Enrichment planting does not improve tree restoration when compared with natural regeneration in a former pine plantation in Kibale National Park, Uganda

Patrick A. Omeja^{1,2}, Colin A. Chapman^{2,3,4}* and Joseph Obua¹

¹Faculty of Forestry and Nature Conservation, Makerere University, PO Box 7062, Kampala, Uganda, ²Makerere University Biological Field Station, PO Box 967, Fort Portal, Uganda, ³McGill School of Environment, 855 Sherbrooke St West, McGill University, Montreal, QC, Canada H3A 2T7 and ⁴Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA

Abstract

Given the high rates of deforestation and subsequent land abandonment, there are increasing calls to reforest degraded lands: however, many areas are in a state of arrested succession. Plantations can break arrested succession and the sale of timber can pay for restoration efforts. However, if the harvest damages native regeneration, it may be necessary to intervene with enrichment planting. Unfortunately, it is not clear when intervention is necessary. Here, we document the rate of biomass accumulation of planted seedlings relative to natural regeneration in a harvested plantation in Kibale National Park, Uganda. We established two 2-ha plots and in one, we planted 100 seedlings of each of four native species, and we monitored all tree regeneration in this area and the control plot. After 4 years, naturally regenerating trees were much taller, larger and more common than the planted seedlings. Species richness and two nonparametric estimators of richness were comparable between the plots. The cumulative biomass of planted seedlings accounted for 0.04% of the total above-ground tree biomass. The use of plantations facilitated the growth of indigenous trees, and enrichment planting subsequent to harvesting was not necessary to obtain a rich tree community with a large number of new recruits.

Key words: arrested succession, enrichment planting, Kibale National Park, pine plantations, regeneration, restoration

Résumé

Étant donné le rythme élevé de déforestation et, par la suite, d'abandon de terres, il y a des demandes croissantes

*Correspondence: E-mail: colin.chapman@mcgill.ca

pour repeupler les terrains dégradés: cependant, de nombreuses surfaces se trouvent dans un état de succession interrompu. Des plantations peuvent mettre fin à cette succession stoppée, et la vente de grumes peut financer les efforts de reforestation. Pourtant, si les prélèvements d'arbres endommagent la régénération naturelle, il peut être nécessaire d'intervenir avec des plantations d'appoint. Malheureusement, il n'est pas toujours facile de savoir quand une intervention est nécessaire. Nous documentons ici le taux d'accumulation de biomasse dans des jeunes arbres replantés par rapport à la régénération naturelle dans une plantation exploitée, à l'intérieur du Parc National de Kibale, en Ouganda. Nous avons établi deux parcelles de deux hectares et, dans une, nous avons repiqué 100 plants de chacune des quatre espèces natives. Nous avons ensuite suivi la régénération de tous les arbres dans cette parcelle et dans la parcelle témoin. Après quatre ans, les arbres provenant de la régénération naturelle étaient beaucoup plus grands, plus gros et plus abondants que les arbres replantés. La richesse en espèces et deux estimateurs nonparamétriques de la richesse étaient comparables dans les deux parcelles. La biomasse cumulée des jeunes arbres plantés comptait pour 0,04% de la biomasse aérienne totale des arbres. Le recours à des plantations a facilité la croissance d'arbres indigènes et la plantation d'appoint faisant suite à l'exploitation ne fut pas nécessaire pour obtenir une communauté d'arbres riche, avec un grand nombre de nouvelles recrues.

Introduction

According to the Food and Agricultural Organization's Global Forest Resources Assessment (FAO, 2005), forest lost between 2000 and 2005 was c. 200 km² of forest per

day. Faced with this rapid rate of forest conversion, it is clear that the survival of many forest dependent species will depend on the capacity of disturbed areas to support their populations (Putz, Dykstra & Heinrich, 2000). However, unlike tree fall gaps and other 'naturally' disturbed areas, the regeneration of secondary forests on anthropogenically disturbed lands does not always follow predictable pathways (Guariguata & Ostertag, 2001) and regeneration is often arrested (Lugo, Parrotta & Brown, 1993; Brown & Lugo, 1994; Paul et al., 2004). Such arrested succession has been attributed to a number of factors including degraded soils, competition from undesirable species, and the action of animals (Lieth & Lohmann, 1993; Chapman & Chapman, 1999; Chapman et al., 1999; Lawes & Chapman, 2005). Usage of fertilizers, weeding or enrichment plantings can break arrested succession and encourage forest development (Parrotta, Turnbull & Jones, 1997: Duncan & Chapman, 2003a). However, it is often not clear when intervention is necessary.

