Journal of Applied Ecology
2000, **37**,
267–283

Simulated effects of logging on carbon storage in dipterocarp forest

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Summary

1. As the role of forestry-based options for reducing or mitigating greenhouse gas emissions is debated by policymakers, there is a need to inform the debate by synthesizing existing information on carbon dynamics in tropical forest systems and by applying this information to a range of possible interventions in forestry.

2. To investigate the consequences of reductions in logging damage for ecosystem carbon storage, we constructed a model to simulate changes in biomass and carbon pools following logging of primary dipterocarp forests in south-east Asia. We adapted a physiologically driven tree-based model of natural forest gap dynamics (FORMIX) to simulate forest recovery following logging.

3. Following selective logging, simulated ecosystem carbon storage declined from prelogging levels (213 Mg C ha^{-1}) to a low of 97 Mg C ha^{-1}, 7 years after logging. Carbon storage in biomass approached prelogging levels about 120 years after logging.

4. The relationship between fatal stand damage and ecosystem carbon storage was not linear, with biomass recovery following logging severely limited by 50–60% stand damage.

5. Results from simulations suggest that when 20–50% of the stand is killed during logging, replacing persistent forest species with pioneer tree species can reduce the site's potential for carbon storage by 15–26% over 40–60 years.

6. Reducing fatal damage from 40% to 20% of the residual stand, as was the case with a pilot project in Malaysia, was associated with an increase of 36 Mg C ha^{-1} in mean carbon storage over 60 years.

7. Efforts to monitor and verify the benefits, either through carbon sequestration in new growth or carbon retention in existing biomass, of offset projects involving tropical forests and natural forest management should focus on above-ground biomass, particularly the large trees. Selection of the most appropriate allometric equations for a site and species is important because of their influence on biomass estimates.

Key-words: disturbance, model, recovery, reduced-impact logging, tropical forest.

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Introduction

As signatory nations negotiate the implementation of the Framework Convention on Climate Change (UNCED 1992), the role of forestry-based options for mitigating carbon dioxide emissions continues to be debated (e.g. Kyoto Protocol). To inform the debate there is a need to synthesize existing information on carbon dynamics in tropical forests and to apply this research to case studies, or pilot carbon offset projects, where specific interventions have been made to increase carbon retention or sequestration.

Reductions in logging damage can result in increased carbon retention in forest biomass (Putz & Pinard 1993). This concept provided the rationale for a pilot carbon offset project initiated in 1992 by Innoprise Corporation Sdn. Bhd. (ICSB), a timber concessionaire in Malaysia, and New England Elec-

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tric Systems (NEES), a coal-burning power company in the USA. NEES contributed funds to the timber concessionaire to train staff and to implement reduced-impact logging (RIL) guidelines in 1400 ha of production forest. The guidelines are intended to reduce damage to residual trees and soil through preharvest mapping, vine-cutting, harvest planning, skidding restrictions and site closure (Pinard *et al*. 1995). The short-term benefits, in terms of carbon retention in biomass, of the reductions in logging damage achieved in the project have been described in Pinard & Putz (1996).

In this paper, we examine the effect of this biomass retention on long-term carbon storage over a 60-year period in dipterocarp forest. We present a simulation model of dipterocarp forest development based on FORMIX, a model developed by Bossel & Krieger (1991). Our model tracks carbon stored in forest biomass and necromass pools over time and is intended to simulate forest recovery following logging. The amount of carbon stored in a logged or silviculturally managed forest is influenced by factors and processes that are both internal to the system (e.g. species composition, growth rates, decay rates) and external to the system (e.g. rotation times, logging damage, timber volume extracted). The model provides a tool for organizing this information. We evaluate the model using sensitivity analyses and comparisons with field observations and published data on biomass and necromass stores in primary and logged dipterocarp forest. Finally, we use output from simulations to evaluate the effects of reductions in logging damage on carbon storage.

CARBON STORAGE AND PATTERNS OF RECOVERY FOLLOWING LOGGING

When timber is removed from a forest, total ecosystem carbon storage declines. Selective cutting often involves harvesting only a few trees, but many others are usually damaged. As damaged trees die and logging debris decomposes, total carbon stored declines further. Only when carbon sequestration in growth and recruitment exceeds carbon losses in death and decay will total carbon storage increase. Over time, and in the absence of large-scale disturbance, ecosystem carbon storage may approach an asymptote, the position of which may or may not be the same as before logging.

Logging may influence a site's potential to store carbon (i.e. height of the asymptote) and the rate at which the forest recovers and sequesters carbon. For example, soil compaction, topsoil displacement and erosion, often a consequence of log extraction with bulldozers, may decrease site productivity (Gillman *et al*. 1985; Zabowski, Skinner & Rygiewicz 1994) and, consequently, decrease carbon storage potential. If, after selective logging, the residual stand becomes dominated by vines, grasses and sedges or pioneer trees (Fox 1976; Chai & Udarbe 1977), growth of persistent forest tree species, many with high wood densities and large stature, may be suppressed for several decades. Changes in forest structure associated with selective logging operations in Sabah influence environmental conditions within the forest and increase the forest's vulnerability to fire (Uhl & Kauffman 1990; Holdsworth & Uhl 1997). An increase in fire frequency also reduces the forest's potential to accumulate carbon in biomass (Woods 1989).

