

EXPEDITING REFORESTATION IN TROPICAL GRASSLANDS: DISTANCE AND ISOLATION FROM SEED SOURCES IN PLANTATIONS

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Abstract. Where tropical forests have been cleared and abandoned, forest regrowth is often slow. Because of the increasing extent of such degraded lands and desire for these areas to fulfill conservation and ecosystem functions, it has become important to assess mechanisms that accelerate reforestation. In situations where site conditions limit tree establishment, one option to facilitate reforestation is to establish plantations of fast-growing noninvasive trees that ameliorate site conditions and promote the growth of indigenous trees. To quantify the effect of distance and isolation from seed sources on the regeneration of indigenous trees, we evaluated tree species richness and stem density in four pine plantations surrounded by natural forest within Kibale National Park, Uganda, and one isolated pine plantation surrounded by agriculture near Kibale. Tree regeneration in these plantations was compared to that in natural forest and to an anthropogenic grassland similar to those upon which the plantations were established. Tree species richness and stem density were negatively correlated with distance to the plantation edge. The grassland had lower tree species richness and stem density than the isolated plantation, which had lower species richness and stem density than the plantations within Kibale. Leguminous species dominated tree regeneration in the isolated plantation and grassland, whereas small-seeded animal-dispersed species dominated regeneration in plantations adjacent to forest. We suggest that these differences are due to decreased seed dispersal across large distances or unfavorable habitats (e.g., grasslands) and to greater disturbance (e.g., fire) in the isolated plantation and grassland than in plantations within the National Park. This study demonstrates that forest reestablishment can be faster if plantations are established than if grasslands are left to recover without management. However, differences within and among plantations can lead to very different communities with respect to species composition, species richness, and stem density.

Key words: arrested succession; dispersal distance; forest management; grasslands; isolation; plantations; reforestation; seed dispersal; species richness; stem density; tropical forests.

INTRODUCTION

As human populations increase throughout the tropics, local needs for food and fuelwood increase. Concomitant with these changes is an increasing demand from developed countries for tropical timber and agricultural products (Brown and Lugo 1994; Naughton-Treves and Chapman, *in press*). Consequently, forests have been converted rapidly to pasture and agricultural land. Between 1990 and 1995, 12.7×10^6 ha of tropical forest were being converted each year, representing an annual rate of loss of tropical forests of 0.7% (Food and Agriculture Organization of the United Nations 1999). Furthermore, forested lands transformed for agriculture and pasture are frequently abandoned after a few years of use due to soil nutrient depletion and/or invasion by weeds and other pests and pathogens (Brown and Lugo 1994, Dobson et al. 1997).

Forest cover can return to some abandoned areas within years to a few decades through natural succession (Reiners et al. 1994). However, forest succession

often occurs at a much slower rate (Brown and Lugo 1994, Cohen et al. 1995). Succession can be considered arrested (analogous to the inhibition model of Connell and Slayter [1977]) when it does not proceed within several decades. Arrested succession resulting from both anthropogenic and natural causes has been reported throughout the tropics, including Brazil (Nepstad et al. 1991), Colombia (Aide and Cavelier 1994), Ecuador (Zahawi and Augspurger 1999), Sri Lanka (Ashton et al. 1997), Singapore (Corlett 1991), and Uganda (Chapman et al. 1999). For example, in Sri Lanka, Cohen et al. (1995) found that, after forest clearance, the fern, *Dicranopteris pectinata*, and frequent fires inhibited rain forest regeneration. Similarly, in Panama, Brokaw (1983) found sapling density was reduced in dense thickets of the terrestrial bromeliad *Aechmea magdalenae*. Many factors have been suggested to lead to arrested succession, including a lack of tree seeds or resprouts, high seed or seedling mortality (Cohen et al. 1995, Nepstad et al. 1996, Ashton et al. 1997; but see Aide and Cavelier 1994), inhospitable abiotic (e.g., light, temperature, water, moisture, pH, or nutrients) and biotic site conditions (e.g., lack

of mycorrhizal or bacterial symbionts or high predation or disease attack; Janos 1980, Corlett 1991, Guariguata et al. 1995, Nepstad et al. 1996, Otsamo et al. 1996, Johnson and Wedin 1997), competitive dominance of invasive herbs and shrubs (Brokaw 1983, Putz and Canham 1992), and fire (Kellman 1980, Uhl and Kauffman 1990). In regions that receive little rainfall or where flammable biomass accumulates during a dry season, if fire is not suppressed, forest regeneration is typically not initiated.

Under such circumstances, human intervention may be required to release this arrested state of succession and facilitate reforestation. One frequently suggested option to rehabilitate degraded areas is to suppress fire and plant an initial crop of fast-growing trees (Brown and Lugo 1994, Parrotta et al. 1997, Evans 1999). These trees can promote seed dispersal by attracting dispersers and ameliorate site conditions leading to increased seed germination and seedling establishment of native trees (Lugo 1992, Parrotta 1993). Subsequently, the plantation trees could be harvested for profit or left to senesce, leaving a native tree community. If the plantation is to be harvested, a method must be used to reduce the impact of the harvest on the regenerating native trees or the reforestation process may be substantially set back. Such reduced impact methods are not typically used in logging operations.

This study investigated the potential use of tree plantations to facilitate regeneration of indigenous trees in successional arrested grasslands, focusing on how characteristics of the plantations and native species could determine the type of regeneration occurring. We considered three components that may affect tree regeneration in an area: (1) location within plantations (i.e., small-scale distance to plantation edge), (2) large-scale distance and habitat between seed sources and plantations, and (3) dispersal mode of tree species.

Location within plantations may be important because dispersers (e.g., primates, birds, wind) differ in their abilities to carry seeds into plantations and thus may determine regeneration success of native tree species within plantations (Parrotta 1993, Kuusipalo et al. 1995, Parrotta et al. 1997). On a larger scale, plantations may have limited regeneration of animal-dispersed trees when they are not adjacent to seed sources but are surrounded by landscapes serving as barriers to animal dispersers (da Silva et al. 1996, Bierregaard and Stouffer 1997). For example, particular dispersers of forest tree seeds may be wide-ranging but may refuse to cross even small grassland gaps (Tucker and Murphy 1997, Duncan and Chapman 1999).