Considering that restored forests in these degraded lands can be useful for conservation, timber production, carbon sequestration and variety of other ecosystems services (Lugo, 1992a; Brown & Lugo, 1994), there has been a recent shift in management strategies to accelerate recovery of degraded lands. In some situations, tree plantations can facilitate indigenous tree restoration in their understories (Chapman & Chapman, 1996; Lugo, 1997; Parrotta et al., 1997). Plantations can cause changes in light, temperature and moisture at the soil surface, enabling germination and growth of native tree species (Lugo, 1992b; Chapman & Chapman, 1996; Parrotta et al., 1997). However, such positive outcomes are not always the case and concerns have been raised about short-rotation plantations and monospecific rehabilitation programs revolving around the use of some exotic species (Parrotta & Knowles, 1999; Yirdaw, 2001). For example, it is often alleged that exotics, particularly Eucalyptus species which are commonly used by reforestation programs in Sub-Sahara Africa (Yirdaw, 2001; Yirdaw & Luukkanen, 2003), Central America (Schaller et al., 2003) and South America (Rhoades, Eckert & Coleman, 2000), rapidly deplete soil nutrients and water and inhibit the development of native flora.

Timber sales will be needed to help pay for the restoration efforts in many tropical countries. However, if this harvest seriously damages the native regeneration that has been able to establish, it may be necessary to intervene with programs such as enrichment planting to promote

the desired rate of native forest restoration (Tucker & Murphy, 1997; Duncan & Chapman, 2003a). The cost of such planting can be very high (Parrotta & Knowles, 1999) and the success of enrichment planting relative to natural regeneration is largely unknown in many environmental conditions. As a result, it is important to contrast the rate and character of natural regeneration versus enrichment planting programs on areas where plantations have been harvested to determine the relative value of these management options.

The aim of this study was to contrast the size, height and biomass accumulation of natural regeneration versus enrichment planting in an area where a pine plantation had been harvested in Kibale National Park, Uganda.

Materials and methods

Study area

The study was conducted between May 2002 and May 2006 in Kibale National Park, Uganda. The park (795 km²) is located in western Uganda (0°13′-0°41′N and 30°19′-30°32′E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997; Chapman & Lambert, 2000). Kibale is a mid-altitude, moist-evergreen forest receiving 1712 mm of rain annually (1990-2007).

Pine plantations (Pinus caribaea Morelet, Pinus patula Schltdl. & Cham, Cupressus lusitanica Mill.) were established in Kibale between 1953 and 1977 on grasslands that were previously forested lands that had been cleared and cultivated by agriculturalists. These lands were abandoned when rinderpest devastated the livestock in the area shortly after 1900 (Osmaston, 1959; Kingston, 1967; Wing & Buss, 1970). Active fire exclusion was initially important to protect young pine seedlings, but became less important as the plantation matured. Similar areas not planted with exotics are still largely fire-maintained grassland (Zanne & Chapman, 2001; Lwanga, 2003). Once the plantations matured, native tree species and shrubs invaded the understory and were not removed by the plantation managers (Chapman & Chapman, 1996; Zanne & Chapman, 2001; Duncan & Chapman, 2003b). Management plans changed when Kibale became a national park in 1993, plantations started to be harvested and the harvested pine areas were left to regenerate to native forest. The study was conducted in the Mikana plantation that was harvested in 1998. Timber felling was carried out using chain saws, and the felling of these pines damaged many indigenous trees. Subsequently, the logs were rolled or winched to portable mills, pitsawing stations or roadsides, damaging more native trees. There was no regeneration of softwood pine species. The area was left to regenerate naturally from the few remaining indigenous trees, resprouts from trees that were damaged by the harvest (often cut at the ground level), seeds in the soil seed bank or newly arrived seeds deposited in the area by animal dispersers or wind. This site was surrounded by natural forest where the interior of former pines was <250 m from natural forest and in the natural forest, there was an abundance of avian and mammalian seed dispersers.