The current state-mandated management plan for timber-producing dipterocarp forests in Sabah calls for 60-year cutting cycles (Sabah Forestry Department 1989). Consequently, logging impacts that influence the rate of carbon storage between logging and 60 years postlogging are of particular interest to this study. The degree to which total carbon stores decline during and after logging depends on many factors, including timber volume extracted and how this volume is distributed among diameter classes, incidental damage to the residual stand, and the degree to which the vegetation responds to opening. Recovery rates will be influenced by site productivity, species composition, changes in necromass stores, long-term effects of non-fatal tree damage, the duration of elevated mortality rates following logging, and impacts of soil damage on vegetation recovery.

In this paper we use a computer simulation model of carbon flow in dipterocarp forest following logging to explore the potential influence of several factors on carbon recovery. Specifically, we use output of simulations to address the following questions. (i) Over 60 years, how does mean carbon storage in a logged forest change with reductions in logging damage? (ii) How do changes in postlogging mortality rates affect mean carbon storage and the final biomass storage over 60 years? (iii) How might a temporary postlogging shift in species composition affect ecosystem carbon storage patterns over time?

Materials and methods

BACKGROUND AND BASIC MODEL STRUCTURE

Previous research has clarified some aspects of forest development and the carbon cycle in dipterocarp forest. Primary productivity and organic matter dynamics were studied in a dipterocarp forest ecosystem in the early 1970s, as part of the International Biological Program (IBP) in Malaysia (synthesized in Kira 1978). The researchers presented a pool and flux model of ecosystem carbon cycling for steady-state conditions (Kira 1987). Using a portion of the IBP data, Bossel & Krieger (1991) developed a physiologically driven model of

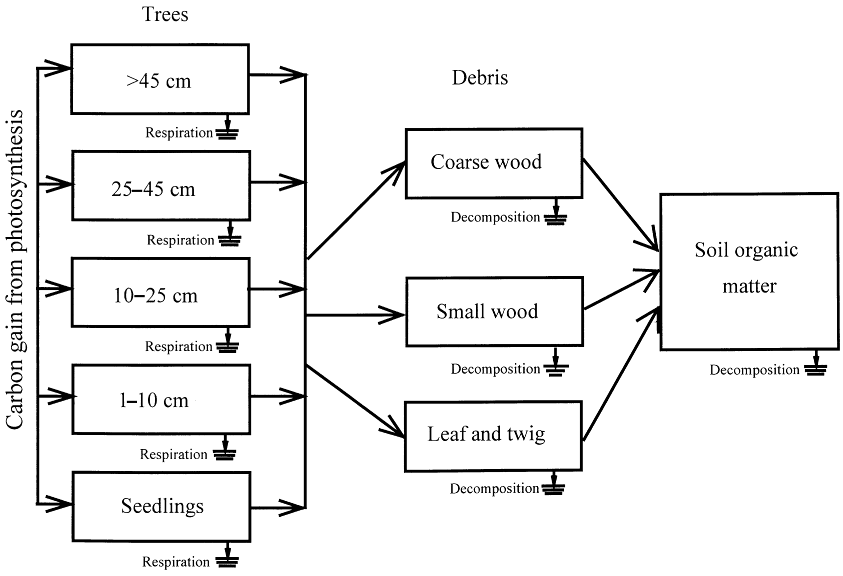

Fig. 1. Diagram of storages, transfer pathways and atmospheric exchanges in our model of carbon flow in a dipterocarp forest. Tree sizes refer to cm d.b.h.

dipterocarp forest development and natural tree-fall gap dynamics called FORMIX. FORMIX is useful for looking at forest growth and structural development and, in combination with the IBP data, provides a base for modelling carbon flow in dipterocarp forest. As originally published, however, FORMIX does not adequately simulate forest recovery from logging with bulldozers because it does not incorporate community-level and ecosystem changes fundamentally associated with soil disturbance and logging in Sabah (but see Huth, Ditzer & Bossel 1997). Changes we have identified as potentially important to carbon storage are elevated postlogging mortality rates, changes in seedling survival, and increased representation of pioneer trees among the recruits.

Our model tracks carbon stored in dipterocarp forest and is intended to simulate forest dynamics both before and after logging. The basic system is scaled to 1 ha, uses annual time steps, and includes carbon pools for above-ground biomass and necromass (Fig. 1). Carbon storage in the pools is followed as trees grow, shed litter, die and are replaced. The basic structure of our model is identical to FORMIX, as are processes describing carbon gain through photosynthesis, transition rates between layers, recruitment and mortality rates. Our model differs from FORMIX in that it simulates carbon transfer from biomass to necromass through tree mortality and litter fall. Necromass decomposition is simulated as proportional to necromass (Olson 1963). Coarse woody, small woody and fine debris decay include transfer of carbon to soil organic matter. Carbon is lost from the soil organic matter pool at 5% mass loss per year (based on Yoneda, Yoda & Kira 1977; Kira 1978). Carbon stored in roots, shrubs, herbs, vines and in mineral soil below 50 cm is not included in our model.

