

Tree–Shrub Interactions During Early Secondary Forest Succession in Uganda

R. Scot Duncan^{1,2} and Colin A. Chapman^{1,3}

Abstract

One of the greatest challenges for ecologists this century will be restoring forests on degraded tropical lands. This restoration will require understanding complex processes that shape successional pathways, including interactions between trees and other plants. Shrub species often quickly invade disturbed tropical lands, yet little is known about whether they facilitate or inhibit subsequent tree recruitment and growth. We examined how shrubs and other vegetation (e.g., vines, grasses, herbs) affect tree recruitment, survival, and growth during the first 6 years of forest succession in Kibale National Park, Uganda. The study was undertaken in two recently logged exotic softwood plantations. We studied the successional trajectories in two recently logged areas that varied in their initial densities of trees and shrubs. Analyses suggested tree seedling presence and density were not strongly related to shrub density or height during succession. Tree sapling presence and density were positively significantly related to shrub density and height. We found little response in the tree

community to experimental shrub removal, and although removal of all nontree vegetation temporarily enhanced tree growth, the effect disappeared after 2 years. Some early-successional trees benefited from reduced competition, whereas some mid-successional trees benefited from the presence of other vegetation. Some specific tree species responded strongly to vegetation removal. We interpret our findings in light of designing manipulations promoting forest restoration for biodiversity conservation and conclude with four tentative guidelines: (1) manage at the species level, not the community level; (2) increase facilitation for seedlings, reduce competition for saplings; (3) be cautious of assumptions about plant interactions; and (4) be adaptable and creative with new strategies when manipulations fail.

Key words: competition, degraded lands, facilitation, inhibition, management, regeneration, restoration, secondary forests, shrubs, thinning treatments, timber plantations, trees, tropical forest succession.

Introduction

During the 1990s, tropical lands were deforested at a rate of 127,300 km²/yr (FAO 1999). Restoring forests on these and other degraded lands will be one of the greatest challenges for restoration ecologists in this century (Brown & Lugo 1994). These forests will be important for providing extractable resources (e.g., timber), ecosystem services (e.g., soil and watershed protection), and habitat for animal and plant populations (Ewel 1986; Finegan 1992; Brown 1993; Brown & Lugo 1994). However, restoring these forests requires understanding principles of forest regrowth. In particular, managers need to know when, where, and how to intervene to initiate or accelerate forest succession for meeting management goals.

One important affect on forest succession is the interaction between trees and other plants of the successional community. On severely degraded lands, fast-growing nontree species, often vines, ferns, or grasses, can prevent or slow tree invasion (Borhidi 1988; Uhl et al. 1988; Kuusipalo et al. 1995; Chapman & Chapman 1999; Zanne &

Chapman 2001). Although shrubs often quickly invade degraded habitats, their role in forest succession is unclear. They may compete with trees for resources (e.g., light, nutrients) and slow forest regrowth (Putz & Canham 1992; Berkowitz et al. 1995; Holl 1998; Rogers & Hartemink 2000). Alternatively, shrubs may buffer harsh abiotic conditions and facilitate tree recruitment because abiotic conditions of degraded lands are often unfavorable for tree seedling recruitment (Nepstad et al. 1991; Vieira et al. 1994; Aide et al. 1996; Li & Wilson 1998; Raffaele & Veblen 1998; Zahawi & Augspurger 1999). Because unfavorable abiotic conditions increase with increasing site degradation, Bertness and Callaway (1994) and Callaway and Walker (1997) suggested that shrubs may facilitate tree recruitment in heavily degraded systems and hinder tree recruitment in less degraded systems. Similarly, shrubs could initially facilitate tree seedling recruitment in younger successional habitats and compete with trees in older successional habitats when conditions for tree seedling recruitment are more favorable (Callaway & Walker 1997).

We investigated how shrubs and other nontree vegetation (vines, grasses, herbs) affect tree recruitment and growth during the first 6 years of natural forest succession after clear felling in timber plantations in Kibale National Park, Uganda. First, we looked for correlations between shrub density and height and tree recruitment. Second, we removed shrubs from plots in an early-successional habitat

¹Department of Zoology, University of Florida, Gainesville, FL 32611, U.S.A.

²Author for correspondence: Division of Science and Mathematics, Birmingham-Southern College, Box 549022, 900 Arkadelphia Road, Birmingham, AL 35254, U.S.A., email sduncan@bsc.edu.

³Wildlife Conservation Society, Bronx, NY 10460, U.S.A.

and compared tree recruitment and growth between these and control plots. Third, we removed all nontree vegetation from plots in early-successional habitats and compared tree recruitment and growth between these and control plots. Because initial availability of on-site tree recruits after disturbance may affect interactions between trees and other vegetation, we compared positive and negative interactions between tree and nontree vegetation in two successional habitats differing in initial on-site recruit availability. We interpret our results in light of designing manipulations to promote forest succession.