Further, depending on their dispersal mode (e.g., animal, wind) and seed size, species vary in the distances to which the majority of their seeds are moved from parent trees (Howe 1990, Parrotta 1993). With respect to animal-dispersed seeds, morphological constraints often limit small animals from ingesting and moving large seeds (Wheelwright 1985). Thus, dispersal of

large-seeded species is limited by the movement patterns of large-bodied animals. Dispersal may also depend on how attractive particular sites within the plantation are to dispersers. For example, understory plants may act as focal points of regeneration for species dispersed by animals attracted to fruits of these understory plants. Factors, such as distance to seed sources or availability of understory plants, may differ among sites within a region and lead to variability in tree species composition, species richness, and stem density among sites.

The goal of this study was to determine if pine plantations established in abandoned anthropogenic grasslands in Kibale National Park, Uganda, encouraged native tree establishment and to compare this regeneration with unplanted grassland and natural forest. Specifically, we explored the impacts that distance into plantations and distance and isolation from seed sources had on levels of regeneration. We predicted that plantations would facilitate forest reestablishment as they could attract seed dispersers and ameliorate site conditions hostile to regenerating trees. Increasing small-scale distance into plantations' interiors and large-scale distance and isolation of plantations from seed sources were predicted to impact negatively regeneration; however, the influence of distance and isolation on regeneration was expected to differ depending on the dispersal strategy of the tree species.

While the limiting factors to regeneration in the grasslands were not determined in this study, fire and competition with aggressive grasses and shrubs (Chapman and Chapman 1999, Chapman et al. 1999; Naughton-Treves and Chapman, *in press*) occur in other locations within Kibale and were expected to limit regeneration in grasslands in this study. It should be noted that while four plantations within the park were examined, only one isolated plantation of comparable age and plantation species was accessible. Comparisons between the Kibale plantations and isolated plantation are still useful especially for situations similar to those found in Kibale. Such situations are likely common in the tropics as plantations are often isolated from forests since they are planted for economic purposes close to urban areas or businesses (e.g., tea plantations) for fuelwood or for environmental purposes in areas already deforested (e.g., damaged watersheds).

STUDY SITE AND METHODS

Study site

This study was conducted in Kibale National Park (766 km²; 0°13'–0°41' N and 30°19'–30°32' E), located in western Uganda, ~24 km east of the Rwenzori Mountains. Kibale consists of mature, midaltitude, moist, semideciduous and evergreen forest (57%), grassland (15%), woodland (4%), swamp (4%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusitanica*, *Pinus patula*, *P.*

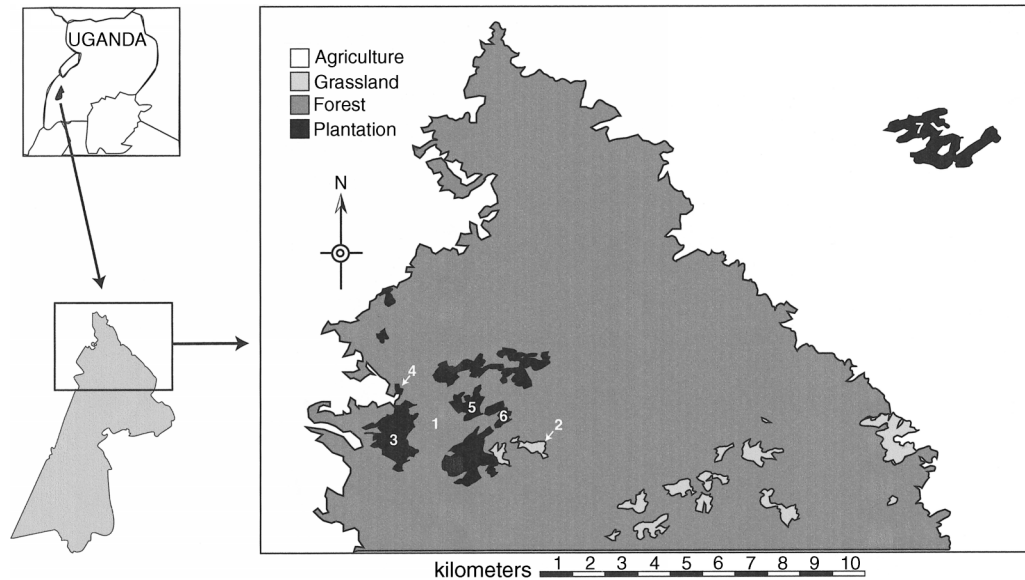


FIG. 1. Kibale National Park, Uganda, and surrounding areas with plantations, grasslands, agriculture, and forest denoted. Study locations: 1 = K-30 forest, 2 = Kyenjura grassland, 3 = Nykatojo Plantation, 4 = Kanyawara Plantation, 5 = Butanzi Plantation, 6 = Nyamusika Plantation, 7 = Oruha Plantation. The map is based on 1996 data from the National Biomass Study, Forestry Department, Government of Uganda.

caribaea, and *Eucalyptus* spp.; Chapman and Lambert 2000). Our work was conducted near the Makerere University Biological Field Station at Kanyawara in the northern portion of the park (1500 m elevation). This region has annual mean daily minimum and maximum temperatures of 15.5 and 23.7°C, respectively, and annual mean rainfall of 1700 mm (1990–1996; C. Chapman and L. Chapman, unpublished data). Rainfall is bimodal, with two rainy seasons occurring from March to May and September to November.

Our study was conducted in four plantations surrounded by forest within Kibale (Nykatojo 86.2 ha, Kanyawara 3 ha, Butanzi 82.4 ha, Nyamusika 28.4 ha, Fig. 1; Kaumi 1989) and one plantation ~7 km from the park and surrounded by agriculture (Oruha 262 ha; Kaumi 1989; Fig. 1). Kibale forest received national park status in 1993. Prior to 1993, it was declared a Forest Reserve in 1932 with the stated goal of providing a sustained production of hardwood timber through selective logging and softwoods from plantations established on anthropogenic grasslands. The grasslands were sites of human settlement; however, the villages were abandoned during the early 1900s due to an increase in rinderpest that killed cattle (Kingston 1967). Pines (especially *P. patula* and *P. caribaea*) and cypress (*C. lusitanica*) were planted on 393 ha of Kibale grassland hilltops between 1953 and 1977 (Kaumi 1989). Plantations were partially to completely weeded to decrease competition between plantation trees and grasses; also some pruning and thinning of plantation trees were done initially (Kingston 1967). During Uganda's political upheaval in the 1970s and 1980s, the plantations were not managed (Kaumi 1989). Since

1993, the planted exotics in Kibale have been extracted (via manual pit saws and portable sawmills) with the ultimate goal of allowing forest regeneration with indigenous species in cleared areas. Pines (*P. patula* and *P. caribaea*) were also planted on Oruha hilltop outside of the park between 1952 and 1967 following methodology similar to what was used in Kibale.