ABOVE-GROUND BIOMASS

As in FORMIX, we divided the forest into five canopy layers (Fig. 1) that correspond to the following: layer 1, canopy trees (> 45 cm diameter at breast height; d.b.h.); layer 2, subcanopy trees (25–45 cm d.b.h.); layer 3, pole-sized trees (10–25 cm d.b.h.); layer 4, saplings (1–10 cm d.b.h.); and layer 5, seedlings (0–1 cm d.b.h.). Initial stem densities are entered for a hectare of representative unlogged forest. Input files contain individual trees identified by a number and d.b.h. (at 1·3 m). Initially all trees are assumed to be persistent forest species characterized by attributes of the *Shorea johorensis–Parashorea* group of the Dipterocarpaceae (e.g. photosynthetic rates, allometric relationships, wood density; Table 1); Dipterocarpaceae dominate this forest in terms of basal area and tree stem density (Pinard & Putz 1996). Using these data, stem, branch, leaf and total biomass are calculated for each tree using diameter–biomass regression equations (Kira 1978; Brown, Gillespie & Lugo 1989). Layers are defined and tracked by total biomass and tree numbers.

CARBON GAIN

Annual gross photosynthate production is calculated for each layer and is based on total layer leaf

Table 1. Characteristics (with code name) of the two types of tree species used in the model. Values that differ from those used in FORMIX (Bossel & Krieger 1991) are noted by superscripts

	Persistent forest species	Pioneer species
Maximum rate of photosynthesis at light saturation ($P_{\max}$; g CO_2 m^{-2} h^{-1})	1·5	2·5[a]
Initial slope of the light response curve (M; g CO_2 h^{-1} W^{-1})	0·015–0·025	0·04[b]
Leaf proportional energy use efficiency (PR)*	0·50	0·35[c]
Photosynthetic production for litter fall (PSD; proportion)	0·10	0·10
Stemwood fraction (TR)	0·70	0·70
Wood density (G; g cm^{-3})	0·52[d]	0·33[d]
Crown diameter ratio (CD; m m^{-1})	25	32[c]

*Accounts for leaf and fine root respiration.
[a] Bazaaz (1979).
[b] Walters & Field (1987).
[c] Fox (1968).
[d] Burgess (1966).

area, incident solar radiation, light attenuation through the canopy, and photosynthetic capacity (following a light response curve; Tables 1 and 2). Litter production and respiration by fine roots, leaves and stems are subtracted from gross photoproduction to yield net annual biomass production per layer. A complete description of the basic model is found in Bossel & Krieger (1991).

TRANSITIONS

Allometric relationships are used to calculate mean stem diameters and crown projection areas for each layer (Table 3). When a layer's mean stem diameter exceeds the maximum diameter set for the layer, a given proportion of the trees (and associated biomass) is transferred to the next layer. Transition probabilities were calculated by Bossel & Krieger (1991). Each layer is associated with two specific mortality rates, a standard rate and a higher rate that applies to crowded conditions. Crowded conditions exist when the layer's canopy is completely closed, as determined by crown area/stem diameter ratio, mean stem diameter and number of trees per layer (Tables 1 and 3). Recruitment into the seedling layer is controlled by the number of trees > 25 cm d.b.h.; each mature tree contributes 1000 seedlings per year (Table 1); the base survival rate for established seedlings is 50% per year.

NECROMASS

Necromass exists in five compartments: coarse woody debris (branches or logs with diameter > 15 cm); small woody litter (diameter ranging from 2 to 15 cm); fine litter (leaves, fruits, twigs < 2 cm

Table 2. Equations describing carbon gain (taken from Bossel & Krieger 1991). Subscripts refer to specific layers that are defined in the text and Fig. 1

Solar radiation received by a layer	$I_I = I_{I+1} \times \exp(-K_{I+1} \times LAI_{I+1})$
Gross photosynthetic production	$PS_I = C \times (P_{\max}/K_i) \times \log_e((1+(M/P_{\max}) \times I_I)/(1+(M/P_{\max}) \times I_{I-1}))$
Photosynthetic production adjusted for crown area	$PT_I = PS_I \times AT_i$
Photosynthetic production adjusted for leaf and root respiration	$PB_I = PT_I \times PR_I$
Photosynthetic production adjusted for stem respiration	$C\text{gain}_I = PB_I - (R_i \times B_I)$

I = radiation above the canopy, 335 W m^{-2}.
K = light extinction coefficient (values per layer in Table 3).
LAI = layer leaf area index (maximum values per layer in Table 3).
C = conversion factor from g CO_2 m^{-2} h^{-1} to metric tons of oven dry mass ha^{-1} $year^{-1}$.
M – definition and values in Table 1.
$P_{\max}$ – definition and values in Table 1.
AT = current crown fill ratio; represents crown cover per layer.
PR – definition in Table 1.
R = biomass proportional energy loss rate; accounts for stem respiration, 0·06.
B = layer total biomass (Mg oven dry mass ha^{-1}).