Methods

Study Site

We studied forest succession in unlogged and logged exotic softwood plantations near Makerere University Biological Field Station (0°34'N, 30°21'E) in Kibale National Park, Uganda. Kibale is dominated by moist evergreen forest; mean elevation is approximately 1,500 m, and rainfall averages 1,543 mm/yr (1903–1999). Most plantations were established during the 1950s and 1960s on fire-maintained grasslands (*Pennisetum purpureum*, *Poaceae*; Osmaston 1959). These hilltop grasslands were present when the area was first described in 1914. Evidence suggests the grasslands were once forested, cleared for agriculture, and then abandoned when rinderpest invaded in the early 1900s (Osmaston 1959). Plantations were managed only for the first few years, and many species of native trees and shrubs colonized their understories as they matured (Zanne & Chapman 2001). Logging of plantations began in 1993 when Kibale became a national park, and current plans are to allow natural forest regrowth after logging. During logging, nearly all stems of plantation species are cut, and there is no regeneration of these softwood species at Kibale.

Pine (*Pinus caribaea* and *P. patula*, *Pinaceae*) and cypress (*Cupressus lusitanica*, *Cupressaceae*) were the main timber species planted at Kibale. Native trees in unlogged plantation understories are taller and denser in pine than in cypress (Fimbel & Fimbel 1996), and hereafter we refer to these plantations as “high density” and “low density” sites, respectively. Native stem recruitment differences between high and low density sites do not appear to result from soil properties, landscape position, or timing of planting (Osmaston 1959; Fimbel & Fimbel 1996). Instead, these differences are probably due to differential timber growth rates and understory light availabilities between plantation types (Fimbel & Fimbel 1996). These differences in preharvest stem density translated into disparities in on-site recruit availability for forest succession after harvesting. Both high and low density sites can be considered moderately degraded after logging, as opposed to heavily degraded habitats where unassisted forest succession proceeds very slowly (successional forest develops >10 years after disturbance). From May 1998 to October

2000, we studied forest succession in a chronosequence of pine and cypress plantations harvested from 1993 to 1998.

Tree and Shrub Interactions

We examined evidence for interactions between shrubs and trees before logging and during the first 6 years of succession after logging. For high and low density sites, we sampled one unlogged plantation, one recently logged plantation 1–3 years after harvest, and one plantation 5–6 years after harvest. The unlogged plantations were similar to the other plantations before logging. These were the only available pairs of similarly aged high and low density sites at Kibale. As is common among large-scale ecosystem manipulations, our design had limited spatial replication. However, this system provided a unique opportunity to study plant interactions between two systems differing in initial on-site recruit availability but sharing similar landscape positions, site histories, and site conditions.

Fimbel and Fimbel (1996) described differences in native stem recruitment below unlogged pine and cypress plantations at Kibale. To confirm these patterns and describe smaller stems not included in their study, we conducted vegetation surveys in the only remaining unlogged low density plantation and an adjacent unlogged high density plantation (thus controlling for landscape position and site history). Within each plantation, 15 nonoverlapping plots were positioned by choosing random distances along a 100-m transect and then choosing a random distance 1–60 m perpendicular to the transect. The open understory of the unlogged plantations allowed use of 25-m² circular plots that were faster to survey than rectangular plots used in logged plantation surveys. In plots we measured density, species richness, and height of all shrub and tree stems more than 1 m tall. We refer to these as “saplings,” though many shrubs were reproductively mature. Smaller stems (ht < 0.25 m) and intermediate stems (0.26–0.99 m tall) were sampled in circular 4-m² subplots. We refer to the smaller stems as “seedlings” and the intermediate-sized stems as “large seedlings,” though stems of either group may have been independent of seed reserves (especially large seedlings) or may have been root sprouts. Plant identification was based on Eggeling and Dale (1952), Polhill (1952), Hamilton (1991), and Katende et al. (1995).

Vegetation during the first 3 years of succession was surveyed with long-term plots (set up July–August 1998) in one recently logged high density site and one recently logged low density site (4 and 9 months after logging, respectively). Twenty-five nonoverlapping plots were randomly placed in each plantation along parallel transects (10 m apart) covering the logged area. These 5 × 5-m plots were surveyed at setup and at 2 and 3 years after harvest. Stems less than 1 m tall were sampled in 2 × 2-m subplots. Vegetation was quantified as in the unlogged plantation. Numbers of early-successional plots sampled after the first year varied because a few plots were destroyed by logging trucks or lost ($n = 22$ low density and 24 high density plots

2 years after harvest; 21 low density and 25 high density plots 3 years after harvest). Plots in heavily disturbed areas were excluded from analysis in this study. Many stems classified as seedlings in the first year (44% and 23% of shrub and tree seedlings, respectively) were actually sprouts from roots or coppice from stems buried during logging (Duncan 2001).

We also surveyed the oldest successional habitats in logged plantations (5–6 years after logging). The vegetation of one logged low density and one logged high density site was sampled once ($n = 28$ and 30 plots, respectively). Plot sampling followed that in recently logged plantations, except we used 2×10 -m plots for sampling the dense vegetation. Some former heavily disturbed areas may have been included in these surveys because these areas were hard to identify.