Control and enrichment planting

In May 2002, two 200 × 100 m (2 ha) plots were established in the harvested pine plantation and each plot was divided into fifty 20×20 m subplots. The plots were adjacent to one another and separated by c. 20 m. One plot was randomly assigned as the enrichment planting plot. At the time of planting, the area was dominated by a variety of grasses, often Pennisetum purpureum Schum. and Hyparrhenia spp. and no seedlings could be seen emerging from the grass. However, dispersed throughout the grasses were small stands of trees that had grown up under the pines and had not been harvested. The control plot had eight trees >30 cm diameter at breast height (DBH) ha⁻¹ and the experimental plot had 25 trees ha⁻¹ of this size. This is in comparison to c. 110 trees ha⁻¹ of this size in the intact forest. These trees are excluded from biomass evaluations, but the presence of the larger number of trees in the experimental plot could have enhanced regeneration.

In the enrichment planting plot, 400 seedlings of fastgrowing species that colonize disturbed areas (Albizia grandibracteata Taub., Celtis africana Burm. f., Celtis durandii Engl. and Milletia dura Dunn.) were planted, with two of each of these species being planted in each 20 × 20 m subplot. To space the seedlings apart, each subplot was divided into four sections and two seedlings of one of the four species were planted in the middle of these sections, c. 2 m apart. The area around the planted seedling was weeded removing competitors. If a seedling died, a new seedling was planted in its place and this replacement continued until the end of the monitoring. If a seedling survived past the first month following planting, the probability of surviving to the end of the 4 years was very high. The four species were selected because they were

species that typically colonize disturbed areas and the seedlings were easily available under mature mother trees, which reduced the cost and time of raising seeds under nursery conditions. The remaining plot was the control; however, similar subplots were established to aid in quantifying regeneration and to ensure that each area received similar treatment.

Species richness, stem density and above-ground biomass estimation

For each of the tree stem >2 m tall, we identified the species and measured their heights, DBH and diameter at ground height (DGH). For resprouting trees that had multiple stems, the largest stem was measured; however, stems often divided above the ground, so this did not influence the measurement of DGH. Plant identification was based on a number of recognized plant keys (Eggeling & Dale, 1952; Polhill, 1952; Hamilton, 1991; Katende, Birnie & Tengrias, 1995; Lwanga, 1996).

Biomass accumulation is important to quantify as it enables estimation of carbon sequestration. To estimate biomass, trees in forest lands that were adjacent to the park were identified, DBH and DGH measured, and the trees were felled at ground level. Trees of species commonly found in the regenerating areas were selected so that they were of size similar to those regenerating in the harvested area (i.e. DBH 1.1-10.0 cm and DGH 1.6-11.0 cm; within the dry weights of 0.25-10 kg; total n = 200 stems). The species included Albizia grandibracteata Taub., Bridelia micrantha Baill., Celtis africana Burm. f., Celtis durandii Engl., Clausena spp, Maesa lanceolata Forssk., Funtumia latifolia Stapt, Milletia dura Dunn. and Trema orientalis Blume. First, the branches were removed and the total dry weight of stems and leaves was determined. Second, the tree stems were cut into smaller sections and air dried until a constant mass was attained.

Data analysis

We compared the size and number of seedlings that were planted into the regenerating forest relative to natural regeneration occurring without management. Tree height and DBH were compared between the plots using Mann-Whitney U-test where subplots were considered the independent unit. Nonparametric analyses were appropriate because the dataset contained many small individuals and thus was skewed to smaller sizes. Biomass data per subplot

were normally distributed and comparisons were made with a *t*-test. Regression equations were developed to predict above-ground dry biomass from DGH with log transformed data. Two nonparametric estimators of species richness [Abundance-based Coverage Estimator (ACE) and Chao 1] were computed using the software EstimateS version 7.5 (Colwell, 2005). Chao1 is based on the number of singletons (species with one individual) and doubletons (species with two individuals), whereas ACE is based on the number of species found with ten or fewer individuals (Chazdon, Colwell & Guariguata, 1998). The sample order was randomized 50 times without replacement and the mean and standard deviation were computed for each value of N, where N is the number of subplots within each

site (Colwell, 2005). Unless otherwise stated, large stems

that survived the harvesting of the pines were excluded

Results

from the analyses.