Table 3. Variables describing the two species groups represented in the model, by layer. Persistent species refers to tree species able to establish in shade and that maintain a seedling bank rather than a seed bank. Pioneer species refers to tree species that require relatively high light for seedling establishment and do not maintain a seedling bank

	Layer 1 > 45 cm	Layer 2 25–45 cm	Layer 3 10–25 cm	Layer 4 1–10 cm	Layer 5 Seedlings
Persistent species					
Mortality rate (mn_i)[a]	0·005	0·008	0·01	0·05	0·10
Crowding mortality rate (mc_i)[a]	0·10	0·15	0·20	0·50	0·50
Postharvest mortality rate (ml)[a]	0·05	0·05	0·05	0·05	0·05
Maximum leaf area index (LAI_i)	2·00	2·00	2·00	2·00	1·00
Transition rate (TS_i)[a]	NA	0·02	0·05	0·08	0·10
Pioneer species					
Mortality rate (mn_i)[a]	0·01	0·01	0·05	0·05	0·10
Crowding mortality rate (mc_i)[a]	0·25	0·25	0·25	0·50	0·50
Postharvest mortality rate (ml)[a]	NA	NA	NA	NA	NA
Maximum leaf area index ($LAIP_i$)	2·00	2·00	2·00	2·00	2·00
Transition rate (TSP_i)[a]	NA	1·00	1·00	1·00	1·00
Common to both groups					
Light extinction coefficient (K_i)[b]	0·86	0·86	0·54	0·54	1·00
Form factor (F_i)	0·38	0·42	0·44	0·45	0·50
Height diameter (HD_i; m m^{-1})	40	48	56	67	140
Maximum diameter (DM_i; m)	NA	0·45	0·25	0·10	0·01

[a] Expressed as proportions of individuals per hectare.
[b] Kira & Yoda (1989).

diameter); and soil organic matter. Dead roots are not included in the model. Initial pool sizes and decay rates were taken from published data for Malaysian dipterocarp forests (Table 4). Annual inputs to the necromass pools include biomass from dying trees and photosynthetic production that goes towards litter fall. Soil organic matter receives annual inputs of coarse woody debris, small woody debris and fine litter. A proportion of the soil carbon is evolved as CO_2. Soil carbon below 50 cm depth is assumed to be static and is not included in the model; this probably represents about 40 mg C ha^{-1} (Ohta & Effendi 1992). Root biomass is also not included in the model; this probably represents about 20% of above-ground tree biomass (Pinard & Putz 1996).

LOGGING

Impacts of logging on the forest are variable and depend, in part, on timber volume extracted, the harvesting system used, and the extent of damage to the residual stand and to the soil. Selective logging, as currently practised in Sabah, removes a proportion of trees > 60 cm d.b.h. (generally 8–15 trees ha^{-1}), damages a portion of the residual stand, and generates logging debris. The model incorporates the effects of logging in a sequence of steps.

Table 4. Variables (with code names) describing necromass stores and fluxes, initial conditions listed with reference. o.d.m. refers to oven dry mass

	Initial conditions	Reference
Coarse woody debris (qc)	49·5 Mg o.d.m. ha^{-1}	Yoneda, Yoda & Kira (1977)
Woody litter conversion to carbon	50% carbon by mass	Kira (1978)
Small woody litter ($qswl$)	2·5 Mg o.d.m. ha^{-1}	This study
Fine litter (qfl)	2·4 Mg o.d.m. ha^{-1}	Burghouts *et al.* (1992)
Fine litter conversion to carbon	46·9% carbon by mass	Burghouts *et al.* (1992)
Soil organic matter ($qsoil$)	33 Mg C ha^{-1}	Ohta & Effendi (1992)
Leaf litter decay rate ($fldk$)	71% mass loss year^{-1}	Burghouts *et al.* (1992)
Leaf litter to soil ($fltoS$)	2·2% transfer to soil year^{-1}	Burghouts *et al.* (1992)
Small woody decay rate ($swldk$)	50% mass loss year^{-1}	This study
Woody debris decay rate ($qcdk$)	14·4% mass loss year^{-1}	Yoneda, Yoda & Kira (1977)
Woody debris to soil ($qctoS$)	4·6% mass loss year^{-1}	Yoneda, Yoda & Kira (1977)
CO_2 evolution from soil ($seflx$)	5% loss year^{-1}	Kira (1978)

First, timber volume extracted per ha is entered as a variable (m^3). The value is converted into biomass (Mg) using mean specific gravity (Table 2) and is translated into number of trees per ha based on the assumption that stem biomass represents 52·8% of total tree biomass (biomass expansion factor, taken from Brown, Gillespie & Lugo 1989). The biomass and number of trees felled are subtracted from the top layer of the forest (trees > 45 cm d.b.h.). Non-stem biomass (i.e. branches, leaves, stumps) enters the necromass pools (80% coarse woody debris, 10% small woody debris, 10% fine litter).

Secondly, the proportion of trees receiving fatal damage during logging is entered; a single value is used to describe fatal damage for all diameter classes. This proportion of each layer's biomass and individual trees is transferred to the necromass pools. This input variable (mean proportion of trees fatally damaged across all layers) is then used to represent the proportion of the 1-ha stand that will be colonized by pioneer tree species rather than by persistent forest species during the first 2 years after logging.