We chose binary logistic regression models to explore relationships between tree seedling recruitment and shrub stems. Like multiple regression, a logistic regression model assesses how well several independent variables predict a categorical dependent variable. One advantage of logistic regression is absence of assumptions about data distributions. This attribute was important because our data were highly zero-skewed, even after transformation. Mean tree seedling densities (seedlings/m²) for each plot were rounded to the nearest integer and categorized for two models. In the first model (model 1), plots were scored for the presence (“1”) or absence (“0”) of tree seedlings. In the second model (model 2), plots were scored for low (“0” for <1 seedlings/m²) or high seedling densities (“1” for >2 seedlings/m²). Plots were also categorized for presence (“1”) or absence (“0”) of tree saplings (model 3), and low (“0” for <1 sapling/m²) or high (“1” for >1 sapling/m²) tree sapling densities (model 4). Independent variables in each model included shrub sapling density and height, site (low or high density plantation), and sampling time relative to harvest. Sampling times were categorized as year 0 = before harvest, year 1 = within a year of harvest, year 2 = 2 years after harvest, year 3 = 3 years after harvest, and year 4 = 4–6 years after harvest. For these year categories, year 0 was used as the reference variable against which the effects of other years were compared. Both site and year independent variables were entered using binary coding, and all independent variables were entered simultaneously into the model. To provide a measure of how well these models fit the data, we present the $-2 \log$ likelihood for full models and the initial (null) model built with the constant but no independent variables. We provide the Nagelkerke R square value to describe the proportion of the model’s variance described by the independent variables. We present the model chi-square test of the null hypothesis that no independent variables are linearly related to the log odds (the probability of “0” divided by the probability of “1”) of the dependent variables (Garson 2001) and the percent of cases categorized correctly by the initial and full model. For each independent variable we present the logit coefficient (B) and the probability the coefficient has no effect based on the Wald statistic. Logistic regressions were performed with SPSS 10.0.5 for Windows (1999). This program and the VassarStats website for statistical computation (Lowry 2000) were used to analyze the following experiments.

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Shrub-Removal Experiment

To further examine effects of shrubs on early-successional tree recruitment, we removed shrubs in June 1999 from 19 plots in the only recently harvested plantation (a high density site) available at the time (approximately 8 months after harvest); 19 control plots were also established here. All plots were 5×5 m, a size seemingly appropriate for examining interactions among the small ($ht < 1.6$ m) trees and shrubs in this successional stage. In removal plots, larger shrubs (height approximately > 0.5 m) were cut at the base, whereas smaller shrubs were pulled from the ground. Subsequent shrub removal occurred every 3 months. Care was taken to avoid trampling other vegetation during shrub removal. Immediately after the first clearing and at the end of the experiment 16 months later, tree and shrub saplings were identified, counted, and their heights measured in removal and control plots. The final survey also included stems less than 1 m tall in 2×2 -m subplots in the center of larger plots. Because vines were abundant and may respond to shrub removal more quickly than trees, we ranked vine coverage on a 0–4 scale (0, no vines; 1, 1–25% coverage; 2, 26–50%; 3, 51–75%; 4, 76–100%).

Community-level tree density, species richness, and height were compared between the removal and control plots for saplings ($ht > 1$ m) and short ($ht < 1$ m) stems (heights of short stems were not compared due to the upper limit on their height for inclusion in this category). At the guild level, we compared removal and control plots for numbers of trees belonging to either early-successional or later successional categories. Late-successional species were uncommon and were pooled with mid-successional species for comparisons. Designations were based on identification manuals listed above and our own observations. We also compared species-level responses of individual trees between treatments. In this and the vegetation removal experiment (see below), data were largely zero-skewed and nonparametric analyses were used (e.g., Mann-Whitney, chi-square). Here and throughout, we describe our data with medians but also provide means to aid comparisons with studies reporting parametric data. Significance was set at $p < 0.05$, though nonsignificant differences at $p < 0.10$ are noted as “trends.”

Vegetation-Removal Experiment

To determine whether trees are affected by interactions with the entire plant community, we experimentally removed all nontree vegetation (shrubs, vines, grasses,

herbs) from plots in early-successional habitats. Plots were 5×5 m, with 2×2 -m center subplots for tree seedlings ($ht < 0.25$ m). These vegetation-removal plots were established within a year after harvest (August–September 1998) in the low density and high density sites where undisturbed succession was monitored with long-term plots ($n = 20$ and 22 removal plots, respectively). Sample sizes differed between plantations because some plots were destroyed by logging trucks. Plots were cleared of all nontree vegetation approximately every 4 months. Shrubs were removed as in the shrub-removal experiment; other vegetation was uprooted. During first removal, all remnant branches of plantation timber species were removed. Care was taken not to disturb trees during vegetation removal. Plots were surveyed as in the shrub-removal experiment when first cleared and at 1 and 2 years after initial clearing. Seedlings were quantified only during the final survey. Vegetation-removal plots were compared with long-term plots located within the same logged plantation.

Results

Tree and Shrub Interactions

Both models for tree seedling density fit the data well but showed limited predictive power for the independent variables and their interactions (Table 1, models 1 and 2). The models described less than 30% of the variance and increased the predictive power by less than 18% relative to the initial models. Shrub density and height were not significant predictors of seedling variables. Seedling presence and especially density were predicted significantly by several year variables, probably because seedling abundance fluctuated from year to year in both plantation types.