Seedling physical attributes in the enrichment planted and natural regenerating plots

The mean heights and DBHs of the trees in the experimental plot indicated that naturally regenerating trees were much taller and larger (all stem $\bar{X}=8.47$ m high, DBH = 10.82, n = 1597; excluding stems left standing at the time of pine removal $\bar{X}=6.49$ m, DBH = 7.10, n = 1593), than the planted seedlings ($\bar{X}=0.51$ m, DBH cannot be measured on such small stems, n = 400; Fig. 1). The range of heights of planted seedlings (0.43–1.72 m) is

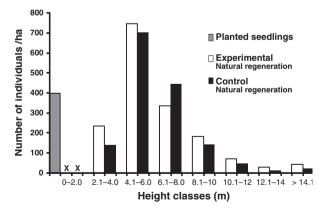


Fig 1 Frequency of trees in different height classes in the control and experimental plots in Kibale National Park, Uganda. Naturally regenerating stems were only recorded if they were >2 m tall

much lower than the height of the naturally regenerating trees [2.0 (smallest size measured)–15 m; excluding stems left standing at the time of pine removal]. There were significant differences in DBH, DGH and canopy height (all Mann–Whitney U P < 0.001) between the enrichment planted plot and the control, with the experimental plot having the higher values. However, any differences documented were not because of the planting, because in both plots, there were large numbers of stems that resulted from natural regeneration in size classes larger than those attained by the seedling used in the enrichment planting.

Density and species richness

The density of stems >2 m tall was very similar between the two plots (enrichment plot = 762 stems ha⁻¹, control 797 stems ha⁻¹). In contrast to this, the density of stems in grasslands similar to those on which the pine plantations were originally planted was only 1.7 stems ha⁻¹ (Zanne & Chapman, 2001).

A total of 44 different tree species were found in the two plots, with 42 tree species in the experimental plot and 35 in the control plot. Abundance-based estimators and Chao1 show a slight difference in species richness between control and experimental plots (Table 1), with experimental plot having a higher ACE index (62.92) compared with that of the control plot (42.26). However, there was a great deal of overlap (80%) in species composition in both sites. The species that were not found in both plots occurred at low densities (maximum 2 stems ha⁻¹). All the tree species that were used as enrichment plant species in the experimental plots were encountered in higher

Table 1 Descriptive statistics and nonparametric abundancebased estimators of species richness by plots in the former pine plantation in Kibale National Park, Uganda

	Plot	
Indices	Experimental	Control
Number of 0.04 ha plots	50	50
Number of species observed	42	35
Number of individuals	1665	1612
Nonparametric estimators		
Abundance-based Coverage	62.96	42.26
Estimator		
Chao1	55.93	41.06
Chao1 S/D	9.52	4.44

Table 2 Mean stand density (stems ha-1) of tree species in the former pine plantation in Kibale National Park, Uganda

Family	Species	Stems ha
Myrsinaceae	Maesa lanceolata	216
Leguminosae	Albizia grandibracteata	144
Euphorbiaceae	Bridelia micrantha	77
Ulmaceae	Trema orientalis	70
Ulmaceae	Celtis durandii	53
Ulmaceae	Celtis africana	46
Papilionaceae	Milletia dura	39
Apocynaceae	Funtumia latifolia	31
Rutaceae	Fagara angolensis	23
Bignoniaceae	Spathodia campanulata	11
Papilionaceae	Erythrina abyssinica	10
Rosaceae	Prunus africana	10
Ebenaceae	Diospyros abyssinica	10
Boraginaceae	Ehretia cymosa	7
Oleaceae	Olea welwitschii	5
Rutaceae	Clausena anistata	5
Moraceae	Ficus natalensis	3
Verbenaceae	Premna angolensis	3
Euphorbiaceae	Croton macrostachyus	3
Euphorbiaceae	Macaranga schweinfurthii	2
Rubiaceae	Vangueria apiculata	1
Euphorbiaceae	Sapium ellipticum	1
Melianthaceae	Bersama abyssinica	1
Mimosaceae	Acacia sp.	1
Sapindaceae	Blighia unijugata	1
Sterculiaceae	Dombeya mukole	1
Flacourtiaceae	Casearia battiscombei	1
Mimosaceae	Dichrostachys glomerata	1
Pittosporaceae	Pittosporum spathicalyx	1
Alangiaceae	Alangium chinense	1
Araliaceae	Polyscias fulva	1
Flacourtiaceae	Scolopia rhamnophylla	1
Borganinaceae	Cordia africana	1
Rutaceae	Teclea nobilis	1
Moraceae	Myrianthus holstii	1
Bignoniaceae	Kigelia moosa	1
Ulmaceae	Chaetacme aristata	1
Euphorbiaceae	Neoboutonia macrocalyx	1
Meliaceae	Guarea cedrata	1
Rubiaceae	Hallea stipulosa	1

numbers among the populations of the naturally regenerating trees in both plots.