Prior to logging, pioneer tree species are uncommon in the dipterocarp forests of Sabah (Whitmore 1978; Corner 1988) but they are a dominant component of logged forests in Sabah, often occurring as monodominant stands (Fox 1968). Pioneer trees are incorporated into the model to provide a way of exploring the impacts of a temporary shift in composition, a shift away from dominance by relatively slow-growing persistent species to relatively fast-growing colonizing species with low wood densities. Pioneer trees are represented by a suite of physiological and allometric attributes distinct from the trees that dominated the site before logging (i.e. the dipterocarps; Table 2).

Bornean species of pioneer trees tend to establish in disturbed sites with open canopy. Establishment patterns suggest that pioneer recruitment increases with some soil disturbance (Putz 1983; Kennedy 1991) but, on compacted soils and subsoils typical of skid trails and log landings in Sabah, pioneer tree recruitment is sparse (Pinard, Howlett & Davidson 1996). In the model, pioneer tree seedlings establish at 13 500 seedlings ha^{-1}, equivalent to 1·25 mg oven dry mass (o.d.m.) ha^{-1} (Pinard & Putz 1996; Pinard, Howlett & Davidson 1996).

The model tracks pioneer tree stand development separately from the residual forest. Carbon gain and transitions within the pioneer tree stand subset follow the same processes described earlier for the persistent forest species, although specific parameters differ (Table 2). Layer transition probabilities for pioneers are set to simulate development of an even-aged (i.e. one layer) stand.

Seedlings of persistent tree species begin to establish under the pioneer tree forest 5 years after logging. Mature residual trees (> 25 cm d.b.h.) provide seedlings to the pioneer tree forest. Generally, fruits of dipterocarp trees do not disperse far from parent trees (Ashton 1982) so both the density and distribution of mature residual trees are important for seedling establishment under pioneers. The model assumes that, as the area occupied by pioneer trees increases (i.e. proportion of stand fatally damaged), the proportion of residual trees able to disperse seeds into the pioneer forest decreases. The following equation describes the relationship used in the model to determine the number of individuals contributing seedlings of persistent forest species under the pioneer stand: $NST = (N_1 + N_2) \times ((1 - DAMF)^2)$, where NST equals the number of trees contributing seeds in a given year, N_i the number of trees in a layer i, and $DAMF$, the proportion of the stand receiving fatal damage.

In Ulu Segama Forest Reserve, observations of planted dipterocarp seedlings suggest that seedlings on skid trails experience higher mortality rates than seedlings off skid trails in logged forest (P. Moura-Costa, personal communication). The relatively high seedling mortality rates on skid trails are due, in part, to an increased incidence of animal browsing and trampling (M.A. Pinard, unpublished data). In the model, survival of seedlings of persistent tree species in the pioneer stand is calculated using the following equation: $survPD = basesurvival \times (1 - AST)$, where $survPD$ equals persistent forest species seedling survival in the pioneer stand, $basesurvival$ is the baseline annual seedling survival rate, and AST is the proportion of area with soil disturbance. This survival rate is maintained over time. Although seedling growth rates are also affected by adverse soil conditions on skid trails (e.g. compacted soils or nutrient-poor subsoils), the model does not incorporate any changes related to carbon gain for trees on skid trails.

Although maximum life spans of colonizing tree species are variable, the maximum life span for the species of *Macaranga* that dominate the pioneers in Ulu Segama is probably close to 30 years (Fox 1968). To simulate senescence of pioneers, annual mortality rates of the pioneer trees increase to 50% at 30 years after logging. The model continues to track the 'pioneer' stand but, after 35 years, the subset is predominantly trees of persistent species.

During logging, a proportion of the residual stand is damaged but some of this damage (e.g. crown or bark damage) does not always cause immediate tree death. This damage is assumed to influence growth rates of affected trees, simulated by removing 25% of the crown area of damaged trees. Newly established trees do not have crown damage. The model represents the elevated mortality due to this damage by a uniform application of 5% mortality rates for 5 years following logging.

METHODS FOR SIMULATIONS AND EVALUATION

Simulations were run under both no logging and logging scenarios. All carbon pools were tracked over a 60-year period. Longer simulations (1000 years) were also performed to evaluate the model's stability. As part of the model evaluation process, a selection of variables, constants and parameters used in the model was increased by 15%, simulations were run, and output values of response variables were recorded. The response variables used in the 'sensitivity' analyses for a no-logging scenario were as follows: mean total carbon storage over 20, 40 and 60 years, ending total carbon storage at 20, 40 and 60 years, and ending total biomass in big trees (> 45 cm d.b.h.) at 60 years. Because a subset of the variables and parameters was applicable only to a logging scenario, another set of 'sensitivity' analyses was conducted assuming 125 m^3 of timber were extracted, 40% of the residual stand fatally damaged, and 20% of the area with soil disturbance and 20% of the residual stand non-fatally damaged. The response variables used in these logging scenario analyses included those listed above but also included total biomass in pioneer-dominated forest at 20 years.

To evaluate the output of the no-logging scenario, we compared estimates of prelogging above-ground biomass and necromass stores from the study site with results from simulations run for 60 and 500 years. To evaluate the output of the logging scenario, we compared simulated densities of pioneer trees at 6 and 18 years after logging to data from logged forest in Ulu Segama. Also, simulated estimates of the amount of coarse woody debris 6 years after logging were compared with measurements of detrital stores in logged forest in Ulu Segama.