Models of tree sapling presence and density also fit the data well but explained little of the variance ($< 56\%$) and were of limited predictive power relative to the initial model ($< 3\%$; Table 2, models 3 and 4). However, shrub density was a significant predictor of both tree sapling presence and density. Spearman rank correlations between shrub sapling density and tree sapling density (as a continuous variable) indicated a significant positive relationship in the low-density plantations (for year 0, year 1, and year 3; $p < 0.05$) but not the high density plantations. Logistic regression revealed shrub height was a significant predictor of tree sapling presence. Spearman rank correlations indicated a positive relationship between shrub height and tree sapling density in the low density plantations (years 0, 1, and 4) and high density plantations (years 1, 3, and 4). Site was a significant predictor of tree sapling density because high density plantations start succession with higher densities of tree saplings than low density plantations.

Shrub-Removal Experiment

Tree sapling density, species richness, and height were initially similar between control and shrub-removal plots (Table 3). However, contrary to what might be expected, at the end of the experiment 16 months later, shrub sapling density, species richness, and height were lower in removal than control plots (Table 3). Shrubs less than 1 m tall were similar between treatments, probably due to resprouting.

At the end of the experiment, no differences existed between control and removal plots for densities or species richnesses of tree saplings or stems less than 1 m tall (Table 3). There was a trend for greater vine cover in removal than in control plots (Mann-Whitney test, $p = 0.091$). No

Table 1. Logistic regression models describing tree seedling ($ht \leq 0.25$ m) presence or absence and high or low density as predicted by shrub sapling ($ht \geq 1$ m) density and height, plantation type (site), and time relative to logging (year).

Model Statistics	Model 1		Model 2	
	Seedling Presence or Absence		Seedling High or Low Density	
Initial -2 log likelihood	306		312	
Model -2 log likelihood	267		253	
Nagelkerke R square	0.21		0.30	
Model chi-square and significance	39		59	
	$p < 0.001$		$p < 0.001$	
% of cases categorized correctly				
Initial model	60		56	
Model	71		74	
Coefficients of independent variables	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>
Shrub density	≥ 0.1	ns	-0.1	ns
Shrub height	0.1	ns	< 0.1	ns
Site	< 0.1	ns	0.1	ns
Year (overall)		≤ 0.001		≤ 0.01
Year 1	0.8	ns	1.5	≤ 0.01
Year 2	-1.2	≤ 0.05	-0.6	≤ 0.01
Year 3	-0.9	≤ 0.10	-0.4	ns
Year 4	0.6	ns	1.9	≤ 0.01

Coefficients (*B*) for the independent variables and their significance are also presented. See text for other details. ns, not significant.

Table 2. Logistic regression models describing tree sapling presence or absence and high or low density as predicted by shrub sapling density and height, plantation type (site), and time relative to logging (year).

Model statistics	Model 3		Model 4	
	Sapling Presence or Absence		Sapling High or Low Density	
Initial -2 log likelihood	173		188	
Model -2 log likelihood	94		156	
Nagelkerke R square	0.56		0.24	
Model chi-square and significance	80 $p < 0.001$		33 $p < 0.001$	
% of cases categorized correctly				
Initial model	87		86	
Model	90		86	
Coefficients of independent variables	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>
Shrub density	1.1	≤0.05	1.0	≤0.01
Shrub height	0.7	≤0.05	0.4	≤0.10
Site	-10.7	ns	-2.4	≤0.001
Year (overall)		ns		ns
Year 1	-0.2	ns	-0.4	ns
Year 2	-0.4	ns	1.0	ns
Year 3	-0.1	ns	-0.4	ns
Year 4	-1.1	ns	-0.8	ns

Coefficients (*B*) for the independent variables and their significance are also presented. See text for other details. ns, not significant.

differences existed in the number of early versus mid- and late-successional tree stems less than 1 m tall (chi-square, $p = 0.740$) or saplings (chi-square, $p = 0.238$). At the species level, only *Diospyros abyssinica* (Ebenaceae) had enough stems less than 1 m tall for comparison ($n > 10$) between treatments; there was a trend for more *D. abyssinica* stems in control than in removal plots ($n = 15$ and 6 stems, respectively; chi-square, $p = 0.081$). For saplings, *Trema orientalis* (Ulmaceae) had over twice as many stems in removal than in control plots, probably because it is a pioneer species (Table 4). All other species with sufficient sample sizes for comparison had similar numbers be-

tween treatments (Table 4). When sapling height was compared between treatments for species with more than six stems per treatment (sufficient for a *t*-test), *T. orientalis* saplings were 1 m taller in removal than in control plots (Table 4). There was a trend for taller *Celtis africana* (Ulmaceae) saplings in control than in removal plots (Table 4).

Vegetation-Removal Plots

After 1 year of vegetation removal in the logged low density site, tree saplings were taller in removal than control plots but tree sapling density and species richness were

Table 3. Initial and final medians (top number) and means (bottom number + SD) for vegetation variables in control and shrub-removal plots.

