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Applying ecological knowledge to decisions about seed tree retention in selective logging in tropical forests

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ABSTRACT

In production forests in the moist tropics, trees are selected for felling or retention primarily by species and size. Tree regeneration requirements and forest stand responses to harvesting are often ignored, and consequently, the regeneration of the residual forest is not ensured. We developed and tested an alternative approach to tree selection, where seed trees were retained as a proportion of harvestable trees, with the proportion defined as a function of species' ecological attributes and local abundance (100 ha), in contrast to the conventional approach which retained 10% of harvestable trees, uniformly across commercial species at the compartmental scale (1000 ha). The study was conducted in Democracia Project, a forest management operation in Amazonas, Brazil. The conventional approach failed to retain any seed trees at the 100 ha block scale for 7 of 37 commercial species, whereas the alternative approach retained a minimum number of seed trees per 100 ha block for all commercial species. The conventional approach resulted in the retention of relatively high proportions of potential seed trees for common species (e.g., 22% for *Eperua oleifera* and 36% for *Maquira sclerophila*) that are shade bearers and recruit readily at the site; alternately, for species with constraints to regeneration, it retained relatively low proportions (e.g., 2% for *Dinizia excelsa* and *Hymenolobium nitidum*). The alternative approach effectively retained lower proportions of common species (e.g., 10% for *E. oleifera* and 13% for *M. sclerophila*) and relatively high proportions of species with regeneration constraints (e.g., 20% for *D. excelsa* and 16% for *H. nitidum*). Our study demonstrates that it is feasible to implement at an operational scale, species-specific retention rules that take into account local abundance when inventory data are digitised and spatially explicit. Monitoring regeneration in the residual stands over time will provide the evidence to assess the ecological benefits of the adoption of our alternative approach.

1. Introduction

Reduced impact logging (RIL) is recognised in the tropics as an important component of natural forest management, with its main objectives to minimize soil disturbance, impacts on wildlife, and damage to residual trees (Sist, 2000). The emphasis on controlling incidental damage associated with logging is important for polycyclic management systems (Dawkins and Philip, 1998), however, RIL is not a silvicultural system, is not meant to promote forest regeneration, and its adoption and implementation is not enough to guarantee sustainability in forest management (Putz et al., 2000; Pinard et al., 1995; De Graaf, 2000; Hammond et al., 2000; Leslie, 2001; Sist, 2001; Sist et al., 2003). A more complete silvicultural approach is needed to ensure adequate regeneration and stand development for future harvests.

Consideration of the regenerative capacity of managed forests begins at the first harvest, with the choice of trees to be retained and felled. In polycyclic management systems, tree selection refers a process by which trees are selected for retention or felling for a given cutting cycle, based on criteria established to achieve the objectives of management. It is an important part of forest management because it represents a synthesis of decisions taken to regulate yield, to plan harvest, to protect residual forest structure and to meet market demands.

In most of silvicultural systems proposed in literature and practiced in the tropics, tree selection is based on minimum felling diameters (MFD) (Dawkins and Philip, 1998; Lamprecht, 1993), and not uncommonly a single MFD is applied for all species (Bruenig, 1996). In some systems, a proportion of the harvestable stock is retained to guarantee the next harvest or as seed trees to favour regeneration. Simplicity and practicability are essential for the

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implementation of management prescriptions to be feasible, however, oversimplification can undermine sustainability.

For example, when MFD is used as the only criterion for selecting trees for harvest, the removal of larger stems from a population can impair subsequent regeneration due to loss of fruit and seed sources (Sheil and van Heist, 2000) and in cases where logging is highly selective for a rare species, and seed trees are not retained, that species can become extirpated over large forest areas (Johns, 1997). Systems that require the retention of a proportion of the harvestable trees as seed trees should have less negative impacts than those that do not. However, a common weakness in the seed tree retention rules that are used across the tropics is that they are often unrelated to the ecology of the forest species (Guariguata and Pinard, 1998). The size of retained trees is commonly based on the MFD and the number of retained trees is generally not species-specific. In tropical forests of Bolivia, the regulation to ensure the retention of seed trees is to reserve 20% of each cutting unit from harvest (Fredericksen et al., 2001). In Ghana, the guideline requires the retention of two to four seed trees of each exploited species in every 120 ha cutting unit (Swaine et al., 1997; Agyeman et al., 1999). Guidelines from Queensland, Australia state that seed trees should be retained at an average spacing of 40 m × 40 m (Vanclay, 1989). Hasanbahri (1997) suggested the retention of one tree per hectare or about 100 trees of different commercial species in every (100 ha) cutting block to manage forests in Indonesia (dipterocarp and non-dipterocarp); and in the Amazon, the retention of 1–2 seed trees per hectare (Projeto Embrapa-CIFOR, 2000) or 10 adult trees per species per 100 ha (Thompson and Yared, 1999) have been recommended.

In the Brazilian Amazon, rules for seed tree retention in production forests were issued by the government in 1995 (Portaria 048/95) (IBAMA, 1995); they require a minimum of 10% retention of trees with DBH ≥ 45 cm per species. In 2002, the rule was restated by the Instruction No. 4 (MMA-Ministério do Meio Ambiente, 2002), as a directive that harvestable volumes should take into account species' regeneration capacity. Species specific regulations were issued later for *Virola surinamensis* (Silva and van Eldik, 2000) and *Swietenia macrophylla* (IBAMA, 2003). More recently, the regulations were revised again, requiring the retention of at least 10% of the harvestable trees per species, chosen over operational units of approximatelly 100 ha (MMA-Ministério do Meio Ambiente, 2006).

As the previous examples attest, seed tree retention rules are considered relevant to natural forest management in many tropical countries. However, the effectiveness of the various rules for enhancing the regenerative capacity of the residual stands remains untested. Concerns about weaknesses in current rules are various, but a primary weakness is that they do not take into account differences in regeneration ecologies of species (Fredericksen et al., 2001); for example, when a single rule is applied across all commercial species, retention requirements may be too stringent for some species and inadequate for others. If species-specific rules were to be devised, it is necessary to establish what attributes should be used to define the rules. Furthermore, experience is needed to determine feasibility and effectiveness of the rules at scales that are relevant to forest managers.

In this paper, we present an approach to seed tree retention based on ecological attributes and forest owner's priorities for timber marketing. We compared the implications of the alternative rules with the conventional rules by applying them to six 100 ha blocks of a harvest compartment, and then examining the effectiveness of the rules at retaining species with limitations for regeneration. We also analyse the composition, density and spatial variability of the pool of trees retained under the two set of rules. We also examined the implications of the two approaches to tree selection in a harvesting experiment, where we compared harvested volume, residual stand damage, soil damage and canopy disturbance (gap numbers and sizes) (Freitas and Pinard, manuscript). The results from the experiment provide an indication of the differences in harvesting impacts of the two approaches, but the longer term regeneration outcomes following the application of the two approaches have not yet been explicitly tested.