The most common tree species in the experimental plot was Maesa lanceolata Forssk., which made up 40.3% of the stand, while Albizia grandibracteata Taub. was most common in the control plot, accounting for 30.2% of regenerating species, (Table 2).

Tree biomass

The dry biomass of trees was predicted by log DGH $(R^2 = 0.653, n = 200, y = 2.053x + 2.056)$. The cumulative biomass of the planted seedlings only accounted for 0.04% of the total above-ground tree biomass found on the experimental plot by the end of the study. Tree species in DGH classes 0.8-10 cm constituted 10.88% of the total biomass in the control plot and 16.19% in the experimental plot (Fig. 2). Considering the subplots as independent units, there was no significant difference between the calculated biomass (t = 1.513, P = 0.130) between the experimental and control plots.

Discussion

This study has demonstrated that the use of fast growing pine plantations facilitated the establishment and growth of indigenous trees and that enrichment planting subsequent to pine plantation harvesting was not necessary to obtain a rich tree community with a large number of new recruits. A number of factors could have contributed to the high level of advanced regeneration in the larger size classes of trees and the trend for substantial woody tree biomass accumulation. The ability of many species to resprout after shoots had been broken, cut or injured significantly contributed to the rapid rate of regeneration. Even though most seedlings and saplings of the indigenous trees were damaged by the pine plantation harvesting so that only small number of woody species were present (except the larger standing trees that were not cut), many of the existing trees with DBH between 5 and 30 cm at the end of the study appear to be the result of resprouting from either broken shoots or even the injured roots (as exhibited by swollen shoots and multiple stems of Albizia grandibracteata Taub., Maesa lanceolata Forssk., Bridelia micrantha Baill. and Milletia dura Dunn.). Such resprouts likely have a well-established root systems that are able to extract nutrients and water from the soil efficiently and thus grow more rapidly than planted seedlings. The importance of resprouting is indicated by the fact that all the trees in these plots with stem densities >10 individuals ha⁻¹ are those trees species that have the ability to resprout from broken shoots or root systems.

A major issue still requiring further study is whether the regeneration in the former pine plantation is of the desired quality. At the present time, most of the species found in the regenerating area are from pioneer genera, e.g. Maesa

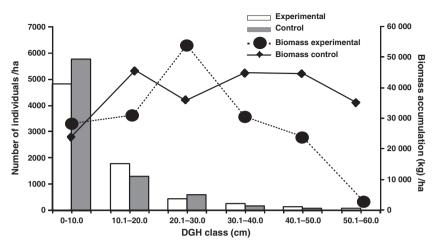


Fig 2 Biomass accumulation among different DGH classes excluding very large stems in the experimental and control plots in Kibale National Park, Uganda. Note that the biomass of stems >60 DGH in the experimental plot is 117,845.5 kg ha⁻¹

lanceolata Forssk., Trema orientalis Blume, Albizia grandibracteata Taub., Milletia dura Dunn, and Bridelia micrantha Baill. These have short lifespan (20-30 years). Further study is needed to determine how soon late-successional forest species become established in these former pine plantations. An additional issue needing investigation concerns the generality of our finding to other regions and environmental settings. The regenerating area studied here was in close proximity to undisturbed forest; an excellent seed source. In similar environmental settings, Zanne & Chapman (2001) found that tree species richness and stem density were negatively correlated with distance to the plantation edge. Thus, it would be valuable to investigate if enrichment planting would assist in the speed or nature of regeneration in harvested plantations that were a long distance from a seed source.