Due to accessibility and similarities in establishment time, we studied portions of Nykatojo and Oruha plantation more intensively than other plantations. The section of Oruha investigated in this study had *P. caribaea* established as the plantation species, while Nykatojo consisted of both *P. caribaea* and *P. patula*. The two *Pinus* species in Nykatojo appeared to influence native tree regeneration in their understories similarly as species richness and stem density were not significant when six *P. caribaea* and six *P. patula* plots paired for distance from plantation edge were compared within Nykatojo. Both areas were planted in 1967–1968. Other sections in Oruha and Nykatojo and the other three Kibale plantations were planted in the 1960s to 1970s (Nykatojo, 1968–1973; Kanyawara, 1963; Butanzi, 1965–1969; Nyamusika, 1962–1974; Oruha, 1952–1968; Kaumi 1989) primarily with *P. caribaea* and *P. patula*.

The forest site, compartment K-30 (300 ha), is near the four Kibale plantations (Fig. 1) and is relatively undisturbed. Prior to 1970, 0.03–0.04 large stems/ha were removed by pitsawyers; the impact on forest structure appears small (Skorupa 1988). The grassland site, Kyenjura (31.5 ha), is the most accessible grassland to the plantations in Kibale (Fig. 1). Grasses (primarily *Pennisetum purpureum*, *Hyparrhenia* spp., or

Cymbopogon afronardus) range between 1.5 and 5 m tall.

Fires have likely burned Kyenjura grassland in the past; however, it has not burned for the past 3 yr, and no record of the frequency of these fires exists. Kyenjura is one of the most isolated grasslands from human contact within Kibale. Other grasslands in and near Kibale are reported to burn frequently and those close to human settlements burn annually. Fires do not appear to burn into closed forest, and no evidence of fire damage is apparent in K-30. No evidence of fire damage is apparent in or recorded for the Kibale plantations, although minor fires burned Oruha in 1972 and 1994. In this study, we cannot separate the effects of fire exclusion from other benefits to regeneration from the plantation trees (e.g., more favorable light environment). The effects of fire exclusion are included as an indirect benefit of plantation establishment just as the benefits of site amelioration are included.

Methods

From May to July 1996, understory tree species richness (species/site) and tree stem density (stems/m²) were quantified in the pine plantations. In 1998, tree species richness and stem density were quantified in the K-30 forest and Kyenjura grassland. Within the focal plantations (Nykatoto and Oruha), seedling, sapling, and tree regeneration were assessed with respect to distance from plantation edge (hereafter termed distance) and various site characteristics. Tree species nomenclature follows the most recent citation of a given species in Hamilton (1991), Katende et al. (1995), or Polhill (1952).

To examine the effect of distance from plantation edge on regeneration, we superimposed a grid on maps of a section of each plantation (Nykatoto, 350 × 700 m; Oruha, 130 × 300 m) and established plots (20 × 5 m) at 30 randomly selected points in the grid for a total of 30 000 m² per plantation.

Trees were divided into three life history stages: seedlings (<0.3 m tall), saplings (≥0.3 m to <2 m tall), trees (≥2 m tall; adapted from Parrotta 1993, Chapman and Chapman 1996). Tree species richness, tree stem density, and site characteristics were measured within each 20 × 5 m plot; due to the expected greater density of stems with decreasing size class, seedlings and saplings were measured in smaller plots within the larger 20 × 5 m plot. In each 20 × 5 m plot, number, species, height, and diameter at breast height (DBH; if ≥2 cm) of all trees were measured, as well as, slope, aspect, and number of stems of the most common understory plants known to be eaten by potential seed dispersers (*Psychotria* sp., Rubiaceae; *Marantochloa leucantha*, Marantaceae; *Ficus asperifolia*, Moraceae; *Aframomum mala*, Zingiberaceae). In a 20 × 1 m strip through the center of each plot, species richness, stem density, and height of saplings were measured. In five 1 × 1 m areas, placed every 4 m

along the central axis of the plot, species richness, stem density, and height of seedlings were measured and percent canopy cover (as measured with a hemispherical canopy densiometer held at arm's length 1 m above the ground) and percent bare ground and ground covered by seedlings, saplings, grass/ferns, herbs, and stones were estimated. In plantations, grassland, and forest, sapling and tree heights were estimated with a 2.5-m pole for reference, and seedling heights were measured directly.

To understand variability in regeneration among plantations within Kibale, we included surveys of Kanyawara, Butanzi, and Nyamusika plantations. Variability among plantations outside the park could not be assessed because relatively undisturbed plantations of comparable age to Oruha were not available. Thirty plots (20 × 5 m) were placed randomly in each plantation; we did not assess the role of distance to plantation edge in these plantations. Number and species only for trees (≥2 m tall), slope, aspect, stem density of *Psychotria* sp., *M. leucantha*, *F. asperifolia*, and *A. mala* were measured as in Nykatoto and Oruha. At five locations 4 m apart along the central axis of the plot, percent canopy cover was measured with a densiometer. In these three plantations, we did not assess the number of seedlings and saplings and percent ground cover.

To compare regeneration in plantations to that in unmanaged grasslands, which represent what the plantation areas would have been like without management, and undisturbed forests, we measured stem density and species richness in unplanted unmanaged grassland (Kyenjura) and in natural forest (K-30) from May to August 1998. Six (50 × 10 m) plots were placed randomly in a grassland within Kibale 30 m off the trail and six (50 × 10 m) plots were placed randomly along trails in the unlogged forest compartment K-30 for a total of 30 000 m² per site (equal to the area sampled in each plantation). The number and species for trees only (≥2 m tall) within each plot were determined.