2. Methods

2.1. Study site

The study was carried out between 2000 and 2003 in Democracia Project, a forest management enterprise located in Manicoré, a district of the State of Amazonas, Brazil (Fig. 1). The project area is alongside the Madeira River, a tributary of the Solimões River. The owner of the enterprise, Gethal Amazonas S.A., managed the forest for timber to supply its plywood factory. In 2000 the project received FSC (Forest Stewardship Council) certification.

The climate is tropical, with mean monthly temperatures of 24–26° and relative humidity of 85–95%. Annual rainfall is 2520 mm (mean calculated from 1970 to 2002). The rainy season starts in October with rainfall peaking from January to April; a dry season typically occurs from July to September. The area, about 40,000 ha, is predominantly covered with 'Terra-firme' Dense Tropical Forest (Pires and Prance, 1985), with an average canopy height of 27 m, and emergent trees to 50 m.

The area was managed according on a polycyclic system, with 25 year cutting cycles and a maximum expected harvest intensity of 12 trees ha^{-1} (Gethal Amazonas, 2001). Harvesting was done following RIL guidelines. The harvest activities were inspired by Tropical Forest Foundation (TFF) methods for RIL (Blate et al., 2001), including a periodic training program for the enterprise's teams. The main commercial species were *Eperua oleifera*, *Brosimum rubescens*, *Scleronema micranthum*, *Brosimum potabile*, *Clarisia racemosa* and *Erisma* spp. The MFD for the majority of the species (67%) was 45 cm DBH, although for some species it was set at 55 or 60 cm DBH, predominantly because of milling requirements.

2.2. Approaches to seed tree retention

The approach used by the enterprise for seed tree retention (hereafter, conventional) consisted of selecting, for each commercial species, a minimum of 10% of total number of trees over 45 cm DBH in a harvest compartment (1000–1500 ha). Trees of any stem quality could be included as potential seed trees (Table 1).

In the experimental approach (hereafter, alternative) the proportion of seed trees to be retained was calculated in reference to species ecological attributes (elaborated below) and the number of potential seed trees within a 100 ha unit. The number of potential seed trees was defined as the number of trees above the species minimum diameter felling (MFD), with stem quality other than poor. Tree selection was done at a 100 ha rather than 1000 ha scale to achieve more uniform retention across the harvest compartment, and to more explicitly match retention to local abundance (number of potential seed trees) and distribution (frequency). In the next few paragraphs, the rationale and methodology used for determining which ecological attributes were considered and how they were applied, along with the method for determining species specific MFDs are elaborated. The main differences between the two approaches are summarized in Table 1.

The ecological attributes used in the alternative approach were identified during a research exercise to characterise the commercial species known at the study site (see Freitas, 2004). Briefly, the

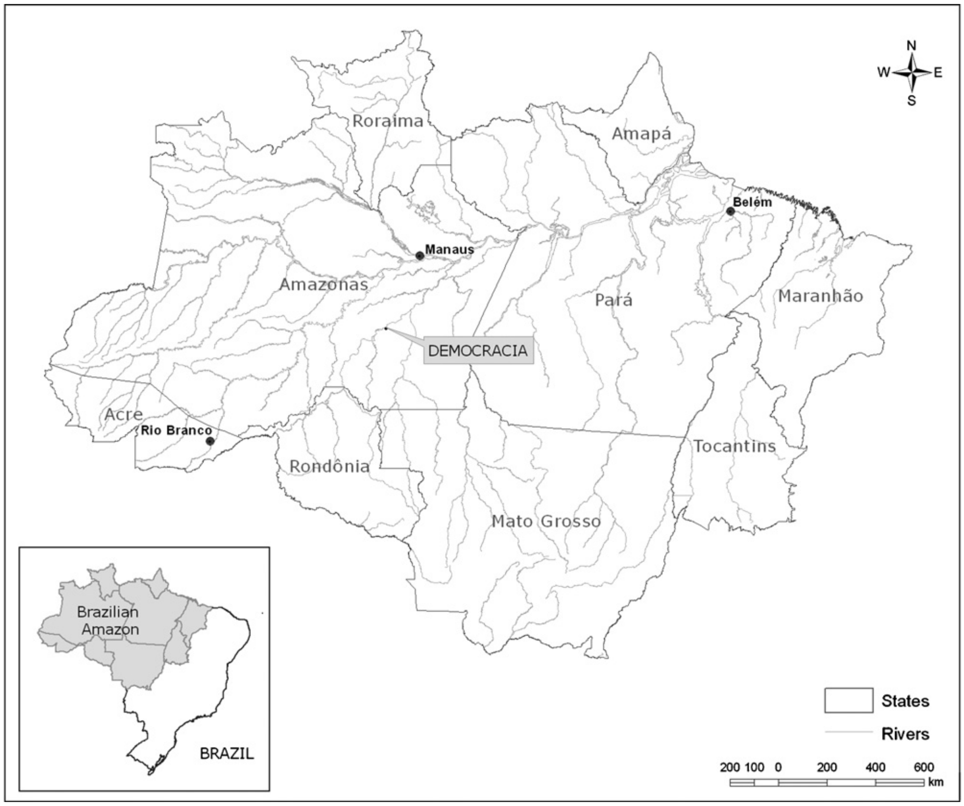

Fig. 1. Map of the Brazilian Amazon, indicating the location of the study site, the Democracia Forest Management Project located on the Madeira River near Manicore.

characterisation was based on information about species' ecologies gathered from the literature, herbarium research and analyses of abundance and distribution data from the study area. The aim was to identify silvicultural interventions that would enhance the regeneration of the commercial species. Data on 55 of the 75 commercial species known in the area were collected and analysed using multivariate analyses and correlation analyses. Of the 11 attributes considered by Freitas (2004), 7 were used in the study presented here to determine the proportion of seed trees to be retained in a given 100 ha unit. These attributes were selected because of their utility in grouping the species by silvicultural requirements.

The seven attributes considered were as follows: (1) shape of the diameter class distribution associated with shade tolerance; (2) seed dispersal mode; (3) sexual system; (4) frequency (percentage of 50 m × 50 m plots in 100 ha with at least one tree ≥35 cm DBH); (5) adult abundance; (6) regeneration abundance and (7) regeneration priority (Table 2).

The maximum level of retention was arbitrarily set at 30% and the minimum level was set at 10%, in accordance to enterprisés method. The seven attributes together were used to determine what percentage, between 10 and 30, should be retained for each species in each 100 ha block. The attributes were weighted subjectively, in relation to our understanding of their relative importance for requirements for regeneration by seed, i.e., the shape of the diameter class distribution and seed dispersal mode had greater relative influence than adult tree abundance (Table 2).

Each attribute was expressed as a categorical variable, with three classes. The three classes within a given attribute were defined such that they represented a state or condition that would justify relatively fewer or more trees to be retained. For example, adult tree abundance (N ha^{-1}) was expressed in three classes: >2 (less); 0.5–2 (intermediate); and <0.5 (more). When a species had on average >2 trees per ha, we assumed that fewer seed trees would need to be retained than when one had <0.5 per ha. In this way, each class within each attribute was associated with a

Table 1
Summary of the two approaches to seed tree retention used in this study

Characteristics	Tree selection for retention treatments	
	Conventional	Alternative
Minimum DBH[a] of potential seed trees[b]	45 cm	45, 55 or 75 cm DBH[c]
Scale of selection	Annual harvesting compartment (>1000 ha)	Stands up to 100 ha within annual compartment
Target percentage of seed tree retention	10	10–30
Species-specific	No	Yes
Stem quality of potential seed trees	All	Very poor not included
Tree-by-tree selection method	Manually on computer screen (worksheet)	Manually on computer screen (GIS)
Minimum retention rules	No	Yes

[a] DBH, Diameter at breast height (1.30 m).
[b] Potential seed tree: a tree with attributes required to be selected as a seed tree.
[c] Based on a minimum felling diameter set considering the species maximum attainable DBH at the study site.