Stem Variable	Stem Height (m)			Density (stems/m ²)			Species Richness (species/m ²)		
	Removal Plot	Control Plot	<i>p</i>	Removal Plot	Control Plot	<i>p</i>	Removal Plot	Control Plot	<i>p</i>
Initial vegetation									
Tree saplings	1.5 1.6 (0.8)	1.3 1.4 (1.0)	0.323	0.2 0.2 (0.1)	0.1 0.1 (0.1)	0.361	0.1 0.1 (0.1)	0.1 0.1 (0.1)	0.231
Shrub saplings	—	1.1 0.8 (0.7)	—	—	0.1 0.1 (0.1)	—	—	<0.1 0.1 (0.1)	—
Final vegetation									
Trees < 1 m tall	—	—	—	0 0.2 (0.3)	0.3 0.2 (0.2)	0.289	0 0.4 (0.6)	0.3 0.2 (0.2)	0.301
Shrubs < 1 m tall	—	—	—	0.3 0.2 (0.2)	0.3 0.4 (0.7)	0.852	0.3 0.3 (0.3)	0.3 0.2 (0.3)	0.875
Tree saplings	1.6 1.7 (0.4)	1.6 1.6 (0.5)	0.665	0.4 0.4 (0.2)	0.4 0.4 (0.2)	0.563	0.2 0.2 (0.1)	0.2 0.2 (0.1)	0.954
Shrub saplings	1.0 0.7 (0.7)*	1.4 1.5 (0.6)	<0.001	<0.1 0.1 (0.1)	0.6 0.7 (0.6)	<0.001	<0.1 < 0.1 (<0.1)	0.2 0.2 (0.1)	<0.001

* Height < 1 m because some plots had no saplings.

Initial shrub variables in removal plots after clearing were nil, and heights of stems < 1 m were not compared (both indicated by “—”).

Table 4. Successional status, numbers, and heights of tree saplings in shrub-removal and control plots 16 months after initial treatment.

Species	Successional Status	Stem Number			Stem Height (m)		
		Removal Plots	Control Plots	p	Removal Plots	Control Plots	p
<i>Albizia grandibracteata</i>	e	29	19	0.195	1.6 (0.5)	1.6 (0.6)	0.971
<i>Celtis africana</i>	m	24	33	0.290	2.0 (0.7)	2.4 (0.9)	0.092
<i>Celtis durandii</i>	m	19	12	0.282	1.9 (0.5)	1.7 (0.9)	0.533
<i>Diospyros abyssinica</i>	m	38	36	0.888	1.4 (0.3)	1.5 (0.7)	0.243
<i>Fagaropsis angolensis</i>	m	3	8	0.227	1.6 (0.5)	1.4 (0.4)	—
<i>Funtumia africana</i>	m	19	14	0.488	1.9 (0.5)	1.7 (0.5)	0.361
<i>Olea welwitschii</i>	m	13	9	0.527	1.6 (0.5)	1.5 (0.3)	0.961
<i>Trema orientalis</i>	e	27	11	0.015	2.5 (1.0)	1.5 (0.5)	0.006

t-test results comparing sapling height and chi-square tests comparing sapling number between treatments are also presented (too few *F. angolensis* saplings were found for height comparisons).

e, early successional; m, mid-successional.

similar between treatments (Fig. 1). In the high density site, tree saplings were of similar height and density between treatments, but species richness was greater in control plots (Fig. 1). By the second year, no differences existed between removal and control plots for any tree variables in either the low or high density site (Fig. 1). Density and species richness of tree seedlings (ht < 0.25) did not differ between removal and control plots in the high density site (Mann-Whitney test, $p = 0.481$ and 0.448 , respectively) or the low density site (Mann-Whitney test, $p = 0.197$ and 0.127 , respectively).

In the high density site, sapling density of early- versus mid- and late-successional species was dependent on treatment, with greater numbers of early-successional saplings in removal than in control plots and greater numbers of mid- and late-successional saplings in control than in removal plots (chi-square, $p = 0.001$). Stems less than 1 m tall (this size category used instead of seedlings to have sufficient sample size for comparisons) showed no significant differences between treatment and successional status (chi-square, $p = 0.256$). In the low density site, interactions between treatment and successional status were not significant for numbers of saplings and stems less than 1 m tall (chi-square, $p = 0.841$ and 0.752 , respectively).

When treatments were compared at the species level, most tree species showing differences in sapling numbers had more stems in control than removal plots, regardless of the site considered (Table 5). The exception was *T. orientalis* in the high density site. In contrast, among stems less than 1 m tall, species differing between treatments usually had more stems in removal than in control plots (Table 5).

At the end of the experiment in the low density site, most tree sapling heights were similar between treatments, with two exceptions (Table 5). *Bridelia micrantha* (Euphorbiaceae) saplings were taller in control than removal plots, and there was a trend for taller *T. orientalis* saplings in removal than control plots. In the high density site, species were usually of similar heights between treatments; *T. orientalis* saplings were shorter in removal than in control plots.

