4.7 \pm 1.4$  cm for *D. abyssinica*, and  $5.8 \pm 1.4$  cm for *U. congensis*. Low vegetation cover removal increased the growth of *T. nobilis* and *D. abyssinica* in the *A. pubescens* patches, but not in the logged forest, resulting in a significant interaction between the environment and the low vegetation cover removal for these two species (Fig. 2A and B; Table S1). Growth of *U. congensis* seedlings was neither influenced by the environment nor by low vegetation cover removal (Fig. 2C; Table S1). Herbivore exclusion did not influence the growth of any of the species.

**NUMBER OF LEAVES.**—After 12 mo, *T. nobilis* and *U. congensis* seedlings transplanted in the *A. pubescens* plots where the low vegetation cover was removed had a greater number of leaves than all other seedlings, indicating a significant interaction between environment and low vegetation cover removal for the two species (Fig. 3A and C; Table S1). Seedlings of *D. abyssinica* transplanted in plots where the low vegetation cover was removed had more leaves than under an intact low vegetation cover in both environments (Fig. 3B; Table S1). Herbivore exclusion had no impact on the number of leaves per seedling.

**ABOVEGROUND BIOMASS.**—Aboveground biomass of *T. nobilis* and *D. abyssinica* followed the same pattern observed for height growth and the number of leaves per seedling. Seedlings transplanted in *A. pubescens* patches in the plots where the low

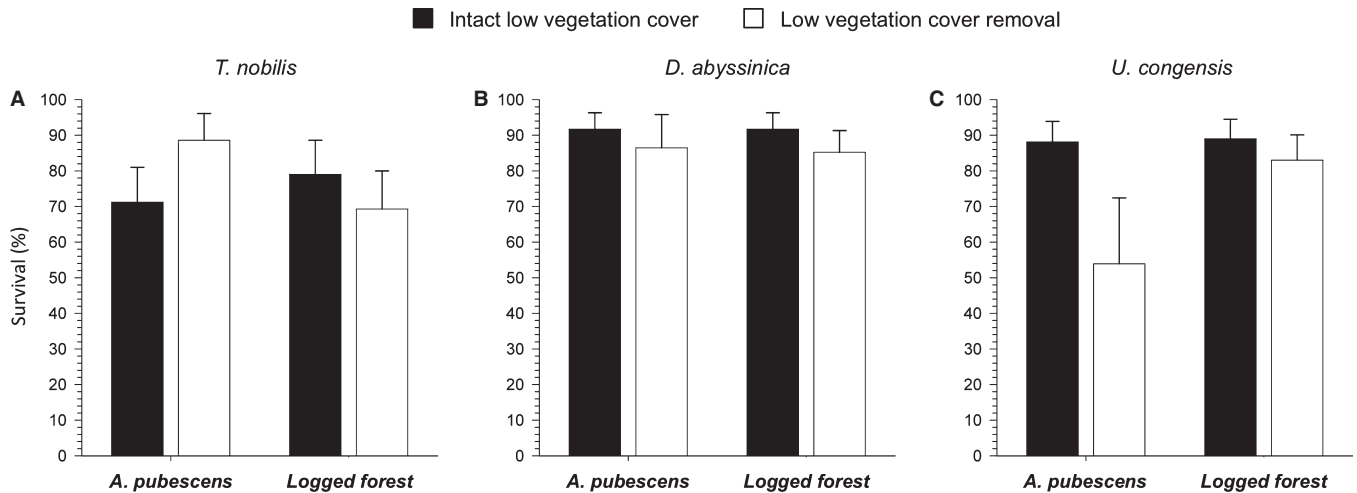


FIGURE 1. Survival  $\pm$  SE (%) of (A) *Teclea nobilis*, (B) *Diospyros abyssinica* and (C) *Uvariopsis congensis* seedlings 12 mo after the inception of the study. Black bars represent plots where the low vegetation cover was left intact; white bars represent plots where the low vegetation cover was removed. The \* indicates a significant main effect of the low vegetation cover removal. Herbivore exclusion had no impact on seedling survival.