Table 2
Attributes with their three classes and associated weightings used to calculate the proportion of trees to be retained as seed trees

Species attribute	Class (weighting)		
	Less	Intermediate	More
Shape of diameter distribution[a]	Type I (0.0)	Type II (0.2)	Type III (0.4)
Seed dispersal mode	Animal (0.0)	Wind (0.1)	Gravity (0.15)
Sexual system	Non-dioecious (0.0)	–	Dioecious (0.1)
Frequency[b] (%)	>60 (0.0)	30–60 (0.05)	<30 (0.1)
Adult abundance (N trees $\geq$ 45 cm DBH ha^{-1})	$\geq$2 (0.0)	0.5–2 (0.03)	<0.5 (0.05)
Regeneration abundance (N trees 5 < DBH < 15 cm ha^{-1})	$\geq$20 (0.0)	5–20 (0.05)	<5 (0.1)
Regeneration priority[c]	3 (0.0)	2 (0.05)	1 (0.1)

The sum of the weightings calculated proportion is applied to 30% of total number of potential seed trees within 100 ha blocks.
[a] Type I, inverse *J*; Type II, irregular number of individuals across all classes; Type III, species with absence of individuals in the smaller classes.
[b] Species frequency within 100 ha blocks – trees DBH $\geq$ 35 cm: percentage of the number of 50 × 50 plots within blocks in which at least on tree DBH $\geq$ 35 cm was found.
[c] 1, High priority for forest owner because of marketability; 2, intermediary priority; 3, with no need for regeneration other than the minimum for less important species.

weighting that, when the weightings from the seven attributes were summed for a given species, that weighting would determine the proportion of trees to be retained. If a species had class A for each of the seven attributes, the minimum proportion would be retained, whereas if a species had class C for each, the maximum proportion would be retained (30%).

Also as part of the alternative method, MFDs were established for all species in reference to the maximum attainable DBH for the area. Maximum attainable DBH was determined by analysing the diameter class structure from the compartment inventory data, and defined as the highest diameter class that included within it and all the classes below it, 90% of the total number of individuals at the compartment scale. No growth data were available from permanent sample plots nearby or for all species from regional studies. MFD for species with a maximum DBH within the 55–65 cm DBH class was set at 45 cm. For those species with maximum DBH between 65 and 95 cm, the MFD was set at 55 cm, and for species whose maximum DBH was greater than 95 cm, the MFD was set at 75 cm.

A series of computational programming routines was written in Microsoft Visual Fox Pro 6.0 to handle data from the main file containing the 100% pre-harvest inventory data and a secondary file containing the species attributes, afterwards calculating the number of potential seed trees and the number of seed trees to be retained per species. The main file (pre-harvest inventory) was shared with a GIS (Geographic Information Systems) (ESRI-ArcView) database for the whole compartment. Additionally to the basic routine to generate the species seed tree numbers additional routines were included with the following instructions, aimed at regulating the minimum number of seed trees retained within 100 ha blocks:

(1) A minimum of 10% of seed tree retention must be achieved for each species: when the calculated number of seed trees was less than 10% of the number of potential seed trees, the number of seed trees was elevated to 10% retention.
(2) If one species had only one potential seed tree, this tree was automatically selected and the species percentage of retention in this case was 100%, assuring that at least one tree greater than MFD was left as a seed tree.
(3) If one species had between 2 and 19 potential seed trees, the calculated number of seed trees was not less than 2, in order to assure that at least 2 trees were selected. When the number of potential seed trees was greater than 19, the minimum of 10% automatically achieved this minimum of 2 retained trees.
(4) Decimal seed tree numbers were rounded up to the next integer.

Finally, the tree-by-tree selection was based on GIS, manually on the screen. For each species, the total number of potential seed trees was searched and retrieved to the screen as the only visible theme, and the calculated number of seed trees selected based on species occurrence within the 100 ha block, as much as possible avoiding selection of trees very close each other (<30 m) as well as trees very far from each other when the number of potential seed trees was small (<10). In the main file (100% pre-harvest inventory data), selected trees received a code to identify them as seed trees so that the next steps could be taken (selection for felling and map plotting) considering their new attribute.

2.3. Experimental design and statistical analysis

The conventional process to select trees for retention as seed trees was carried out by the enterprise's team at the time of harvest planning, at harvest compartment scale (1315 ha), while the alternative process was applied at a smaller scale (100 ha stands). Therefore, for the purpose of the statistical comparisons between treatments to select seed trees, it was assumed that both selected seed trees for the whole compartment, but comparisons were made based on six blocks of 100 ha each (1000 m × 1000 m) Thus, the statistical analysis considered six plots of 100 ha each, in which alternative and conventional approaches were compared for seed tree retention, hereafter blocks (B, C, F, G, K and J). Only the 37 species occurring in all six blocks were included in the analysis and occasionally comparisons were made for 22 species sharing the same minimum felling diameter in the different treatments, in order to compare treatment effects when the potential number of seed trees is not affected by the differences in MFD.

Comparisons between treatments were made on percentage retention (%) of the total number of potential seed trees, as well as specified reference thresholds, and occasionally by stand variables like number of trees and volume. Because both conventional and alternative approaches were compared using data from the same six plots (100 ha blocks), paired *t*-tests were used in most of the statistical comparisons and assumptions for normality were tested for each treatment of each paired analysis using Kolmorov–Smirnov tests (Kinnear and Gray, 2000). When normality was not achieved, transformations (squared root) were used and in this case, when normality was not achieved the treatments were compared using non-parametric Friedman tests, which can be used to compare paired treatments (Sokal and Rohlf, 1995). For comparisons of treatment effects on different species, a split plot general linear model was used (test of between-subjects effects), with block as a random factor and treatment as a fixed factor, for the variable square-root of species percentage of retention. The block effect was not significant therefore, additional analyses were made by species to compare treatments by species, where the number of seed trees were pooled across the blocks to reduce the effect that the low number of potential seed trees may have on the results for each species.