Discussion

Tree and Shrub Interactions

Our analysis suggested shrub saplings had no detectable influence on tree seedling recruitment. This result was surprising considering that many others have found strong influences of shrubs on tree seedling recruitment. For example, Li et al. (1999) found that shrubs inhibited tree growth but enhanced soil nutrients in older subtropical successional forests. Berkowitz et al. (1995) found that nontree vegetation, including shrubs, inhibited tree seedling growth but facilitated tree seedling recruitment. Walker (1994) found a similar relationship between ferns and tree seedlings on landslides. We were also surprised that site type did not affect seedling recruitment given site differences in initial recruit availability. Similarly, Berkowitz et al. (1995) found that tree seedling growth was slow on low-resource sites due to physical stress but was also slow on high-resource sites due to competition with other plants. The only variable to have predictive power in our models was time since logging. This was not as surprising given the strong pattern of seedling recruitment seen through time in these successional habitats. Negative and positive relationships between tree seedlings and other vegetation probably caused these patterns (Duncan 2001). These patterns may change later in succession.

Our results suggest relationships between tree saplings and shrub density and height in the early stage of succession. Both shrub variables were significantly positively related to tree sapling density at several years in both high and low density sites. This pattern could be the result of facilitation of trees by shrubs, as others have found (e.g., increasing shade provides lower temperatures, greater soil moisture; Bertness & Callaway 1994; Callaway & Walker 1997). Alternatively, tree saplings could be facilitating shrub recruitment or growth. However, given the strong site effect on shrub density and that shrub saplings and tree saplings are strongly positively related before logging in the low density planta-

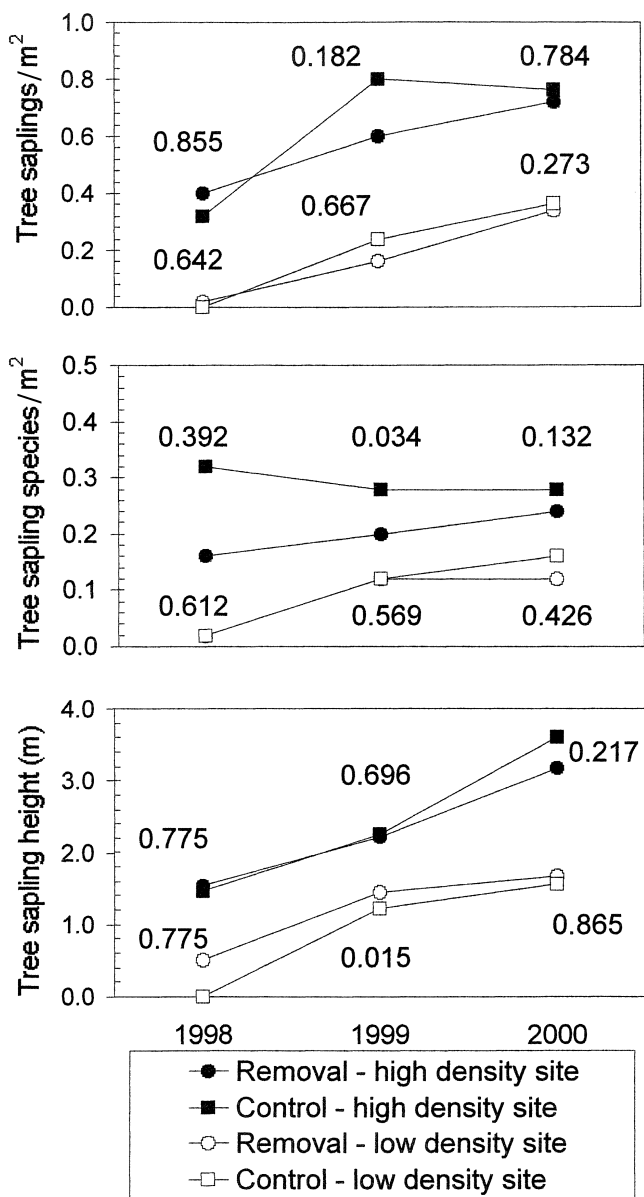


Figure 1. Median tree sapling density, species richness, and height during vegetation-removal experiments in early forest successions on logged high density and low density plantations in Kibale National Park, Uganda. Numbers are probability values of Mann-Whitney comparisons of treatments within plantation types.

tions, it is possible these results partially reflect patterns established before logging.

Our nonexperimental results suggest shrub saplings had little effect on tree seedling recruitment and survival during the first few years of succession. However, tree saplings recruited well in the presence of shrub saplings. This suggests that planting or removing shrub saplings to increase tree recruitment would not affect seedling densities but might improve sapling densities. Given the difficulty of inferring causal relationships from these patterns, removal

experiments are a stronger approach to discerning relationships between trees and other vegetation.

Vegetation- and Shrub-Removal Experiments

Although our correlative analyses suggested facilitative and competitive relationships between shrubs and trees, these patterns could also have been affected by plant responses to other variables (e.g., prelogging stem densities). Thus, we hoped an experimental approach would clearly illustrate interactions between trees and shrubs.