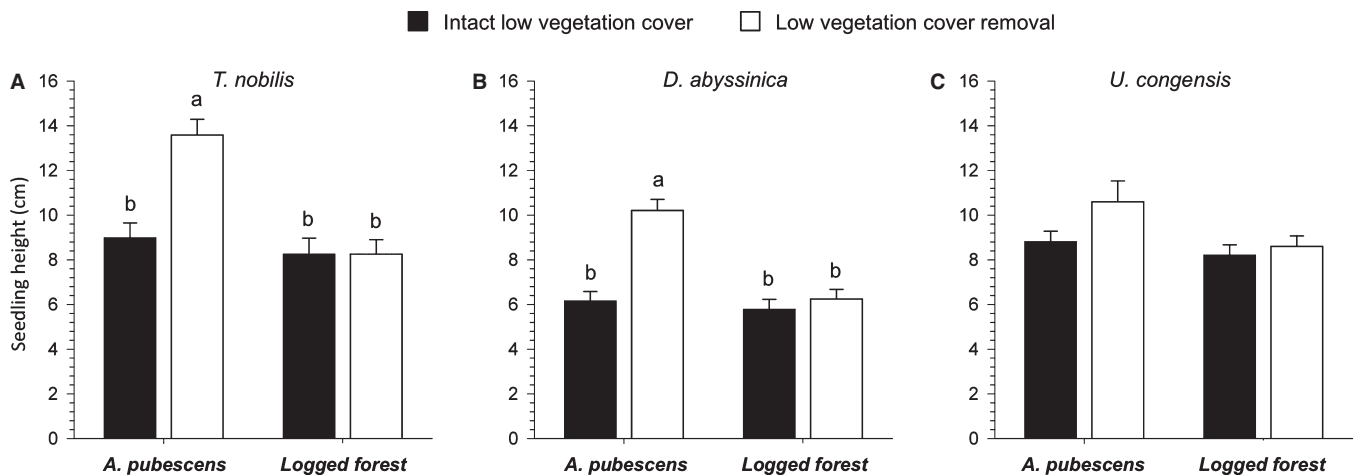


FIGURE 2. Height  $\pm$  SE (cm) of (A) *Teclea nobilis*, (B) *Diospyros abyssinica* and (C) *Uvariopsis congensis* seedlings 12 mo after the inception of the study. Black bars represent plots where the low vegetation cover was left intact; white bars represent plots where the low vegetation cover was removed. Letters a and b indicate significant differences between the different treatment combinations when a significant interaction between Environment and Low vegetation cover was observed. Herbivore exclusion had no impact on seedling height.

vegetation cover was removed had significantly greater biomass than all other seedlings in any other treatment or environment (Fig. 4A and B; Table S1). For *U. congensis*, the positive impacts of low vegetation cover removal on aboveground biomass were observed in both environments (Fig. 4C; Table S1). Herbivore exclusion had no impact on aboveground biomass accumulation.

**ABIOTIC CONDITIONS.**—Only nitrogen and magnesium availability differed among treatments of the experimental design (Table 1). In both environments, total nitrogen was higher in the plots where the low vegetation cover was removed (ANOVA, Low vegetation cover:  $F = 10.1$ ,  $P = 0.008$ ). Magnesium was higher in the *A. pubescens* patches than in logged forests, regardless of the

low vegetation cover treatment (ANOVA, Environment:  $F = 29.0$ ,  $P = 0.002$ ). Results for other nutrients are shown in Table S2. As expected, low vegetation cover removal in both environments resulted in a greater amount of irradiance ( $\mu\text{mol}/\text{s}/\text{m}^2$ ) than under an intact low vegetation cover (ANOVA, Low vegetation cover:  $F = 53.8$ ,  $P < 0.001$ ).

## DISCUSSION

Worldwide impacts of dense shrub or herb cover on forest dynamics, biodiversity and succession have recently been acknowledged (see Royo & Carson 2006). Impacts of native herb/shrub massive colonization in disturbed tropical forests, however, have mainly