Analyses

To examine relationships between distance from plantation edge and tree regeneration in Nykatoto and Oruha, we separated all species in the tree size class (seedling and sapling numbers were too small for analysis by category) into various mutually exclusive categories: exotic species (excluding plantation species), indigenous species, or pine species (plantation species); individual species with stem densities high enough to analyze statistically (>47 stems sampled in a plantation); and dispersal types (wind-dispersed, dehiscent legume, large-seeded animal-dispersed species, or small-seeded animal-dispersed species). Most species occurred at too low a density to analyze individually but we were able to analyze the effect of distance on several common species. The criterion of differentiating common from uncommon species was se-

lected because a natural break occurred separating species with at least 47 stems from the next most common species that had only 25 stems per plantation.

With respect to dispersal types, legumes were species in the Fabaceae with dehiscent fruits, heavy seeds, and no apparent attractive structures, such as arils, for animal dispersers, including *Albizia grandibracteata*, *Dichrostachys cinerea*, *Erythrina abyssinica*, and *Milletia dura*; seeds may be wind-dispersed in the pod but individual seeds are unlikely to be wind-dispersed. Wind-dispersed seeds were species with small seeds and wings or hairs. Animal-dispersed seeds were species with fleshy fruits known to be moved by animals based on observations (C. Chapman and L. Chapman, unpublished data). Morphological constraints of frugivores (e.g., gape width) were assumed to limit the maximum size of seeds an animal disperser could move (Wheelwright 1985). Based on seed sizes in Polhill (1952), measurements of a seed collection at Kibale, and observations of different dispersers, large-seeded animal-dispersed species were those whose seeds had length \times width measurements >1 cm² and small-seeded animal-dispersed species were those whose seeds had length \times width measurement of <1 cm². In all analyses, exotics were excluded unless specifically noted.

Stem density and species richness in plantations were compared between Nykatojo and Oruha using Student's *t* tests adjusted for unequal variance for seedlings and saplings and among all plantations using Kruskal-Wallis tests for trees. One-way analysis of variance was not used because in all cases tests for homogeneity of variance were significant ($P < 0.05$). Differences found among medians with Kruskal-Wallis tests were further analyzed using Mann-Whitney *U* tests with the appropriate Bonferroni correction factor. Descriptive statistics are presented as means \pm 1 SD. Tree community similarity was compared among the five plantations, grassland, and natural forest using Morisita's index of similarity (Wolda 1981, Krebs 1989).

Stem density, species richness, and distance from plantation edge were analyzed using the transformation (untransformed or log-transformed: $\log_{10}[x + 1]$) that allowed the best fit of the model assumptions for linearity between species richness or stem density on distance. When data were not normally distributed even after transformation as determined by a Kolmogorov-Smirnov test, they were analyzed using Spearman rank correlations. Stepwise linear regression was used to determine which continuous site characteristics (percent canopy cover; percentage of ground covered by grass/fern, herb, sapling, seedling, and bare; stem density of *A. mala*, *F. asperifolia*, *M. leucantha*, *Psychotria* sp.; distance; slope) influenced stem density and species richness in the plots. Data recorded as percentages were arcsine square-root transformed. Pearson product-moment correlations between vegetation and site characteristics were calculated for both Nykatojo

and Oruha. Correlations were only performed on data having stem densities of 18 or greater within the plantations.

RESULTS

Comparisons among plantations and grassland

Various site characteristics were compared among the five plantations. Oruha had a greater mean slope (21.1°) than other plantations (Nykatojo 12.2°, Nyamusika 11.5°, Butanzi 10.6°), while Kanyawara had a smaller mean slope (5.7°) than other plantations. Nykatojo (22.4%) had a more open canopy than Oruha (13.1%) and both were more open than the other three plantations (Nyamusika 2.5%, Butanzi 2.9%, Kanyawara 2.2%). Percent ground cover was only measured in Nykatojo and Oruha. Nykatojo (9.7%) and Oruha (8.8%) had very similar levels of ground covered by woody saplings and neither contained exposed stone. Nykatojo had greater seedling cover (0.5%) and herb cover (72.4%) than Oruha (0.2% and 37.4%, respectively), while Oruha had greater grass/fern cover (30.1%) and bare ground (23.2%) than Nykatojo (7.0% and 10.4%, respectively). Vines were equally common in all plantations. The four Kibale plantations were all located within the same forest matrix.

Indigenous seedlings, saplings, and trees grew at higher densities in pine plantations within Kibale than the isolated pine plantation at Oruha (seedlings: Nykatojo 2.5 per 5 m², Oruha 0.6 per 5 m², $t = 2.93$, $P < 0.01$; saplings: Nykatojo 9.5 per 20 m², Oruha 3.8 per 20 m², $t = 2.57$, $P < 0.05$; trees: Fig. 2; all tree comparisons are significant at $P < 0.05$). All five plantations had greater indigenous tree stem density than Kyenjura grassland located within Kibale. Oruha had more exotic stems than the other plantations and Kyenjura grassland and forest within Kibale. The natural forest had similar stem densities to Butanzi plantation but nearly double the density of the other Kibale plantations (Fig. 2).

More tree stems of large- and small-seeded animal-dispersed species were found in the Kibale plantations than Oruha and the grassland. The natural forest had more large-seeded animal-dispersed and wind-dispersed stems than the other areas (Fig. 3; all comparisons are significant at $P < 0.05$). Kyenjura grassland had fewer total stems of any dispersal type than the five plantations and no wind- or large-seeded animal-dispersed stems; the grassland contained a greater percent of legumes than animal-dispersed stems. Species with animal-dispersed seeds (both large and small) dominated the regeneration in the natural forest, whereas species with small animal-dispersed seeds were most common in the Kibale plantations. Species with legumes dominated the regeneration in Oruha (Fig. 3). More species grew in the natural forest than in any other area; however, more species grew in the Kibale