MODEL APPLICATIONS

To evaluate the impacts of timber volume extracted on mean carbon storage, we ran a series of simulations in which damage was held constant and timber volumes were increased from 0 to 200 m^3 in 25-m^3 increments. Mean timber volume extracted from the case study in Ulu Segama was about 125 m^3 ha^{-1} (Pinard & Putz 1996), so we used this value for all subsequent simulations.

The rationale for promoting reduced-impact logging as a carbon offset is based on the assumption that more carbon is retained in forest biomass when logging damage is lessened. To evaluate the importance of reduced logging damage for ecosystem carbon storage, we ran a series of simulations holding constant the volume extracted (125 m^3), non-fatal damage (0%), and area in skid trails (20%), but increased the proportion of residual stand killed in 10% intervals from 10% to 90% killed.

In the ICSB-NEES case study, about 22% of the individuals in the residual stands in both conventional and RIL areas received damage that did not immediately result in tree death (Pinard & Putz 1996). To evaluate the potential importance of nonlethal damage to carbon storage, we ran two series of simulations in which we varied mortality rates following logging. In the first series, the duration of elevated mortality rates (0·01 for all layers) was increased in 1-year increments from 2 to 10 years. In the second series, duration was set at 5 years, and postlogging annual mortality rates ranged from 1% to 12%. To examine the impacts of reducing crown area for the proportion of trees receiving non-fatal damage, we ran simulations reducing the crown area of damaged trees from 80% to 10% of full crown. We also ran a series of simulations in which the proportion of non-fatally damaged trees was increased in 10% increments from 0% to 90%, holding volume extracted, area in skid trails and fatal damage constant.

Conventional and reduced-impact logging differ in terms of volume extracted, fatal damage and soil damage (Pinard & Putz 1996; Pinard, Barker & Tay 2000). To compare the integrated effects of these differences for carbon storage, we ran the model using values observed for each logging method. For conventional logging, the input variables were 154 m^3 ha^{-1} timber extracted, 16·6% area with soil disturbance, 40% of the stand fatally damaged, and 20% of the stand with minor damage. For reduced-impact logging, the input variables were 104 m^3 ha^{-1} timber extracted, 6·8% area with soil disturbance, 20% of the stand fatally damaged, and 20% of the stand with minor damage.

We used mean total carbon storage over time as the response variable for simulations exploring the effects of increasing volume extracted, fatal damage, non-fatal damage and mortality rates. Results from sensitivity analyses indicated that mean carbon storage was relatively insensitive to small changes in parameter values. For the simulations, we used the following three time intervals: 60 years to represent one cutting cycle, 40 years to represent the NEES-ICSB project life span, and 20 years to allow the identification of trends specific to a shorter time period.

Results and discussion

EVALUATION OF MODEL – SIMULATIONS

Over a 1000-year time span, simulated carbon stores in the unlogged forest fluctuated between 200 and 265 Mg ha^{-1} (Fig. 2a); mean carbon storage over a 60-year simulation was 220 Mg ha^{-1} (SD = 11). Above-ground biomass ranged from 130 to 220 Mg C ha^{-1} and showed a mean value of 166 Mg C ha^{-1} (SD = 19·5) over a 60-year simulation, and 170 Mg