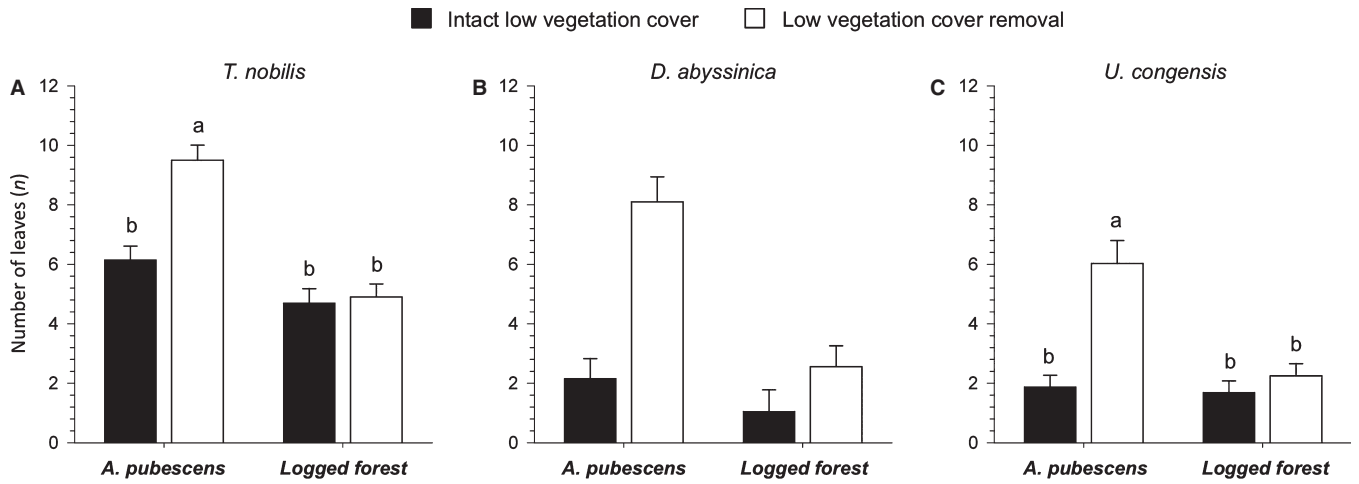


FIGURE 3. Number of leaves ± SE of (A) *Teclea nobilis*, (B) *Diospyros abyssinica* and (C) *Uvariopsis congensis* seedlings 12 mo after the inception of the study. Black bars represent plots where the low vegetation cover was left intact; white bars represent plots where the low vegetation cover was removed. Letters a and b indicate significant differences between the different treatment combinations when a significant interaction between Environment and Low vegetation cover was observed. The \* indicates a significant main effect of low vegetation cover removal. Herbivore exclusion had no impact on the number of leaves of the seedlings.

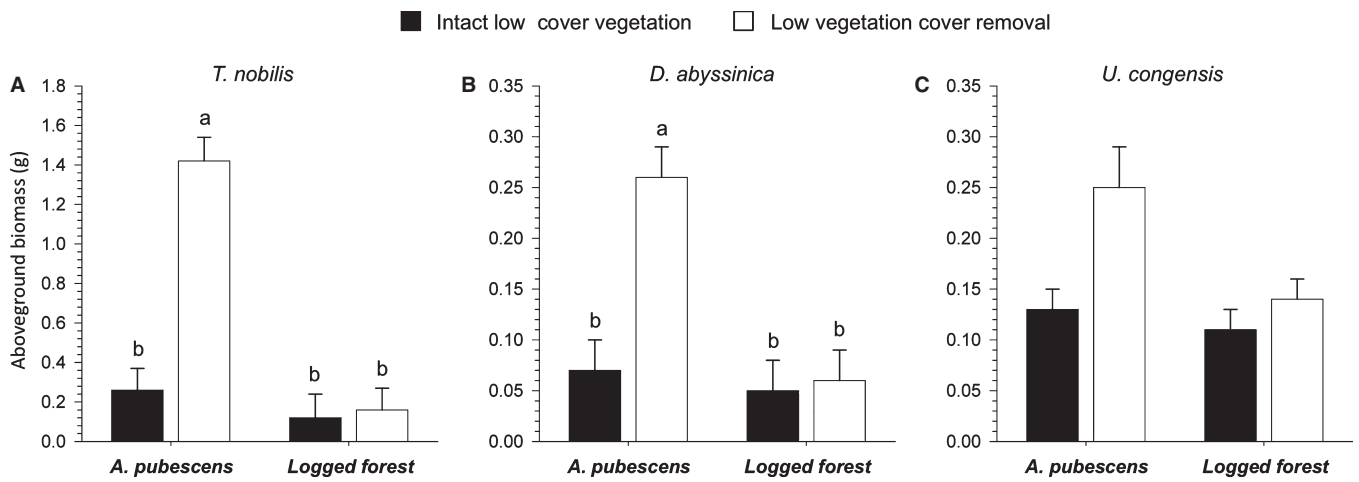


FIGURE 4. Aboveground biomass ± SE (g) of (A) *Teclea nobilis*, (B) *Diospyros abyssinica* and (C) *Uvariopsis congensis* seedlings 12 mo after the inception of the study. Black bars represent plots where the low vegetation cover was left intact; white bars represent plots where the low vegetation cover was removed. Letters a and b indicate significant differences between the different treatment combinations when a significant interaction between Environment and Low vegetation cover was observed. The \* indicates a significant main effect of the low vegetation cover removal. Herbivore exclusion had no impact on seedling aboveground biomass.