Table 3
Descriptive statistics for six 100 ha stands (blocks) within the annual compartment (600 ha)

Variable	Block (100 ha stands within annual compartment)						Average (95% CI)
	B	C	F	G	J	K	
All species							
Number of trees (DBH $\geq$ 35 cm; N ha^{-1})	37.7	33.9	36.6	36.9	39.3	38.2	37.1 ($\pm$1.5)
Basal area (DBH $\geq$ 35 cm; m^2 ha^{-1})	10.0	9.8	9.5	10.2	10.3	10.7	10.1 ($\pm$0.3)
Commercial species							
DBH $\geq$ 35 cm (N ha^{-1})	17.0	16.6	18.6	18.5	15.8	21.0	17.9 ($\pm$1.5)
DBH $\geq$ 45 cm (N ha^{-1})	11.3	11.9	13.1	13.1	11.5	15.7	12.8 ($\pm$1.3)
Volume DBH $\geq$ 45 cm (m^3 ha^{-1})	48.0	56.3	58.8	61.6	54.5	77.1	59.4 ($\pm$7.9)
Volume *Eperua oleifera* (m^3 ha^{-1})	7.9	18.3	22.9	24.2	18.9	46.6	23.1 ($\pm$10.2)
Non-pioneer shade bearers (percentage of N)	72.2	64.8	76.8	73.7	81.5	81.9	75.2 ($\pm$5.2)
Non-pioneer light demanding (percentage of N)	25.3	31.6	19.6	23.5	17.5	16.6	22.4 ($\pm$4.5)
Pioneers (percentage of N)	2.5	3.6	3.6	2.7	1.0	1.5	2.5 ($\pm$0.9)

Values in brackets for average column are confidence intervals (α = 0.05; N = 6). Commercial species include the 37 species considered in this study and the percentages given for ecological groups are based on the 37 commercial species.

3. Results

In the six 100 ha blocks used for the study (Table 3) average tree density (DBH $\geq$35 cm, all species) was 37.1 stems ha^{-1} (CI = $\pm$1.5; α = 0.05) and basal area was 10.1 m^2 ha^{-1} (CI = $\pm$0.3; α = 0.05). The stock of commercial species, considering only 37 species included in the comparisons for seed tree retention, was 12.8 trees (CI = $\pm$1.3) corresponding to a mean volume per hectare of 59.4 m^3 ha^{-1} (CI = $\pm$7.9). Tree volumes were estimated using a regional volume equation (Fernandes et al., 1983). There was variation across blocks for volume of trees DBH $\geq$ 45 cm (Table 3); differences in volumes in the common species, *E. oleifera* were responsible for the differences, Block K had more volume of this species relative to the other blocks, particularly Block B, where its abundance was the lowest. In all six blocks the majority of trees were non-pioneer shade bearers (75.2 $\pm$ 5.2%).

3.1. Seed tree retention for all commercial species

Considering the 37 commercial species, the mean number of trees considered to be potential seed trees was greater in the conventional relative to the alternative tree selection treatment (Table 4), not surprisingly as the conventional approach included trees with poor stem quality and trees to a lower diameter limit for some species (Table 2). As a result, the conventional process selected almost twice as many seed trees the alternative.

The overall percentage of retention, meaning the number of selected seed trees in the compartment (600 ha) divided by the corresponding total number of potential seed trees, was 16.7% for the conventional and 16.1% for the alternative, similar values for the two approaches (t = 1.4; d.f. = 5, p = 0.23).

If only the 22 species that shared the same MFD under the two approaches, the number of potential seed trees was still greater in the conventional than alternative, as well as the number of seed trees retained. The overall percentage of retention for the compartment was again similar for the two approaches, 20.4% for the conventional and 17.8% for the alternative approaches (t = 1.8; d.f. = 5, p = 0.13).

3.2. Seed tree retention for individual species

In every one of the six blocks, the conventional process retained no seed trees for at least one species and, on average, 18% of the

Table 4
Results of seed tree retention statistics for conventional and alternative approaches; results are presented for two groups, the 37 commercial species that occurred in all blocks, and the 22 species that shared the same minimum felling diameter (MFD) within the two tree selection processes

	Conventional approach	Alternative approach	T-statistic (p-value)
Results for 37 species			
Number of potential seed trees per 100 ha block	1275.8 ($\pm$130.2)	718.5 ($\pm$30.3)	8.7 ($p < 0.01$)
Number of seed trees retained per 100 ha block	213.5 ($\pm$16.6)	121.8 ($\pm$3.1)	9.6 ($p < 0.01$)
Average density of seed trees retained per ha	2.1 ($\pm$0.2)	1.2 ($\pm$0)	–
Overall compartment percentage retention	16.7	16.1	–
Average percentage retention per block	16.9 ($\pm$1.8)	16.1 ($\pm$0.3)	1.4 ($p < 0.23$)
Number of stands with 0% seed tree retention	6	0	–
Mean percentage of species with 0% retention (%)	18.0 ($\pm$3.5)	0	10 ($p = 0.01$)
Minimum retention per species (%)	0	10.1 ($\pm$0.1)	−241.0 ($p < 0.01$)
Mean retention per species (%)	20.0 ($\pm$2.3)	31.5 ($\pm$4.2)	−6.5 ($p = 0.01$)
Maximum retention per species (%)	75.8 ($\pm$16.1)	100.0	−2.9 ($p = 0.03$)
Results for 22 species with equal MFD[3]			
Number of potential seed trees per 100 ha block	363 ($\pm$31.2)	335 ($\pm$33.6)	9.9 ($p < 0.01$)
Number of seed trees retained per 100 ha block	74 ($\pm$13.5)	59.5 ($\pm$3.2)	2.6 ($p = 0.05$)
Average density of seed trees retained per ha	0.8 ($\pm$0.1)	0.6 ($\pm$0.1)	–
Overall compartment percentage retention	20.4	17.8	–
Average percentage retention per block	20.3 ($\pm$2.3)	17.9 ($\pm$0.9)	1.8 ($p = 0.13$)
Number of stands with 0% seed tree retention	6	0	–
Mean number of species with 0% retention (%)	30.3 ($\pm$4.4)	0	13.5 ($p < 0.01$)
Minimum retention per species (%)	0.0	10.5 ($\pm$0.3)	−65.9 ($p < 0.01$)
Average retention per species (%)	20.4 ($\pm$1.2)	27.0 ($\pm$3.1)	−3.8 ($p = 0.01$)
Maximum retention per species (%)	71.2 ($\pm$11.7)	86.1 ($\pm$17.7)	−2.5 ($p = 0.06$)

In all cases, N = six 100 ha blocks.

species had no seed trees retained at the 100 ha block scale (Table 4). Conversely, the alternative process retained the minimum of 10% per species in all blocks and achieved higher mean percentage retention per species (32%) than the conventional (20%). The maximum percentage retention per species also was greater for the alternative (100%) than conventional (76%), meaning that the latter did not select all trees for any species, independent of the number of potential seed trees found in the 100 ha block.

Considering only the 22 species with the same MFD, the ANOVA revealed significant treatment ($F = 54.5$; d.f. = 1.5; $p < 0.01$) and species ($F = 6.0$; d.f. = 21.210 $p < 0.01$) effect, as well as an interaction between treatments and species ($F = 6.8$; d.f. = 21.210; $p < 0.01$). The block effect (random factor) was not significant ($F = 0.85$; d.f. = 5.210; $p = 0.57$).