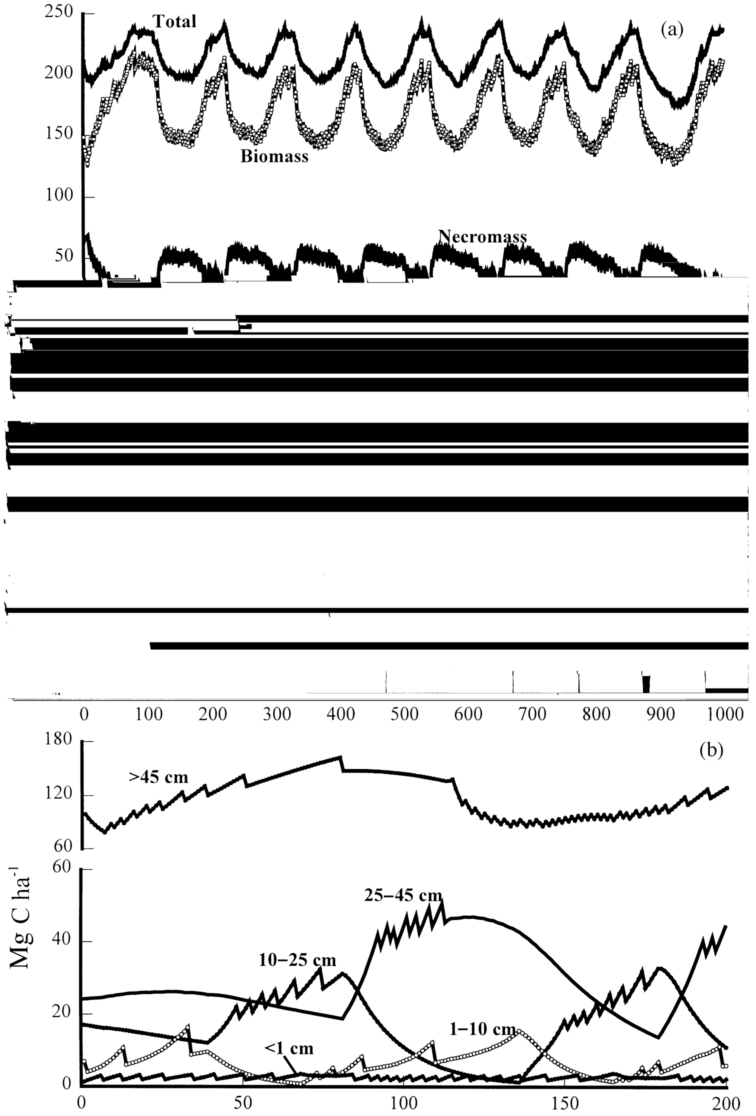

Fig. 2. Results from simulations with no logging. (a) Carbon storage in above-ground biomass, necromass and both (total) over 1000 years. (b) Changes in carbon storage in five canopy layers identified by d.b.h. class. (c) Changes in carbon storage in soil, coarse woody debris, fine litter and small woody litter. Note break and change in scale on *y*-axis in (b) and (c).

C ha^{-1} (SD = 23) over a 500-year simulation. The distribution of biomass across diameter classes fell within the range of values observed in Ulu Segama before logging (Table 5). Mean necromass store over a 60-year simulation was 54 Mg C ha^{-1} (SD = 8·9; Fig. 2c). Coarse woody debris stores fluctuated between 10 and 60 Mg C ha^{-1} and trends were negatively associated with fluctuations in total biomass stores (Fig. 2b,c). The mean quantity of coarse woody debris over a 60-year simulation (13·5 Mg C ha^{-1}, SD = 7·5) was similar to the mean value recorded in our plots in Ulu Segama (mean = 12·2 Mg C ha^{-1}, SD = 2·3; M.A. Pinard, unpublished data).

Simulated biomass stores cycled with an approximate 100-year frequency (Fig. 2a). Stand dynamics involving fluctuations of the magnitude observed in simulation results could be expected in an area prone to regularly occurring large storms, droughts or fires, but would not be expected if individual tree fall gap dynamics were the principal structuring phenomenon in the forest. However, model aggregation at the 1-ha scale limits resolution of finer scale processes. When the overstorey is 'filled' with trees, overstorey mortality rates switch to a higher rate, causing a decline in biomass that uniformly affects the entire hectare unit. Natural forest canopy gaps are generally much smaller, about 0·02 ha. A spa-

Table 5. Mean above-ground biomass (Mg C ha^{-1}) from a simulation of no-logging over 60 years and from plots in Ulu Segama Forest Reserve, Sabah (Pinard & Putz 1996)

d.b.h. class	Model results	d.b.h. class	Field measurements*
> 45 cm d.b.h.	115	> 40 cm	120 (28)
25–45 cm	25	20–40 cm	23 (3)
10–25 cm	17	10–20 cm	11 (2)
1–10 cm	8	1–10 cm	7 (1)
< 1 cm	3	< 1 cm	2 (1)

*Mean values (SD noted parenthetically) from eight logging units of about 50 ha each, subsampled with 15–20 plots (40 × 20 m).

tially explicit model that incorporates a mosaic of interconnected patches might simulate natural forest dynamics more realistically than our model, with damping of extreme fluctuations (e.g. FORMIX2; Bossel & Krieger 1994).

Following selective logging, carbon storage dropped to a low of 97 Mg C ha^{-1} 7 years after harvesting (Fig. 3a). Carbon storage peaked approximately 120 years after logging (about 150 Mg C ha^{-1}), after which time cycling was similar to that seen in simulations without logging. The mean carbon storage over 60 years after logging was 107 Mg C ha^{-1} (SD = 9·9), about 52% of the level for the