TABLE 1. Nutrient availability ± SE (µg/10 cm<sup>2</sup>/4 weeks) and irradiance ± SE (µmol/m<sup>2</sup>/s) in the experimental plots.

|             | <i>Acanthus pubescens</i>   |                              | Logged forest               |                              |
|-------------|-----------------------------|------------------------------|-----------------------------|------------------------------|
|             | Intact low vegetation cover | Removed low vegetation cover | Intact low vegetation cover | Removed low vegetation cover |
| Total N*    | 343.5 ± 49.4                | 417.4 ± 38.9                 | 346.1 ± 44.9                | 450.4 ± 46.9                 |
| Mg**        | 558.9 ± 39.3                | 547.9 ± 44.5                 | 308.1 ± 31.7                | 350.1 ± 45.4                 |
| Irradiance* | 856 ± 532                   | 20 ± 21                      | 17 ± 15                     | 11 ± 7                       |

\*indicates a significant effect of the low vegetation cover removal.

\*\*indicates a significant effect of the environment.



been studied in the Neotropics (Guariguata 1990, Walker 1994) and few studies have been conducted in the Paleotropics (Paul *et al.* 2004, Lawes & Chapman 2006). In Kibale National Park, where a native shrub species (*A. pubescens*) dominates old logging sites (Chapman *et al.* 1999), we used an experimental design to evaluate if the regeneration collapse of tree species in these stands was associated with greater herbivory by small mammals or with habitat changes in light or nutrient availability. We found no evidence to support the hypothesis that herbivory was significantly higher under dense *A. pubescens* cover. However, seedling performance was enhanced by the removal of the *A. pubescens* cover, suggesting that changes in the abiotic environment associated with a dense *A. pubescens* cover might be important.

**SURVIVAL AND GROWTH.**—Species differed in their response to the removal of low vegetation cover. For survival, only *U. congensis* was negatively influenced by the removal of low vegetation cover in both environments, suggesting that this species might be more shade-tolerant than the other two. For height growth and above-ground biomass accumulation, *T. nobilis* and *D. abyssinica* were positively influenced by the removal of *A. pubescens* cover, but not by the removal of low vegetation cover in closed-canopy forest, a result which suggest that *A. pubescens* impede their performance. At last, *T. nobilis* and *U. congensis* number of leaves were positively influenced by the removal of *A. pubescens* cover, but not by the removal of low vegetation in closed-canopy forest whereas the number of leaves in *D. abyssinica* was positively influenced by the removal of the low vegetation cover in both environments.

Overall, these results strongly suggest that changes in habitat light availability produced by dense *A. pubescens* cover is an important factor for seedling growth in *A. pubescens* patches. We hypothesize that removing *A. pubescens* creates conditions similar to those found in canopy gaps, with greater level of photosynthetically active radiation reaching the ground level. By contrast, although removing low vegetation cover under closed-canopy forest did increase the photosynthetically active radiation at the ground level, the magnitude of the increase was different between the two environments (42 and 1.5 times higher in low vegetation removal plots than in plots where low vegetation cover was left intact in *A. pubescens* patches and logged forest, respectively). Previous studies in tropical forest showed that many tree seedlings grow faster when exposed to higher light levels (Kobe 1999, Holste *et al.* 2011) and therefore identify light as the most limiting factor for seedling growth in tropical ecosystems (Percy 2007). This is supported by the fact that regeneration of tropical forests is intimately linked to the presence of natural gaps where light reaches forest ground and modifies biophysical conditions. These light conditions were shown to facilitate the establishment of new seedlings and/or to foster the growth of pre-established seedlings (Brokaw 1985). As pointed out by Young and Peffer (2010), *A. pubescens*, like many other herbs and shrubs, has rapid clonal growth. As a result, although disturbances create gaps in the dense *A. pubescens* cover, the rapid closure of the dense cover quickly reduces light penetration and consequently slows seedling growth.