Removal of shrubs or all nontree vegetation seemed to have little effect on community-level tree recruitment or growth. Removal of nontree vegetation only temporarily enhanced tree growth in the logged cypress plantation and reduced tree species richness in the logged pine plantation. The absence of a strong removal effect suggests competitive-facilitative interactions were weak during this period of succession. However, several other explanations exist. First, these interactions may not have been apparent if resources (e.g., light) were relatively unlimited and there was no competition. Alternatively, shrubs and nontree vegetation both facilitated and limited tree recruitment and growth to similar magnitudes. It is also possible the time between vegetation removal events was so long that during intervening periods, shrubs and other vegetation recruited or regrew, thus reducing treatment effects. For vegetation removal plots, this may not be a likely explanation because nontree biomass appeared to be lower in removal than control plots throughout the experiment. For shrub removal plots, other vegetation may have replaced shrubs, obscuring their effect on tree recruitment and growth. Weak support of this was the trend for more vines in removal than control plots. In any case, shrub densities were sufficiently high at the shrub removal site to expect some response from trees (>1 shrub sapling/m²). Finally, limited arrival of seeds may have reduced the capacity of our experiments to detect strong effects of shrubs and other vegetation on tree seedling recruitment (Symstad & Tilman 2001), but Duncan (2001) estimated high levels of bird-dispersed seeds arriving in these habitats during the second year, with no subsequent increase seen in seedling recruitment. The effects of shrub or all nontree vegetation removal may have stronger effects later in succession as factors influencing these processes change.

In the high-density plantation there was some indication of differences between early- and mid- to late-successional species in response to shrub or nontree vegetation removal. Although these results suggested that nontree vegetation inhibited early-successional species and benefited mid- and late-successional species, no patterns were found among successional guilds in the other experiments. Thus, using successional status to predict tree responses to thinning at the community level may not be successful. However, several seedling species responded significantly (positively or negatively) to vegetation-removal treatments,

Table 5. Successional status, number, and mean (+ SD) heights of trees in vegetation-removal and control plots 2 years after initial treatment.

Species	Successional Status	Stem Number			Stem Height (m)		
		Removal Plots	Control Plots	p	Removal Plots	Control Plots	p
Low density site, saplings ht ≥ 1 m							
<i>Albizia grandibracteata</i>	e	17	29	0.077	2.1 (2.4)	2.6 (1.3)	0.406
<i>Bridelia micrantha</i>	e	29	40	0.163	1.4 (0.4)	1.8 (0.6)	0.010
<i>Celtis africana</i>	m	9	12	0.603	1.9 (0.6)	1.6 (0.4)	0.202
<i>Celtis durandii</i>	m	5	18	<0.001	1.3 (0.2)	1.7 (1.0)	—
<i>Croton macrostachys</i>	m	10	10	1.000	1.5 (0.3)	1.6 (0.4)	0.805
<i>Diospyros abyssinica</i>	m	8	5	0.655	1.2 (0.2)	1.4 (0.3)	—
<i>Maesa lanceolata</i>	e	47	96	<0.002	1.8 (0.8)	1.7 (0.6)	0.626
<i>Millettia dura</i>	e	8	3	0.252	1.7 (0.8)	6.0 (3.3)	—
<i>Trema orientalis</i>	e	27	20	0.467	2.0 (1.3)	1.4 (0.6)	0.078
Low density site, stems ht < 1 m							
<i>Albizia grandibracteata</i>	e	21	5	0.005	—	—	—
<i>Diospyros abyssinica</i>	m	15	5	0.054	—	—	—
<i>Maesa lanceolata</i>	e	2	13	0.007	—	—	—
<i>Millettia dura</i>	e	9	3	0.166	—	—	—
<i>Trema orientalis</i>	e	7	4	0.590	—	—	—
High density site, saplings ht ≥ 1 m							
<i>Albizia grandibracteata</i>	e	37	54	0.538	2.5 (1.5)	2.5 (1.2)	0.814
<i>Celtis africana</i>	m	24	50	0.050	2.7 (1.4)	2.9 (1.3)	0.373
<i>Celtis durandii</i>	m	18	21	1.000	1.8 (1.2)	2.6 (1.9)	0.156
<i>Clauseana anisata</i>	e	17	24	0.823	1.9 (0.8)	2.1 (0.9)	0.318
<i>Diospyros abyssinica</i>	m	64	80	1.000	2.2 (0.8)	2.4 (0.9)	0.120
<i>Fagaropsis angolensis</i>	m	5	9	0.708	3.4 (1.4)	2.9 (1.1)	—
High density site, saplings ht ≥ 1 m							
<i>Funtumia africana</i>	m	10	7	0.354	1.9 (0.5)	1.5 (0.5)	0.149
<i>Maesopsis eminii</i>	e	1	11	0.027	1.7	2.9 (1.3)	—
<i>Millettia dura</i>	e	10	25	0.083	3.4 (1.8)	3.8 (1.6)	0.549
<i>Mimusops bagshawei</i>	l	5	8	0.862	1.7 (0.8)	1.7 (0.8)	—
<i>Polyscias fulva</i>	e	8	12	0.862	2.3 (0.9)	2.8 (1.5)	0.430
<i>Teclea nobilis</i>	m	4	17	0.035	2.2 (0.4)	2.1 (1.0)	—
<i>Trema orientalis</i>	e	251	185	<0.001	4.5 (2.2)	5.8 (1.8)	<0.001
High density site, stems ht < 1 m							
<i>Albizia grandibracteata</i>	e	16	6	0.014	—	—	—
<i>Celtis durandii</i>	e	12	14	1.000	—	—	—
<i>Clauseana anisata</i>	e	7	8	1.000	—	—	—
<i>Diospyros abyssinica</i>	m	8	14	0.578	—	—	—

p values from comparisons between treatments of sapling height (*t*-test) and stem number (chi-square) are also presented. Heights were not compared for species with < 6 stems per treatment nor for stems < 1 m tall (both indicated by “—”).

e, early-successional; m, mid-successional; l, late successional.

suggesting a species-level approach to designing vegetation manipulation treatments may be advantageous.