To illustrate the variability among the percentage of retention based on species ecological and silvicultural attributes in the alternative process, the results for 23 species (percentage of retention) only in blocks where the number of potential seed trees were greater than 9 are presented in Table 5. The results show that the alternative tree selection process was sensitive to the species ecological characteristics, retaining more seed trees for species with more limitations to regeneration. For example, the species that are in the top of the table have a diameter distribution that follows an *inverted-j* curve (principally, non-pioneer shade bearers) and adequate recruitment; they had seed tree percentage retention close to the minimum (10%), varying up to 12%. Amongst them was *E. oleifera* (10.4%), the most important species in the forest structure within the experimental blocks. Species with adequate recruitment, but with light demanding regeneration (i.e., have an irregular diameter distribution), had intermediate levels of retention, ranging from 13.4 up to 16.9%. This group included *Parkia pendula*, *Andira* spp., *Hymenolobium nitidum* and *Peltogyne paniculata*. Those few shade bearer species identified as having inadequate recruitment, achieved retention rates ranging from 12.2 up to 13.5%, values slightly above the percentage achieved by the majority of shade bearers. Finally, a different pattern of seed tree retention is shown for the species at the bottom of Table 5, with retention rates ranging from 15.4 up to 25.4%. Most of the commercial species included in this group are non-pioneer light demanding species, which were identified as having inadequate recruitment and rare as adults; each species in this group presents a particular limitation for regeneration. For example, *Simarouba amara* (23.2%) is dioecious species, and *Piptadenia suaveolens*, *Dinizia excelsa* and *Hymenolobium excelsum* are wind dispersed.

On the other hand, because the conventional process did not consider any species ecological information, it achieved inadequate retention for some species and potentially excessive retention for others. For example, *E. oleifera*, *Copaifera multijuga* and *Maquira sclerophila* are all species with adequate recruitment, with individuals present in the forest across all diameter classes. *Eperua* and *Maquira* are also common species, and the latter is a low priority species to regenerate. For these species, retention rates were higher than the minimum required (21.8; 20.4; and 35.6%, respectively). For some species with constraints to regenerate, the percentages of retention were lower than the minimum required. This group included *S. amara* (8% seed tree retention), *D. excelsa* (2.3%), *H. nitidum* (2.3%) and *H. excelsum* (9.3%). *Goupia glabra* was classified as a pioneer species because it requires large gaps for seedling establishment (Mory and Jardim, 2001) and the alternative process was more sensitive to its constraints retaining more seed trees (20%) than the conventional process (7%).

4. Discussion

In this study we compared the performance of two methods for selecting trees for retention as seed trees, with the main differences between the two methods being the scale at which retention decisions are made and allowances for species differences in terms of abundance and constraints for regeneration. In the first part of the discussion, we consider the relevance of our results to the overall objective of promoting regeneration of

Table 5
Species ecological characteristics and percentage seed tree retention (with standard deviation noted parenthetically) for conventional and alternative approaches to selection

	Recruitment status	Regeneration guild	Abundance pattern	Priority	Conventional	Alternative
Eperua oleifera	Adequate	NPSB	Common	1	21.8 (±4.6)	10.4 (±0.3)
Brosimum potabile	Adequate	NPSB	Rare	1	12.5 (±5.4)	11.0 (±0.4)
Hymenaea courbaril	Adequate	NPSB	Rare	1	2.6 (±2.2)	12.3 (±1.8)
Copaifera multijuga	Adequate	NPSB	Rare	1	20.4 (±8.6)	11.4 (±0.9)
Brosimum rubescens	Adequate	NPSB	Common	2	8.0 (±2.2)	10.7 (±0.6)
Clarisia racemosa	Adequate	NPSB	Rare	2	9.2 (±7.5)	11.5 (±1.1)
Maquira sclerophylla	Adequate	NPSB	Common	3	35.6 (±11.2)	12.5 (±1.9)
Couratari guianensis	Adequate	NPSB	Rare	3	22.6 (±4.6)	11.9 (±1.7)
Parkia nitida	Adequate	NPLD	Rare	1	22.4 (±10.8)	16.8 (±2.0)
Stryphnodendron guianensis	Adequate	NPLD	Rare	2	54.4 (±17.4)	16.1 (±2.5)
Andira spp.	Adequate	NPLD	Rare	3	13.6 (±10.5)	16.9 (±3.9)
Hymenolobium nitidum	Adequate	NPLD	Rare	3	2.3 (±2.8)	15.5 (±1.7)
Peltogyne paniculata	Adequate	NPLD	Rare	3	7.2 (±4.9)	13.4 (±05)
Cariniana decandra	Inadequate	NPSB	Rare	1	5.3 (±3.4)	13.5 (±0.7)
Mezilaurus itauba	Inadequate	NPSB	Common	2	8.0 (±4.4)	12.2 (±1.4)
Hymenaea sp.	Inadequate	NPSB	Rare	3	39.7 (±6.2)	12.4 (±1.1)
Dipteryx odorata	Inadequate	NPLD	Rare	1	16.0 (±6.1)	20.9 (±5.9)
Simarouba amara	Inadequate	NPLD	Rare	1	8.0 (±9.8)	23.2 (±5.4)
Dipteryx magnifica	Inadequate	NPLD	Rare	2	7.4 (±2.1)	17.2 (±0.7)
Piptadenia suaveolens	Inadequate	NPLD	Rare	2	47.2 (±7.9)	15.4 (±2.3)
Dinizia excelsa	Inadequate	NPLD	Rare	3	2.3 (±7.5)	19.5 (±3.9)
Hymenolobium excelsum	Inadequate	NPLD	Rare	3	9.3 (±8.5)	25.4 (±4.6)
Goupia glabra	Inadequate	Pioneer	Rare	3	6.9 (±5.1)	20.3 (±1.3)

Twenty-three species were included in the analysis, selected from blocks where the total number of potential seed trees was at least 9. Species are sorted by ecological attributes, with species showing relatively more constraints to regeneration further down the table. Cruitment status, adequate refers to occurrence of Species individuals in the smallest diameter class (5 < 15 DBH); regeneration guild, NPSB (non-pioneer shade bearer); NPLD (non-pioneer light demanding); abundance pattern, common (>3 trees ha^{-1}; 15 cm < DBH < 45 cm). Priority: 1 (species with high priority to be promoted); 2 (species with intermediary priority to be promoted); 3 (species for which no additional incentive should be given to their regeneration after logging).

commercial species in residual stands. In the second part, we discuss the strengths and weaknesses of our methodology and the characteristics used to determine retention levels.

4.1. The effectiveness of the retention rules at promoting regeneration

The aim of seed tree retention in selective harvesting systems is to ensure that there are mature trees in the residual stand that provide propagules for the regeneration of the species over subsequent cutting cycles. Overall, the alternative approach performed better than the conventional approach, in that the pool of trees retained included relatively more trees of species with constraints to regeneration, and retained at least two individuals of all species within each 100 ha block of forest.