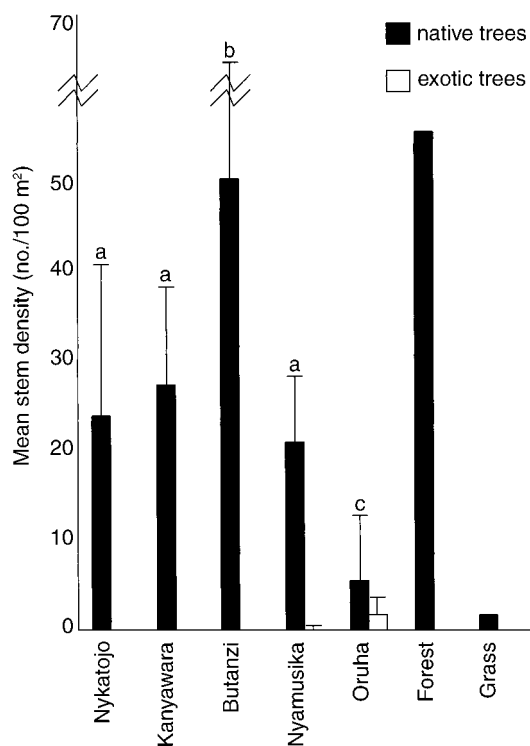


FIG. 2. Mean stem density (≥ 2 m tall) of native tree species and exotic tree species (excluding planted pines) per 100 m² in four plantations contiguous to forest, one forest, and one grassland in Kibale National Park, Uganda, and one isolated plantation (Oruha) near the park. Results of Kruskal-Wallis tests with Mann-Whitney *U* multiple comparisons using a Bonferroni correction factor are denoted with letters. Comparisons are made between plantations within the native category. Bars with the same letter are not statistically different at $P > 0.05$. Standard deviation bars and statistical analyses are presented for all plantations but do not appear for forest and grassland because plot size in forest and grassland was 500 m², and thus standard deviation could not be calculated for a 100-m² area (mean [1 SD] stems per 500 m²: forest plot, native = 280.5 [94.6], exotic = 0.2 [0.4]; grassland plot, native = 8.3 [6.0], exotic = 0.0 [0.0]). Note that low means (e.g., number of exotics in the forest) are not detectable in this figure.

plantations than either the isolated plantation or grassland (Table 1).

Kyenjura grassland results (Figs. 2 and 3) are supported by a separate study which surveyed six grasslands within Kibale (including Kyenjura grassland) in which all trees (> 2 m) were recorded in 20 plots (40 \times 50 m). Stem density in the grasslands was much lower than the plantations and forest (native trees, 1.35 per 100 m²; large-seeded animal-dispersed, 0.008 per 100 m²; small-seeded animal-dispersed, 0.045 per 100 m²; wind-dispersed, 0.005 per 100 m²; dehiscent legumes, 1.27 per 100 m²). Further, only 15 species occurred in the entire 40 000 m² grassland area surveyed (as compared to 3000 m² surveyed in the forest and each plantation in this study).

Variability among the four Kibale plantations was

high for tree (≥ 2 m) stem density, species richness, and species composition. Mean stem density per 100 m² plot ranged from 21.3 in Nyamusika to 51.0 in Butanzi (Fig. 2). The high density of regeneration in Butanzi was due primarily to a few species, such as *Diospyros abyssinica*, Ebenaceae (17.1 ± 14.9 stems/100 m², $n = 30$) and *Teclea nobilis*, Rutaceae (10.2 ± 13.2 stems/100 m², $n = 30$), which together comprised 53.7% of all stems growing in Butanzi. Fewer stems of *D. abyssinica* (6.6 ± 8.9 stems/100 m², $n = 30$) and *T. nobilis* (0.1 ± 0.4 stems/100 m², $n = 30$) were growing in Nykatojo. The plantations also varied in the relative importance of different dispersal types. Kany-

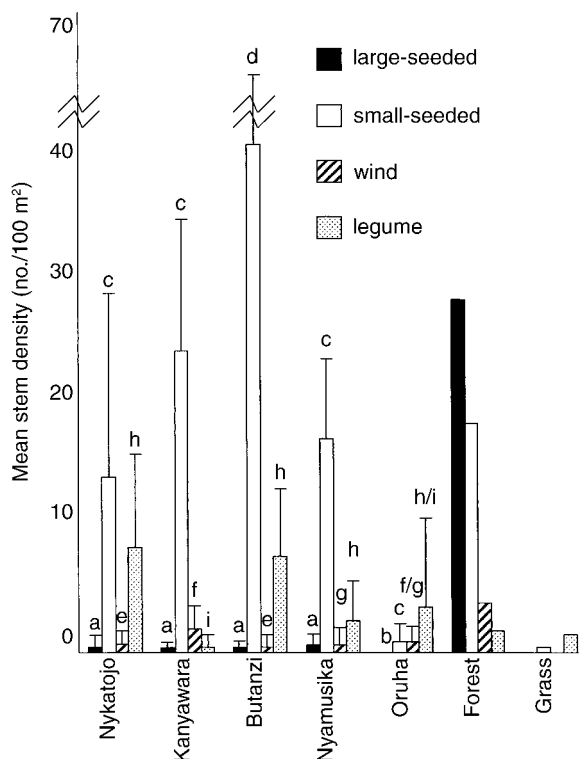


FIG. 3. Mean stem density (≥ 2 m tall) of large-seeded animal-dispersed, small-seeded animal-dispersed, wind-dispersed, and legume tree species per 100 m² area in four plantations contiguous to forest, one forest, and one grassland in Kibale National Park, Uganda, and one isolated plantation (Oruha) near the park. Results of Kruskal-Wallis tests with Mann-Whitney *U* multiple comparisons using a Bonferroni correction factor are denoted with letters. Comparisons are made between plantations within the dispersal type categories. Bars with the same letter are not statistically different at $P > 0.05$. Standard deviation bars and statistical analyses are presented for all plantations but do not appear for forest and grassland because plot size in forest and grassland was 500 m², and thus standard deviation could not be calculated for a 100-m² area (mean [1 SD] stems per 500 m²: forest plot, large-seeded, animal-dispersed = 145.2 [74.4], small-seeded, animal-dispersed = 93.3 [57.2], wind-dispersed = 20.5 [14.7], legume = 9.0 [6.6]; grassland plot, large-seeded, animal-dispersed = 0.0 [0.0], small-seeded, animal-dispersed = 1.2 [1.9], wind-dispersed = 0.0 [0.0], legume = 7.2 [5.5]).