Is this lack of a strong removal effect interesting? We believe it is considering there is much evidence for positive and negative interactions between trees and other vegetation in tropical successions. Holl (1998) found that shrubs and grasses inhibited tree seedling growth through both above- and belowground competition. Guariguata (1999) found that thinning of nearby vegetation helped trees grow in a 4.5-year-old successional forest. Li et al. (1999) found that shrub removal increased tree biomass only in forests older than 25 years and had no effect on tree density across a chronosequence. In Indonesia, Otsamo (1998a) found that removal of planted nurse crop trees improved growth of tree saplings planted several years earlier.

Zanne and Chapman (2001) found tree density and species richness was negatively related to shrub and herb density in unlogged pine plantations at Kibale.

In contrast to the above studies, growing evidence suggests that facilitation of trees by other vegetation is common in tropical forest successions. Chapman et al. (2002) found that tree survival was lower in vegetation removal than in control plots 4–6 years after logging in a cypress plantation at Kibale. Fast-growing exotic tree species planted in degraded areas can initiate natural recruitment of native tree species (Lugo 1997; Parrotta et al. 1997; Otsamo 1998b; Zanne & Chapman 2001), and several studies provided strong evidence that shrub species can facilitate tree recruitment in abandoned pastures (Vieira et al. 1994; Aide et al. 1996; Da Silva et al. 1996; Zahawi & Augspurger

1999). Thus, the limited positive and negative interactions between trees and other vegetation types found in this study contrasts with other studies of plant interactions.

Management Implications of Plant Interaction During Succession

Given that strong positive and negative interactions between trees and other vegetation seem to be widespread in most other tropical successions, when should managers encourage facilitation by planting and/or retaining nurse plants or limit competition by removing vegetation? Facilitation of tree seedling recruitment and growth by taller vegetation may be most successful as a management strategy in harsh habitats (e.g., hot, cold, dry; Bertness & Callaway 1994; Callaway & Walker 1997; Holmgren et al. 1997). Manipulations promoting facilitation may be most successful early in successions before a tall canopy develops and abiotic conditions improve. In less stressful habitats, facilitation strategies may help to reduce competition with grasses and vulnerability to fire (Kuusipalo et al. 1995; Holl 1998).

Predicting when and where plant competition will be important has been vigorously debated by plant ecologists (Grace 1991). One prominent argument is that intensity of competition across ecosystems varies depending on environmental stress (Grime 1979). Another is that competition can be high in all ecosystems (Tilman 1985). In either case, competition can be expected to be less important early in succession when resources are abundant and/or plant biomass is low (Lambers et al. 1998). Furthermore, because seedlings can temporarily rely on seed energy reserves and overall demands for resources are small relative to larger plants (Fenner & Kitajima 1999), competition is more likely among older stems than among seedlings (Callaway & Walker 1997). Thus, managers may expect a shift from facilitative to competitive interactions as successional forests develop, and vegetation thinning treatments may be helpful only later in succession when competitive interactions have intensified. However, in the early-successional habitats we studied, we found only limited support for these trends, suggesting managers should be cautious about assumptions regarding plant interactions in their systems.

Our results and those of others suggest four guidelines for determining when and how to intervene to guide forest succession towards species-rich mature forest. First, species-level responses to manipulations may be more important to consider than community-level responses. Thus, instead of conducting manipulations over a uniform area, managers should target individuals of species whose growth responses to manipulation are known (Guariguata 1999). This approach would also give managers a more active role in guiding forest composition to meet management goals (e.g., biodiversity conservation or timber production). Second, as described above, manipulations to encourage facilitation should target seedlings, whereas manipulations to

limit competition should target older trees. One exception may be small-seeded early-successional tree seedlings that require high light levels immediately after germination (Finegan 1984; Foster & Janson 1985; Fenner & Kitajima 1999). Third, as our study and others have found, plant interactions during succession tend to be complex. Thus, managers should be cautious when designing manipulations. Finally, our results show that manipulations to enhance tree recruitment can fail. Thus, managers should monitor the success of manipulations relative to control treatments and should be ready with new strategies if manipulations fail.

Currently, a great opportunity exists for advancing the field of tropical forest dynamics by conducting more studies of plant interactions during succession. In particular, we believe two types of studies are needed: experimental studies to separate complex interactions between species and broad-scale comparative studies to identify how plant interactions vary across ecosystems and disturbance types. Both approaches will be essential for advancing the ability of restoration ecologists to design successful management strategies.

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