Lastly, an issue requiring further study concerns when enrichment planting might yield ecological gains worth the economic price. The replanting of a mix of early and late-successional tree species has been recommended as viable means of restoring diversity much more rapidly than waiting for natural regeneration to occur (Yirdaw, 2001). However, the potential application of enrichment planting to facilitate restoration and biodiversity conservation is based on the premise that the increase in seedling recruitment would lead to a greatly enhanced regeneration of mature trees that would be worth the investment that replanting programs require (Plumptre, 1995; Chapman & Chapman, 1996). Even though performance of the trees in enrichment planting has a high probability of success, especially when planting is timed to optimize survival rates (Duncan & Chapman, 2003a), enrichment planting generally involves high costs in nursery maintenance and field labour. For example, forest restoration is estimated to cost US\$250,000 per km² on bauxite mined land in Amazon (Parrotta & Knowles, 1999) and US\$120,000 per km² in Kibale National Park, Uganda (UWA-FACE, 2005). Given the positive rate of restoration both in terms of biomass and species richness quantified in the non-enrichment planted site and the magnitude of the costs of enrichment planting, it is valuable to evaluate whether natural regeneration will meet management needs prior to suggesting enrichment options.

Acknowledgement

This research was supported by Canada Research Chairs Program, Wildlife Conservation Society, Natural Science and Engineering Research Council of Canada, the Committee on Scientific and Technological Cooperation of the Organization of Islamic Conference, Islamabad, Pakistan and the International Foundation for Science, Stockholm, Sweden. We would also like to thank Uganda Wildlife Authority, Uganda National Council for Science and Technology and Makerere University Biological Field Station for granting permission to conduct this research. The field assistants of Kibale Fish and Monkeys Projects provided very valuable help. The manuscript benefited from comments by Aerin Jacob and Mike Lawes.

References

Brown, S. & Lugo, A.E. (1994) Rehabilitation of tropical lands: a key to sustaining development. *Restor. Ecol.* 2, 97–111.

- CHAPMAN, C.A. & CHAPMAN, L.J. (1996) Exotic tree plantations and the regeneration of natural forests in Kibale National Park, Uganda, Biol. Conserv. 76, 253-257.
- CHAPMAN, C.A. & CHAPMAN, L.J. (1999) Forest restoration in abandoned agricultural land: a case study from East Africa. Conserv. Biol. 13, 1301-1311.
- CHAPMAN, C.A. & LAMBERT, J.E. (2000) Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. Am. J. Primatol. 50, 169-185.
- CHAPMAN, C.A., CHAPMAN, L.J., KAUFMAN, L. & ZANNE, A.E. (1999) Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. Afr. J. Ecol. 37,
- CHAZDON, R.L., COLWELL, J.L. & GUARIGUATA, M.R. (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northern Costa Rica. In: Forest Biodiversity Research, Monitoring and Modelling: Conceptual Background and Old World Case Studies (Eds F. DALLMEIR and J. A. Comiskey). UNESCO/The Parthenon Publishing Group, Paris.
- COLWELL, R.K. (2005) EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 7.5. User's Guide and Application Published at: http://purl.oclc.org. estimates (last accessed on 23 September 2008).
- DUNCAN, R.S. & CHAPMAN, C.A. (2003a) Consequences of plantation harvest during tropical forest restoration in Uganda. For. Ecol. Manage. 173, 235-250.
- DUNCAN, R.S. & CHAPMAN, C.A. (2003b) Tree-shrub interactions during early secondary forest succession in Uganda. Restor. Ecol. 11, 198-207.
- EGGELING, W.J. & DALE, I.R. (1952) The Indigenous Trees of the Uganda Protectorate. Government of Uganda Printer, Entebbe, Uganda.
- FAO (2005) Global Forest Resources Assessment 2005: Progress towards Sustainable Forest Management. FAO Forestry Paper 147.
- GUARIGUATA, M.R. & OSTERTAG, R. (2001) Neotropical forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148, 185-206.
- Hamilton, A.C. (1991) A Field Guide to Uganda Forest Trees. Makerere University Printery, Kampala.
- KATENDE, A., BIRNIE, A. & TENGRIAS, B. (1995) Useful Trees and Shrubs for Uganda: Identification, Propagation and Management for Agricultural and Pastoral Communities. Regional Soil Conservation Unit, Nairobi.
- KINGSTON, B. (1967) Working Plan for Kibale and Itwara Central Forest Reserves. Uganda Forest Department, Entebbe, Uganda.
- LAWES, M.J. & CHAPMAN, C.A. (2005) Does the herb Acanthus pubescens and/or elephants suppress tree regeneration in disturbed Afrotropical forests? For. Ecol. Manage. 221, 274-284.
- LIETH, H. & LOHMANN, M. (1993) Restoration of Tropical Ecosystems. Kluwer Academic Publishers, London.
- Lugo, A.E. (1992a) Comparison of tropical tree plantations with secondary forests of similar age. Ecol. Monogr. 62, 1-41.