TABLE 1. Native (and exotic) total species richness (number of species/30,000 m²) and Morisita's index of similarity of tree species (≥ 2 m tall) for five plantations in and near Kibale National Park, Uganda, and an unlogged portion of natural forest and grassland inside the park.

Site	Total species	Similarity (Morisita's index)					
		Nykatojo	Kanyawara	Butanzi	Nyamusika	Oruha	Natural forest
Nykatojo	26 (0)						
Kanyawara	32 (0)	0.71					
Butanzi	33 (0)	0.76	0.67				
Nyamusika	34 (0)	0.75	0.78	0.93			
Oruha	16 (4)	0.10	0.03	0.05	0.10		
Natural forest	69 (1)	0.07	0.14	0.21	0.18	0.02	
Grassland	7 (0)	0.57	0.03	0.27	0.20	0.50	0.00

Note: The closer the value is to 1, the greater the similarity between areas.

awara had fewer legume stems and more wind-dispersed stems than did the other plantations (Fig. 3).

Based on Morisita's index of similarity, the four Kibale plantations had similar understory tree communities (Table 1). Kyenjura grassland shared more species with Nykatojo and Oruha than the other plantations. The species composition of natural forest was more similar to Butanzi than to other areas. Oruha had little species overlap with the natural forest or with the Kibale plantations.

The effect of distance on regeneration

Indices of species richness and stem density were negatively correlated with distance from plantation edge in Nykatojo and Oruha (where distance from plantation edge was measured; Table 2). In Nykatojo, dis-

tance from plantation edge was negatively correlated with species richness and stem density of indigenous seedlings, saplings, and trees (Table 2). Besides plantation species, no exotic species were growing in Nykatojo. In the isolated plantation at Oruha, distance from plantation edge was negatively correlated with stem density of exotic trees and native trees and with species richness of native trees (Table 2).

Only four tree species (*Albizia grandibracteata*, Fabaceae; *Celtis africana*, Celtidaceae; *C. durandii*; *D. abyssinica*) in Nykatojo and two tree species (*Cedrela odorata*, Meliaceae (exotic); *Millettia dura*, Fabaceae) in Oruha were considered abundant (≥ 47 stems ≥ 2 m tall per 3000 m² sampled in a plantation). Together these species made up 85.3% and 90.5% of the stems growing in Nykatojo and Oruha, respectively. Stem

TABLE 2. Correlations between species richness or stem density and distance from plantation edge for various size classes (seedlings, saplings, and trees), common species (≥ 2 m tall), and dispersal type (≥ 2 m tall) in 30 100-m² plots each sampled in Nykatojo and Oruha.

Plantation	Parameter	Response variable	<i>r</i>	<i>P</i>	Transformation
Nykatojo	species richness	native seedlings	-0.610	<0.001	normal, log
		native saplings	-0.594	0.001	log, log
		native trees	-0.676	<0.001	normal, log
	stem density	native seedlings	-0.474	0.008	normal, log
		native saplings	-0.555	0.001	log, log
		native trees	-0.582	0.001	normal, normal
		<i>Albizia grandibracteata</i>	-0.412	0.024	log, log
		<i>Celtis africana</i>	-0.501	0.005	normal, normal
		<i>Celtis durandii</i>	-0.316	0.089	normal, normal
		<i>Diospyros abyssinica</i>	-0.441	0.015	normal, log
		legume	-0.439	0.015	log, log
		small-seeded, animal dispersed	-0.469	0.009	normal, normal
		large-seeded, animal dispersed	-0.520	0.003	Spearman
		wind dispersed	-0.121	0.525	Spearman
Oruha	species richness	native trees	-0.522	0.003	normal, log
	stem density	native trees	-0.430	0.018	normal, log
		exotic trees	-0.398	0.029	normal, normal
		<i>Millettia dura</i>	-0.340	0.066	Spearman
		<i>Cedrela odorata</i>	-0.264	0.158	normal, normal
		legume	-0.222	0.238	Spearman
		small-seeded, animal dispersed	-0.377	0.040	Spearman
		wind dispersed	-0.154	0.418	Spearman

Notes: Comparisons are only made when stem density in a plantation within a category is at least 18; thus comparisons are different for the two plantations. Seedlings were < 0.3 m tall; saplings were 0.3–2 m tall; trees were ≥ 2 m tall. The most appropriate transformation is indicated; the first transformation is for distance, and the second transformation is for vegetation with “normal” meaning untransformed.

TABLE 3. Stepwise linear regression analyses of species richness or stem density on various site characteristics (percentage of canopy opening; percentage of bare ground; percent cover by grass/ferns, herbs, saplings, and seedlings; stem density of *Psychotria* sp., *Marantochloa leucantha*, *Ficus asperifolia*, and *Aframomum mala*; distance; slope) for 30 100-m² plots each in Nykatojo and Oruha.

Plantation	Parameter	Response variable	Site characteristics	R ²	P
Nykatojo	species richness	native seedlings	% herb cover	0.426	<0.001
		native saplings†	<i>A. mala</i> density, % herb and seedling cover	0.677	<0.001
		native trees†	<i>A. mala</i> and <i>F. asperifolia</i> density, % herb and seedling cover	0.747	<0.001
	stem density	native seedlings†	distance	0.225	0.008
		native saplings†	% herb cover	0.428	<0.001
		native trees	% herb, grass/fern, and seedling cover	0.673	<0.001
Oruha	native trees†	slope	0.288	0.002	
	species richness	native trees†	distance	0.185	0.018
	stem density	exotic trees	slope, % grass/fern cover	0.433	<0.001

Notes: All coefficient signs were negative except those for percent seedling cover which were positive, and all model terms had $P < 0.05$. Seedlings were <0.3 m tall; saplings were 0.3–2 m tall; trees were ≥ 2 m tall.

† $\log(x + 1)$ transformed.

densities of *A. grandibracteata*, *C. africana*, and *D. abyssinica* were each negatively correlated with distance from plantation edge (Table 2). The stem density for *C. durandii* showed a weak trend for a negative correlation with distance from plantation edge (Table 2). In Oruha, distance from plantation edge was weakly negatively related with stem density for *M. dura* but was not correlated with stem density for the exotic, *C. odorata* (Table 2). Reproductive adults were found within the plantations for three species: *C. odorata* and *M. dura* in Oruha and *A. grandibracteata* in Nykatojo.