The greater response of tree seedlings to the removal of the vegetation in *A. pubescens* patches could also be partly explained by differential nutrient availability. Although we acknowledge that trenching could have helped us to discriminate between the effect of below- and aboveground competition (Lewis & Tanner 2000, Schnitzer *et al.* 2005), the woody intricate low stem network of *A. pubescens* makes it very difficult to cut all stem and root connections. We found that nitrogen availability was higher when the low vegetation cover was removed in both environments, while magnesium was higher in the *A. pubescens* patches. Higher nutrient availability following the removal of *A. pubescens* could be linked to a decrease in uptake following the removal of the low vegetation cover. Such results are corroborated by other studies showing that disturbances like clear-cutting increases nitrogen availability in forest soils (Matson & Vitousek 1981, Vitousek & Matson 1985). Differential nitrogen availability could also be the result of higher decomposition rates following the increase in soil temperature over a short time period (Kirschbaum 1995). An increase in soil temperature, however, probably decreased substrate humidity, which could impede decomposition rate. Although the ecological process underlying this different N-availability will remain speculative, the observed significant differences in N availability could lead to better seedling growth. In fact, mountain tropical soils (>1,500 m asl) are often shown to be limited in nitrogen (Tanner *et al.* 1998). As for magnesium, its higher availability in *A. pubescens* patches than in the logged forest, without any influence of low vegetation removal, could contribute to enhance seedling growth as it is an essential element for chlorophyll synthesis (Shabala & Hariadi 2005), although it is unlikely to be the main driver of seedling performance.

**HERBIVORY.**—Herbivore exclusion did not enhance seedling survival, height growth, number of leaves or aboveground biomass in *A. pubescens* patches and in logged forests. This result was unexpected as the most abundant rodent species (*Praomys jacksoni* de Winton, *Hylomyscus stella* and *Hybomys univittatus*) in the study area, even if mainly frugivorous, consume up to 15 percent of leaves and soft stems in their diets (Struhsaker 1997). Moreover, blue (*Cephalophus monticola*) and red (*Cephalophus natalensis*) duikers are as abundant in logged forest as in mature forest (Struhsaker 1997). An increase in their activity under dense cover of *A. pubescens* could have led to greater herbivory, reducing seedling growth and survival. Our results suggest that mammal herbivory is not a major constraint in *A. pubescens* patches. They support those of Tsvuura *et al.* (2007), who showed that the negative impacts of dense *Isoglossa woodii* (Acanthaceae) cover on tree species seedling survival and growth in coastal dune forests of South Africa were not associated with higher mammalian herbivory. Such results contrast with other studies for which shrub and herb cover were shown to modify rodent behavior, limiting establishment and growth of native plant species (Meiners 2007, Orrock *et al.* 2008). Observed evidence of insect herbivory (which was not excluded) on most seedlings suggests that it might be of greater importance for seedling performance, although our data are too qualitative to draw any conclusion. The

lack of a significant impact of mammalian herbivory on seedling performance could reflect the difficulty of detecting such an effect in a complex system. In fact, seed predation trials conducted in the same experimental design revealed high spatial variability in seed predation (V. Duclos, unpubl. data).

## CONCLUSION

Our study experimentally demonstrates that habitat changes produced by *A. pubescens* cover on light availability and, to a lesser extent, on nutrient availability could be detrimental for tree seedling growth. Mammal herbivory, however, does not appear to be a significant factor for seedling performance in such environments. Manipulative studies like ours are lacking in the literature, although they are necessary to understand forest succession dynamics in disturbed habitat in order to design and implement management policies to control the spread and dominance of opportunistic species like *A. pubescens*. From the perspective of habitat restoration, our results strongly suggest that the permanent removal of *A. pubescens* cover is the first step towards the restoration of the forest ecosystem, although characterization of the seed rain in *A. pubescens* patches would also be necessary to determine if artificial seeding is needed.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Results of the paired ANOVAs for seedling survival and aboveground biomass and of the paired ANCOVAs for height and the number of leaves.

TABLE S2. Mean nutrient availability  $\pm$  SE ( $\mu\text{g}/10\text{ cm}^2$ ) in experimental plots.

FIGURE S1. Study site, Kibale National Park, Uganda.

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