However, retaining seed trees is not the same as achieving recruitment and development of new stems in the residual stand. The ultimate measure of the effectiveness of retention rules would be evidence of favourable levels of regeneration of the target species in the residual forest. In this study we did not set out to answer the question, "Does the alternative method of selection result in greater recruitment of target species than the conventional method?" Long-term observations of post-harvest stand dynamics would be required to fully address that question. Many factors can constrain tree recruitment post-harvest, even where seed trees are present in a stand. For example, low fecundity of seed trees, irregularity of fruiting cycles, high levels of seed predation or lack of appropriate microsites for seedling establishment and development. It is partly because of the unpredictability and complexity in natural regeneration that some tropical silviculturalists promote artificial regeneration strategies (e.g., Wyatt-Smith, 1987). For species with regeneration requirements that are not created from disturbances typical of selective logging, silvicultural intensification may be required (Fredericksen and Putz, 2003) or reliance on alternative selection systems (e.g., group selection or patch cutting, Nyland, 1996). Seed tree retention rules are only one component of a silvicultural system.

Seed tree retention is particularly important for rare species because selective logging can result in their extirpation over large forest areas (Johns, 1997) or the reproductive isolation of survivors (Ghazoul et al., 1998). In Democracia, more than 70% of the commercial species occurred at very low densities (<0.5 trees ha^{-1}). The failure of the conventional approach to retain any seed trees for an average of 30% of the species at the 100 ha stand level (Table 4) highlights the limitations of the application of retention rules at the compartment level. However, more knowledge is needed about tree size at first reproduction related to MFD, for it is the species that become reproductively active at sizes above the MFD that are most at risk of extirpation (Sheil and van Heist, 2000). For the few species for which data on size at first reproduction have been published, the results are variable. Some studies suggest little reproductive activity until trees reach sizes above the MFD (e.g., Snook, 1996), but a study of 15 commercial species in moist forest in Ghana, Adam (2003) found that 14 had reproductive thresholds below their MFD. It is often most practicable to link retention rules to the data routinely collected during harvest planning, and because pre-harvest inventories are often limited to trees at or above MFDs, the implementation of rules for retention that include smaller sized trees may require investment in additional data collection at the time of pre-harvest planning.

Decisions about seed tree retention are typically made alongside decisions about tree selection for felling; therefore, any change in tree retention levels (or composition of retained trees) will have implications for the pool of trees available for felling. In this study, after selecting trees for retention, the harvestable volume was less in the alternative relative to the conventional (37 commercial species, conventional = 40 m^3 ha^{-1}; ($CI_{95\%} = 7$); alternative = 35 m^3 ha^{-1} ($CI_{95\%} = 3$); $t = 2.7$; $p = 0.04$). However, when only the 22 species with the same MFD in the two treatments were considered, the harvestable volumes were similar (the average difference between treatments was <1 m^3 ha^{-1}).

We conducted a field experiment at our study site to examine the impacts of the alternative approach on harvest production and post-logging forest conditions (Freitas and Pinard, manuscript). Tree selection for felling in both conventional and alternative approach followed the previous seed tree selection presented in this study. Post-logging conditions differed between the two treatments (i.e., canopy openness and soil disturbance), but the majority of these differences could be attributed to the rules for selecting trees for felling rather than the seed tree retention rules. The one variable that was a consequence of the retention rules was distance between mature conspecifics, where the average distance between conspecifics of rare species was less following the alternative approach relative to the conventional.

4.2. Ecological characteristics used to determine seed tree retention rules

Many studies have been published where species ecological attributes are examined in relation to forest management problems (e.g., Pinard et al., 1999; Mostacedo and Pinard, 2001; Hammond et al., 1996; Martini et al., 1994). In addition, there is a considerable body of information scattered throughout many ecological studies that are potentially useful for forest management (Sheil and van Heist, 2000), as is foresters' informal knowledge based on field experience (Swaine, 1996). The challenge, however, is to compile information for local management problems and determine how to apply the information at operational scales.

In this study we relied on seven attributes that have relevance for understanding species regeneration ecologies and constraints. For our study site, terra firme forest in Amazonia, these characteristics proved useful for grouping species according to their silvicultural requirements (Freitas, 2004). In our forest, non-pioneer light demanding species and non-pioneer shade bearers were similarly represented among the commercial species; both ecological groups contained species with inadequate regeneration (Freitas, 2004). The attributes that we used in this study were chosen for their associations with shade tolerance, presence or absence of advanced regeneration, potential fecundity and seed dispersal.

Stem diameter distributions were assigned a relatively high weighting in the alternative approach. We assumed that the shape of species' diameter distributions were related to their regeneration ecology (Rollet, 1979), and would therefore be useful for increasing the retention levels of pioneer and non-pioneer light demanding species. The shape of diameter distributions, however, does not always provide reliable insights into species' regeneration ecologies. For example, sample size and forest history influence the shape of a species diameter class distribution (Swaine, 1992; Poorter et al., 1996). Reference to growth data and wood density data from the literature (Alder and Silva, 2000; Silva et al., 1995, 1996; da Silva et al., 2002; Alder et al., 2002; Loureiro et al., 1979a,b) increased the robustness of our classification.

Seed dispersal mode was assumed to influence the extent of effective dispersal, and the alternative rules retained fewer seed trees when dispersal was assumed to be relatively good, and more when dispersal was assumed to be relatively poor. Seed dispersal mode is expected to affect the distance from the parent tree that seeds can reach, and therefore influences the probability of escaping density-dependent mortality (Janzen, 1970, 1971). Several studies support this assumption, demonstrating differences in dispersal distance depending on dispersal mode, however, dispersal distances vary enormously and the great majority of seeds fall within 30 m of the parent (Augspurger, 1986; Forget, 1989; Medjibe and Hall, 2002; Agyeman et al., 1999), independent of the dispersal mode. Fredericksen et al. (2001) suggested that this pattern diminishes the importance of seed dispersal mode for seed tree retention guidelines.

In this study we assumed wind dispersed species would be at a disadvantage over animal dispersed species not for the potential dispersal distance, but because of local site conditions. The study site is flat and winds are typically absent, and it is a large area of old growth forest with a low incidence of hunting or fragmentation, reducing any relative advantage of wind over animal dispersal.

Dioecious species were assumed to require greater retention than hermaphroditic species. Like most of tropical tree species, many dioecious species are pollinated by small insects, thus a reduced inter-plant distance may favour the movement of their pollinators (Bawa and Opler, 1975). Published seed tree retention guidelines suggest retaining twice the number of seed trees of dioecious species (Fredericksen et al., 2001; Guariguata and Pinard, 1998) and to maximize male density around female trees to increase the potential for adequate regeneration. However, information about plant sexuality is scarce, and although flower dimorphism frequently occurs (Bawa and Opler, 1975), it would be difficult to recognise such differences in the field (Wheelwright, 2000) during the 100% pre-harvest inventory. For dioecious species, a conservative alternative would be to increase the number of seed trees to prevent high numbers of reproductively isolated trees, independent of sex ratio (Crawley, 1997), but see (Wheelwright and Bruneau, 1992). In this study the alternative process did not double the seed tree number for dioecious species, but used this attribute to retain more seed trees, although the final number of retention was a combination with other species attributes showing low or high constraints to regeneration.

Species frequency was included as an attribute to influence retention rates, assuming that more homogeneous distribution would require the retention of fewer trees. This attribute proved influential for only four species with an outstandingly even distribution and with high abundance.