In Nykatojo, distance from plantation edge was negatively correlated with tree stem density for legume, large-seeded animal-dispersed, and small-seeded animal-dispersed species, but distance was not correlated with tree stem density for wind-dispersed species (Table 2). In Oruha, tree stem density of legume and wind-dispersed species was not related to distance from plantation edge, whereas density of small-seeded animal-dispersed species was negatively related to distance from plantation edge (Table 2). No large-seeded animal-dispersed species were present at Oruha.

The effect of site characteristics on regeneration

Stepwise linear regression analyses indicated that variation in tree stem density in Nykatojo was related primarily to percent herb, grass/fern, and seedling cover, and sapling stem density was related primarily to percent herb cover. Variation in seedling density was attributable mostly to distance from plantation edge (Table 3). Variation in tree species richness was explained by *A. mala* and *F. asperifolia* stem density and percent herb and seedling cover (Table 3). Variation in sapling species richness was attributable to percent seedling and herb cover and *A. mala* stem density, and variation in seedling species richness was best explained by percent herb cover (Table 3). All relation-

ships were negative except those with percent seedling cover which were positive.

In the isolated plantation in Oruha, variation in indigenous tree stem density was attributable primarily to distance from plantation edge (Table 3). Variation in exotic tree stem density was explained by slope and percent grass/fern cover. Variation in indigenous tree species richness was attributable mainly to slope. Again all relationships were negative.

DISCUSSION

In severely degraded areas where forest succession is slower than desired by forest managers, plantations of fast-growing trees can facilitate establishment and growth of indigenous tree species (Lugo 1992, Parrotta 1993, Parrotta et al. 1997, Harrington 1999). Our study demonstrated that this management method could be used for landscapes similar to those found in Kibale. While all five plantations still differed in species composition and stem density from forest, all plantations had higher tree species richness and stem density than anthropogenic grassland. These results suggest that establishment of these plantations facilitated forest regeneration in grasslands more quickly than grassland left to regenerate through natural succession. However, not all plantations had equal amounts of regeneration.

Several findings from this study have implications for use of plantations to encourage forest reestablishment on degraded lands. These include: (1) the effect of small-scale distance from plantation edge (distance effect); (2) the effect of large-scale distance and habitat between seed sources and plantations (isolation effect); (3) the effect of understory plants (understory plant effect); and (4) variability among plantations at the same site.

We found a negative correlation between distance from plantation edge and density of trees in different

size classes and dispersal types in both Nykatojo and Oruha plantations. Similar effects have been observed elsewhere (Parrotta 1993, Hardwick et al. 1997, Parrotta et al. 1997). For example, Parrotta (1993) found that most species dispersed into a plantation had seed sources within 100 m, although some bird- or mammal-dispersed species were carried more than 200 m.

In our study, the strength of this relationship between abundance and distance differed among common species. Small-seeded animal-dispersed species tended to show a strong distance effect with decreasing density as distance increased (*C. africana* and *D. abyssinica* in Nykatojo), but one such species (*C. durandii* in Nykatojo) showed only a weak decrease in density with increasing distance. Two species with reproductive adults in plantations showed little or no distance effect (*C. odorata* and *M. dura* in Oruha), but *A. grandibracteata* in Nykatojo had reproductive individuals within the plantation and still showed a strong distance effect. It is unclear why *M. dura* and *A. grandibracteata* (both legumes with similar fruit and seed morphology) differed in how their densities changed with distance. It is also unclear why the two *Celtis* species that have very similar fruits and seeds had different densities with increasing distance. These results suggest forest reestablishment will occur faster in regions that have many species with densities that are little affected by distance from plantation edge than in regions that have many species with densities that decrease rapidly with increasing distance from plantation edge. Characteristics that confer the ability to colonize throughout plantations could include effective dispersal and fast maturity so that dispersal within plantations begins quickly. Understanding which species and which characteristics of those species facilitate colonization far into plantations will assist in designing plantations to promote regeneration.

The second major finding of this study was that the isolated plantation (Oruha) had lower species richness and stem density than plantations located adjacent to natural forest. While only one isolated plantation was available to study and variability found among Kibale plantations suggests that extrapolating findings from one plantation to another must be done with caution, the results point to areas where future work is needed. Furthermore, these results are comparable to results found by Tucker and Murphy (1997), although in their study, they detected differences due to isolation at around 500 m from forest and we were measuring isolation at ~7 km from forest. In the current study, Kibale plantations had 5.5 times the native stem density and 2.0 times the native species richness of the isolated plantation at Oruha. These results can likely be attributed to the fact that animal dispersers inhabiting forests will often not enter disturbed areas such as pastures (da Silva et al. 1996, Bierregaard and Stouffer 1997, Tucker and Murphy 1997), and in fact in a month long study of terrestrial mammal abundance, wild mammals

were 8.1 times more frequent in Nykatojo than Oruha (Zanne et al., *in press*). Thus, Oruha may be visited less by seed dispersers than Kibale plantations due to habitat barriers such as agricultural land. The isolation effect is supported by the fact that a greater percentage of species established in Kibale plantations were animal dispersed, while a greater percentage of species established in Oruha and the grassland were legumes. In fact, no large-seeded animal-dispersed species grew in Oruha or the grassland. Large-seeded species tend to be more limited in abundance by infrequent dispersal events than small-seeded species (Hardwick et al. 1997, Tucker and Murphy 1997). The impoverished tree communities in the grassland and Oruha suggest that forest recovery on isolated lands will be very slow.

Results from this study suggest that strategies such as intercropping plantations with desirable native species especially dispersal-limited large-seeded species (Tucker and Murphy 1997) or species that attract a variety of seed dispersers, such as, *Ficus* (Parrotta 1995, Thornton et al. 1996) may accelerate reforestation in isolated plantations. Dispersal-limited species could mature and become seed sources for those species within the plantation. Species, such as *Ficus*, that are attractive to a large number of seed dispersers (Thornton et al. 1996) could attract more dispersers to the plantation and increase seed rain.