- Lugo, A.E. (1992b) Tree plantations for rehabilitating damaged forest lands in the tropics. In: Ecosystem Rehabilitation: Ecosystem Analysis and Synthesis (Ed. M. K. WALI), Academic Press, The Наопе
- Lugo, A.E. (1997) The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. For. Ecol. Manage. 99, 9-19.
- Lugo, A.E., Parrotta, I.A. & Brown, S. (1993) Loss in species caused by tropical deforestation and the recovery through management. Ambio 22, 106-109.
- LWANGA, J.S. (1996) Trees and shrubs. In: Kibale Forest Biodiversity Report (Ed. P. C. HOWARD, L. DAVENPORT and R. A. MATTHEWS). Forestry Department, Kampala, Uganda.
- LWANGA, I.S. (2003) Forest succession in Kibale National Park, Uganda: implications for forest restoration and management. Afr. J. Ecol. 41, 9-22.
- OSMASTON, H.A. (1959) Working Plan for the Kibale and Itwara Forests. Ugandan Forest Department, Entebbe.
- PARROTTA, J.A. & KNOWLES, O.H. (1999) Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. For. Ecol. Manage. 7, 1-7.
- PARROTTA, J.A., TURNBULL, J.W. & JONES, N. (1997) Catalyzing native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 1-7.
- PAUL, J.R., RANDLE, A.M., CHAPMAN, C.A. & CHAPMAN, L.J. (2004) Arrested succession in logging gaps: is tree seedling growth and survival limiting? Afr. J. Ecol. 42, 245-251.
- PLUMPTRE, A.J. (1995) The importance of seed trees for the natural regeneration of selectively logged tropical forest. Commonw. Forest. Rev. 74, 253-258.
- POLHILL, R.M. (1952) Flora of Tropical East Africa. A.A. Balkema, Rotterdam, The Netherlands.
- PUTZ, F.E., DYKSTRA, D.P. & HEINRICH, R. (2000) Why poor logging practices persist in the tropics. Conserv. Biol. 14, 505-508.
- RHOADES, C.C., ECKERT, G.E. & COLEMAN, D.C. (2000) Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. Ecol. Appl. 10, 497-505.
- SCHALLER, M., SCHROTH, G., BEER, J. & JIMENEZ, F. (2003) Species and site characteristics that permit the association of fast-growing trees with crops: the case of Eucalyptus deglupta as coffee shade in Costa Rica. For. Ecol. Manage. 175, 205-215.
- STRUHSAKER, T.T. (1975) The Red Colobus Monkey. University of Chicago Press, Chicago.
- STRUHSAKER, T.T. (1997) Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation. University of Florida Press, Gainesville.
- Tucker, N.I.J. & Murphy, T.M. (1997) The effects of ecological rehabilitation on vegetation recruitment: some observations from the Wet Tropics of North Queensland. For. Ecol. Manage. 99, 133-152.
- UWA-FACE (2005) Project Plan of Operation Report January to December 2005. Uganda Wildlife Authority, Kampala, Uganda.

- WING, L.D. & BUSS, I.O. (1970) Elephants and forests. Wildl. Monogr. 19, 1-92.
- YIRDAW, E. (2001) Diversity of naturally-regenerated native woody species in forest plantations in the Ethiopian highlands. NewForest. 22, 159-177.
- YIRDAW, E. & LUUKKANEN, O. (2003) Indigenous woody species diversity in Eucalyptus globulus Labill. plantations in the Ethiopian highlands. Biodivers. Conserv. 12, 567-582.
- ZANNE, A.E. & CHAPMAN, C.A. (2001) Expediting reforestation in tropical grasslands: distance and isolation from seed sources in plantations. Ecol. Appl. 11, 1610-1621.

(Manuscript accepted 1 July 2008)

doi: 10.1111/j.1365-2028.2008.01016.x