Regeneration priority was included in order to promote species according to their commercial value. The rationale is in line with the concept of forest domestication proposed by Lamprecht (1993) and also supported by De Graaf (2000), in which the forest is gradually transformed over time, by favouring valuable species and eliminating less desirable ones. In this study, the adjustment of seed tree retention for regeneration priority was additional promotion of valued species, but without an associated effort to eliminate less desirable species. However, it seems unlikely that the retention of an additional 5% of a species potential seed trees would make a difference to recruitment and long-term composition.

5. Conclusions

Our study demonstrates that it is feasible to implement at an operational scale, species-specific retention rules that take into account local abundance when inventory data are digitised and spatially explicit. The implementation of reduced impact logging techniques, particularly harvest planning, produces information on trees. The spatial data produced can be manipulated through computer systems to support harvest planning, improve efficiency and cost reduction. This important tool should be also used to improve forest management systems based on species characteristics and appropriate silvicultural strategies to promote target commercial species regeneration.

The methodology developed here was aimed at illustrating how species characteristics could be used to choose trees for retention wisely, not necessarily to increase the number of trees retained in residual stands. Monitoring regeneration in the residual stands over time will provide the evidence to assess the ecological benefits of the adoption of our alternative approach.

Species regeneration in managed forest is determined by a complex set of ecological processes in which biotic and abiotic factors are important, and because typical logging disturbances do not mimic natural disturbances regimes, much remains to be learned about tree regeneration in logged forests. However, developing tree selection approaches that translate ecological information and knowledge into practical procedures and forest management decisions is a step forward.

References

Adam, K.A., 2003. Tree selection in selective logging: ecological and silvicultural considerations for natural forest management in Ghana. Ph.D. Thesis. University of Aberdeen, Aberdeen, 201 pp.

Agyeman, V.K., Abu-Juam, M., Hawthorne, W.D., 1999. Towards Better Forest Harvesting. Forestry Research Institute of Ghana, Kumasi.

Alder, D., Silva, J.N.M., 2000. An empirical cohort model for management of Terra Firme forests in the Brazilian Amazon. Forest Ecol. Manage. 130, 141–157.

Alder, D., Oavika, F., Sanchez, M., Silva, J.N.M., Van der Hout, P., Wright, H.L., 2002. A comparison of species rates from four moist tropical forest regions using increment-size ordination. Int. Forestry Rev. 4, 196–205.

Augspurger, C.K., 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. Am. J. Bot. 73, 353–363.

Bawa, K.S., Opler, P.A., 1975. Dioecism in tropical forest trees. Evolution 29, 167–179.

Blate, G., Putz, F.E., Zweed, J.C., 2001. Changing harvesting practice in the Amazon. Tropical Forest Update ITTO Newsletter 11, pp. 8–9.

Bruenig, E.F., 1996. Conservation and Management of Tropical Rain Forests: An Integrated Approach to Sustainability. CAB International, Wallingford, UK.

Crawley, M.J., 1997. Sex. In: Crawley, M.J. (Ed.), Plant Ecology. Blackwell Science, Oxford, pp. 156–213.

da Silva, R.P., Santos, J., Tribuzy, E.S., Chambers, J.Q., Nakamura, S., Higuchi, N., 2002. Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. Forest Ecol. Manage. 166, 295–301.

Dawkins, H.C., Philip, M.S., 1998. Tropical Moist Forest Silviculture and Management: A History of Success and Failure. Wallingford.

De Graaf, N.R., 2000. Reduced impact logging as part of the domestication of neotropical rainforest. Int. Forestry Rev. 2 (1), 40–44.

Fernandes, N.P., Jardim, F.C.S., Higuchi, N., 1983. Tabelas de volume para a floresta de terra firme da Estação experimental de Silvicultura Tropical. Acta Amazonica 13 (3–4), 537–545.

Forget, P.-M., 1989. La Régéneration Naturelle D'une Espéce Autochore de La Forêt Guyanaise *Eperua falcata* Aublet (Caesalpiniaceae). Biotropica 21, 115–125.

Fredericksen, T.S., Putz, F.E., 2003. Silvicultural intensification for tropical forest conservation. Biodiversity Conserv. 12, 1445–1453.

Fredericksen, T.S., Mostacedo, B., Justiniano, J., Ledezma, J., 2001. Seed tree retention considerations for uneven-aged management in Bolivian tropical forests. J. Trop. Forest Sci. 13 (2), 352–363.

Freitas, J.V., 2004. Improving tree selection for felling and retention in natural forest in amazonia through spatial control and targeted seed tree retention: a case study of a forest management project in Amazonas State, Brazil. Ph.D. Thesis. University of Aberdeen, 184 pp.

Gethal Amazonas, S.A., 2001. Projeto de Manejo Floresta Democracia+. Gethal Amazonas Indústria de Madeira Compensada S.A.1a Revisão (Fev. 2001). Manicoré-AM.

Ghazoul, J., Liston, K.A., Boyles, T.J.B., 1998. Disturbance-induced density-dependent seed set in Shorea siamensis (*Dipterocarpaceae*), a tropical forest tree. J. Ecol. 86, 462–473.

Guariguata, M.R., Pinard, M.A., 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. Forest Ecol. Manage. 112, 87–89.

Hammond, D.S., Van der Hout, P., Cassels, D.S., Zagt, R.J., Evans, J., Marshall, G., 2000. Benefits, bottlenecks and uncertaintes in the implementation of reduced impact logging techniques. Int. J. Geographical Inf. Syst. 2 (1), 45–53.

Hammond, D.S., Gourlet-Fleury, S., van der Hout, P., ter Steege, H., Brown, V.K., 1996. A compilation of known Guianan timber trees and the signficance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. Forest Ecol. Manage. 83, 99–116.

Hasanbahri, S., 1997. The selection of some mature commercial tree species as parent trees before logging on the natural production forest. BIOTROP Spec. Publ. 60, 73–80.