The density of understory plants is a third major factor that influenced tree regeneration in this study. It might be expected that understory plants found in plantations and commonly eaten by seed dispersers (e.g., *A. mala*) would act as focal points for seed deposition. In Kibale, chimpanzees (*Pan troglodytes*) are an important seed disperser and 42.9% of chimpanzee dung samples contained *A. mala* (Wrangham et al. 1994). Besides *A. mala* seeds, these samples contained various tree species (e.g., *Uvariopsis congensis*, Annonaceae; *Mimusops bagshawei*, Sapotaceae). Since chimpanzees travel through Kanyawara pine plantations (Zanne et al., *in press*) and disperse seeds from ~30% of the species found within the plantations, they could be an important seed disperser to plantations. However, in the current study, understory plants (such as *A. mala*) were negatively correlated with tree species richness and stem density. Understory plants have been documented to inhibit forest succession by restricting access to water, sunlight (Walker 1994), or nutrients (Corlett 1991, Ashton et al. 1997), by physically blocking growth (Cohen et al. 1995, Hardwick et al. 1997), and/or by allelopathy (Otsamo et al. 1996). In Costa Rica, Powers et al. (1997) found that grass/fern cover was negatively correlated with species richness and density of woody stems. In the current study, while trees grew at low densities in dense patches of understory plants, these understory plants may still attract potential seed dispersers increasing seed deposition in plantations. Seedling establishment may be higher within plantations outside dense patches of understory plants, but

if so this effect occurred at a larger spatial scale than measured (100-m² plots).

Finally, while most studies of regeneration of indigenous trees in plantations have shown an increase in species richness and stem density in plantations vs. unmanaged grasslands, only a few studies have documented variation between different plantations located in the same region. In the current study, species composition and stem density were highly variable among Kibale pine plantations. For example, *Teclea nobilis* stem density was much higher in Butanzi than any of the other Kibale plantations (Butanzi density = 102.3 times Nykatojo density, 12.8 times Kanyawara density, and 5.0 times Nyamusika density), and no *T. nobilis* stems were present in the isolated Oruha plantation. This variability may be due to many factors that differ among the plantations (e.g., differences in plantation size or shape). Heterogeneity (e.g., species composition) in the surrounding natural forest may be important as it may determine which and how frequent dispersers move through different plantations and the nature of the seed sources. While forest directly surrounding plantations was not quantified, this forest does show some heterogeneity; adults of species, such as *Uvariopsis congensis*, occur in high density stands in some areas in the forest but are nearly absent in other parts. In an Australian study, variation between plantations in regeneration levels was attributed to increasing diversity in adjacent forests (Tucker and Murphy 1997).

The observed variation in regeneration among pine plantations in Kibale suggests that extrapolations about forest regeneration based on data from one or a few plantations may not reflect regeneration in other plantations. For example, if species composition were estimated only in Nykatojo, the species *A. grandibracteata* would have been the most common regenerating species (229 stems/3000 m²), but *A. grandibracteata* is not among the top two most common species in any of the other three plantations. In fact, Kanyawara has only 13 *A. grandibracteata* stems per 3000 m². In the other three plantations, small-seeded animal-dispersed species (*C. durandii* or *D. abyssinica*) are the most common species.

In summary, this study found plantations facilitated understory forest regeneration over levels found in unmanaged grasslands. Thus in some situations, plantations can act as nurse crops for reestablishing forest cover. This investigation contributes information about important physical and biological characteristics influencing indigenous species richness and stem density within a plantation's understory. Increasing distance from plantation edge, isolation from seed sources of native species, and dense understory plant abundance all negatively affected forest regeneration. Variability in species composition, species richness, and stem density was high among plantations. Plantations will accumulate more stems and species when established ad-

jacent to natural forest or older plantations already with established regeneration than isolated from forest. These results suggest that plantations established around natural forest as buffer zones, for example, may facilitate high levels of indigenous species establishment in their understories.

The success of restoration using plantations will depend not only on location but also on time frame. The speed at which plantations begin facilitating regeneration is unclear from this study as only 30-yr-old plantations were studied; it would be expected that these effects would begin as soon as the pines could out-compete the grasses. Determining the time that plantations become beneficial to regeneration would be useful and would be expected to occur within years to a few decades.

Future studies should determine if regenerating trees can survive extraction of planted pine trees and form a closed forest canopy. If forest trees are able to establish in the pine understory but are unable to survive pine extraction, applications of this management scheme would be limited to using pines as facilitators that are left to die in place. Chapman and Chapman (1996) found a trend for greater tree regeneration in unlogged versus logged plantations of *P. patula*, *P. caribaea*, and *Cupressus lusitanica* in Kibale National Park two years after logging, but two years is perhaps insufficient to evaluate regeneration success given that successional processes occur over a much longer time frame.

This study assessed when plantation establishment is recommended from a biological perspective. However, our research in Uganda led us to realize that other factors (e.g., social and economic) may be very important in determining success of a reforestation project. For instance, in Uganda, grasslands at Oruha hill-top were used originally as public land for growing crops. When the Forest Department established plantations at this location, local access to these lands was restricted. Such impacts on local users need to be taken into consideration. A study in the Philippines suggests that reforestation projects had increased success when they were viewed by local people as economically beneficial to them, were made compatible with local resource use and land tenure, incorporated local knowledge and skills, recruited the support of local social groups and organizations, and were compatible with local policies and political factors (Walters 1997).

Further, the use of plantations as nurse crops may be limited because of the costs of plantation establishment. Most studies of plantations that foster understory tree regeneration were established for other purposes (e.g., industrial). Understory regeneration competes with plantation species, so an understory has been allowed to flourish only in failed or small experimental plantations. Researchers have shown that in some situations it is biologically possible to use plantation species as nurse crops for increasing tree diversity and

richness. However, because studies have been conducted primarily on these failed plantations, researchers have yet to show whether it is financially feasible to establish such plantations (Kosonen et al. 1997).

If establishment costs are financially, economically, or socially high in areas such as public lands, then use of plantations as nurse crops may be restricted to situations such as occurred within Kibale, where public land use is limited and the goal of the park is to promote forest diversity. While future studies should focus on biological aspects, such as fire exclusion, and which species and harvesting practices facilitate forest reestablishment, these studies need to be conducted in plantations designed for the purpose of encouraging forest regrowth. Furthermore, future studies need to consider potential biological benefits of plantations in conjunction with social, economic, and financial aspects.

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