IBAMA, 1995. Portaria N (48 sobre a exploração das florestas primitivas e demais formas de vegetação arbórea na Bacia Amazônica. Diário Oficial N 48, Brasilia-DF, 3-7-2002.
IBAMA, 2003. Instrução Normativa No. 7 sobre os Planos de Manejo Florestal que contemplem a exploração da espécie mogno (*Switenia macrophylla*, King). Diário Oficial N 164, Brasilia-DF, 22-8-2003.
Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528.
Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Systematics 2, 465–492.
Johns, A.G., 1997. Timber Production and Biodiversity Conservation in Tropical Rain Forests. Cambridge University Press, Cambridge.
Kinnear, P.R., Gray, C.D., 2000. SPSS for Windows Made Simple—Release 10. Psychology Press Ltd., Hove.
Lamprecht, H., 1993. Silviculture in the tropical natural forests. In: Pancel, L. (Ed.), Tropical Forestry Handbook. Springer Verlag, Berlin, pp. 728–810.
Leslie, A., 2001. The trouble with RIL. Tropical Forest Update ITTO Newsletter 32.
Loureiro, A.A., Silva, M.F., Alencar, J.C., 1979a. Essências Madeireiras da Amazônia, vol. I. CNPq/INPA, Manaus, 245 pp.
Loureiro, A.A., Silva, M.F., Alencar, J.C., 1979b. Essências Madeireiras da Amazônia, vol. II. CNPq/INPA, Manaus, 187 pp.
Martini, A.M.Z., De, A., Rosa, N., Uhl, C., 1994. An attempt to predict which Amazonian tree species may be threatened by logging activities. Environ. Conserv. 21 (2), 152–162.
Medjibe, V., Hall, J.S., 2002. Seed dispersal and its implications for silviculture of African mahogany (*Entandrophragma* spp.) in undisturbed forest in the Central African Republic. Forest Ecol. Manage. 170, 247–249.
MMA-Ministério do Meio Ambiente, 2002. Instrução Normativa N (4 sobre Manejo Florestal Sustentável de Uso Múltiplo na Amazônia Legal. Diário Oficial 1 N 45, Brasilia-DF, 3-7-2002.
MMA-Ministério do Meio Ambiente, 2006. Instrução Normativa No. 5 sobre procedimentos técnicos para elaboração, execução e avaliação técnica de Planos de Manejo Florestal na Amazônia Legal. Brasilia-DF, 11-12-2006.
Mory, A.M., Jardim, F.C.S., 2001. Comportamento de *Goupia glabra* Aubl. (Cupiúba) em diferentes níveis de desbastes por anelamento em florestas tropicais. Revista de Ciências Agrárias 36, 55–66.
Mostacedo, B., Pinard, M.A., 2001. Ecologia de semillas y plantulas de arboles maderables en bosques de Bolivia. In: Mostacedo, B., T. S. Fredericksen (Eds.), Regeneracion y Silvicutlura de Bosques Tropicales en Bolivia. Proyect de Manejo Forestal Sostenible (BOLFOR), Santa Cruz, Bolivia, pp. 11–30.
Nyland, R.D., 1996. Silviculture: Concepts and Applications. McGraw-Hill Companies, USA, 608 pp.
Pinard, M.A., Putz, F.E., Tay, J., Sullivan, T.E., 1995. Creating timber harvest guidelines for a reduced-impact logging project in Malaysia. J. Forestry 93, 41–45.
Pinard, M.A., Putz, F.E., Rumiz, D., Guzman, R., 1999. Ecological characterization of tree species to guide forest management decisions – an exercise in classification of species in the semideciduous forests of Lomerio, Bolivia. Forest Ecol. Manage. 113, 201–213.
Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon. In: Prance, G.T., Lovejoy, T.E. (Eds.), Amazonia: Key Environments. Pergamon Press, Oxford, pp. 109–145.
Poorter, L., Bongers, F., van Rompaey, R.S.A.R., de Klerk, M., 1996. Regeneration of canopy tree species at five sites in West African moist forest. Forest Ecol. Manage. 84, 61–69.
Projeto Embrapa-CIFOR, 2000. Diretrizes Técnicas para a Exploração de Impacto Reduzido em Operações Florestais de Terra Firme na Amazônia Brasileira. CIFOR, Belem, 24 pp.
Putz, F.E., Redford, K.H., Robinson, J.G., Blate, G.M., 2000. Biodiversity Conservation in the Context of Tropical Forest Management. The Word Bank Environment Department, Washington, 80 pp.
Rollet, B., 1979. Application de diverses méthodes d'analyse de données à des inventaires forestiers détaillés levés en forêt tropicale. Œcology Plantarum 14, 319–344.
Sheil, D., van Heist, M., 2000. Ecology for tropical forest management. Int. Forestry Rev. 2 (4), 261–271.
Silva, J.N.M., van Eldik, T., 2000. Approaches adopted towards yield regulation in Brazilian Amazon. In: Wright, H.L., Alder, D. (Eds.), Proceedings of Workshop on Humid and Semi-humid Tropical Forest Yield Regulation with Minimal Data. Occasional Papers 52. Oxford Forestry Institute-O.F.I., Oxford, pp. 70–72.
Silva, J.N.M., Carvalho, J.O.P.D., Lopes, J.C.A., Almeida, B.F., Costa, D.H.M., Oliveira, L.C.D., Vanclay, J.K., Skovsgaard, J.P., 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. Forest Ecol. Manage. 71, 267–274.
Silva, J.N.M., Carvalho, J.O.P.D., Lopes, J.C.A., Oliveira, R.P.D., Oliveira, L.C.D., 1996. Growth and yield studies in the Tapajós region, Central Brazilian Amazon. Commonwealth Forestry Rev. 75, 325–329.
Sist, P., 2000. Reduced impact logging in the tropics: objectives, principles and impact of research. Int. Forestry Rev. 2 (1), 3–10.
Sist, P., 2001. Why RIL won't work by minimum-diameter cutting alone. Tropical Forest Update ITTO Newsletter 11.
Sist, P., Fimbel, R., Sheil, D., Nasi, R., Chevallier, M.-H., 2003. Towards sustainable management of mixed diperocarp forests of Southeast Asia: moving beyond minimum diameter cutting limits. Env. Conserv. 30, 364–374.
Snook, L., 1996. Catastrophic disturbance, logging and the ecology of mahogany (*Swietenia macrophylla* King): grounds for listing a major tropical timber species in CITES. Bot. J. Linnean Soc. 122, 35–46.
Sokal, R.R., Rohlf, F.J., 1995. Biometry. W.H. Freeman and Company, New York.
Swaine, M.D., 1992. Characteristics of dry forest in West Africa and the influence of fire. J. Veg. Sci. 3, 365–374.
Swaine, M.D., 1996. The Ecology of Tropical Forest Tree Seedlings. Man and the Biosphere Series, vol. 17. UNESCO, Paris.
Swaine, M.D., Agyeman, V.K., Kyereh, B., Orgle, T.K., Thompson, J., Veenendaal, E.M., 1997. Ecology of Forest Trees in Ghana. ODA Forestry Series No. 7. ODA, London, 75 pp.
Thompson, I.S., Yared, J.A.G., 1999. Seleção de árvores: uma decisão chave no manejo sustentável de florestas para produção de madeira em florestas de terra firme da Amazônia Oriental. Embrapa/DFID. Simposio SILVICULTURA NA AMAZONIA ORIENTAL: Contribuicoes do Projeto Embrapa/Dfid, Belém, pp. 248–252.
Vanclay, J.K., 1989. Modelling selection harvesting in tropical rain forest. J. Trop. Forest Sci. 1 (3), 280–294.
Wheelwright, N.T., 2000. Sex ratios and distribution of male and female trees. In: Nadkarni, N.M., Wheelwright, N.T. (Eds.), Monteverde: Ecology and Conservation of A Tropical Cloud Forest. Oxford University Press, New York.
Wheelwright, N.T., Bruneau, A., 1992. Population sex ratios and spatial distribution of *Ocotea tenera* (Lauraceae) trees in a tropical forest. J. Ecol. 80, 425–432.
Wyatt-Smith, J., 1987. Problems and prospects for natural management of tropical moist forests. In: Mergem, F., Vincent, J.R. (Eds.), Natural Management of Tropical Moist Forests: Silviculture and Management, Prospects of Sustained Utilization. Yale University, New Haven, pp. 5–22.