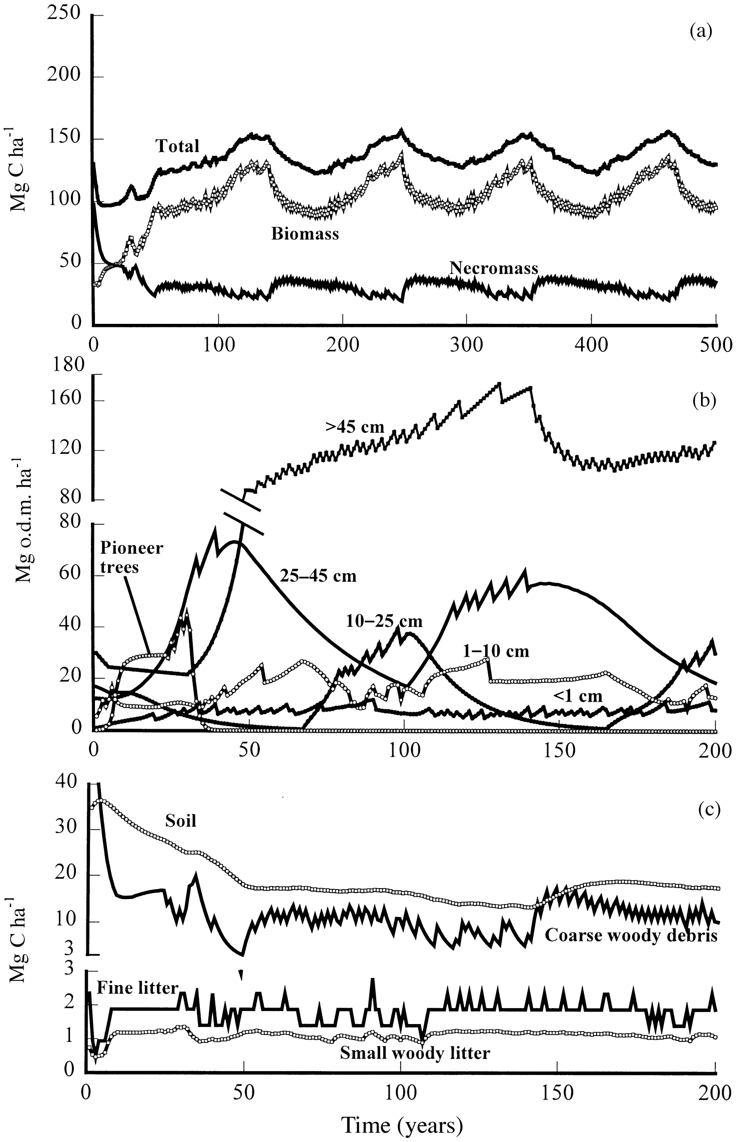

Fig. 3. Results from simulations following logging (125 m^3 extracted, 20% soil disturbance, 40% fatal damage, 20% other damage). (a) Carbon storage in above-ground biomass, necromass and both (total) across 500 years following logging. (b) Carbon storage in canopy layers (by d.b.h. class) and pioneer trees. (c) Carbon storage in soil, coarse woody debris (CWD), small woody litter (SWL) and fine litter. Note break and change in scale on *y*-axis in (b) and (c).

no-logging scenario. The small peak in carbon storage that occurred about 30 years after logging was related to a peak in pioneer tree biomass and necromass production associated with the death of the pioneer trees (Fig. 3).

Ecosystem carbon storage did not reach prelogging levels (213 Mg C ha^{-1}) within 500 years after logging (Fig. 3a). While it is possible that these forests would not fully recover after 500 years, the model was not designed for simulating long-term dynamics. Long-term dynamics are difficult to simulate correctly due to the heterogeneous decomposition of the necromass components, including very long turnover time of some soil organic matter components, and to the difficulty in correctly simulating forest succession over that time frame.

During the first 35 years after logging, only 23% of mean total forest biomass was in pioneer trees, even though the pioneer forest dominated 40% of the site (Fig. 3b). During the first 60 years after logging, 84% of the mean biomass was in residual trees (Fig. 3b). Persistent tree species that establish beneath the pioneer tree canopy increase in importance (for biomass storage) beyond 50 years after logging. Prior to this, these trees represent only 8% of the mean biomass stored per year (7 Mg C ha^{-1}). Before logging, the model forest plot contained 41 trees > 45 cm d.b.h. ha^{-1}; 60 years after logging, the layer contained 19·3 trees > 45 cm d.b.h. ha^{-1}.

Results from a simulation of logging (125 m^3, 20% soil disturbance, 40% fatal damage, 20% non-fatal damage) generated pioneer tree densities similar to those observed in logged forest in Ulu Segama Forest Reserve. At 6 years after logging, simulated pioneer tree density was 1603 stems ha^{-1}, with trees belonging to layer 4 (1–10 cm d.b.h.). At 18 years after logging, simulated density was 51 stems ha^{-1}, at which time all pioneer trees were in the uppermost layer (> 45 cm d.b.h.). Observed pioneer tree densities in logged forest, 18 years after logging, overlapped with simulated values (pioneer trees > 5 cm d.b.h., mean = 188, SD = 244; M.A. Pinard, unpublished data) but few pioneers were found with a d.b.h. greater than 45 cm.

Necromass stores reached a low point at 49 years after logging (Fig. 3a,c). The initial decline in coarse woody debris, evident during the first 10 years after logging, reflects carbon losses with the decomposition of logging debris; soil organic matter storage increases only slightly during this time. The rapidly growing pioneer forest contributes a relatively large amount of coarse woody debris between years 10 and 40. For most of this period, conditions in the pioneer forest are crowded, so mortality rates are relatively high. The plateau that is reached in pioneer tree biomass at year 10 (Fig. 3b) reflects crowded conditions when the trees are passing through layer 2 (25–45 cm d.b.h.); pioneer tree density is high, carbon gain is relatively high, mean diameter is increasing, and many trees are dying due to competition. Once the threshold diameter (45 cm) is reached (at approximately year 23) the stand again shows an increase in biomass. The decline in coarse woody debris that occurs at about year 23 reflects the low input of debris associated with low tree densities and less mortality. Pioneer tree senescence causes the necromass peak 30–40 years after logging. By 60 years after logging, the pattern of carbon storage in the coarse woody pool begins to resemble simulation results for the no-logging scenario. Fine litter and small woody litter decline during the first 5 years but by 10 years both pools begin to exhibit fluctuations similar to that observed in results from simulations of the no-logging scenario (Fig. 3c).

The results of simulations of logging are similar to direct calculations of logging debris produced (Pinard & Putz 1996) and field measurements of coarse woody debris in logged forest 6 years after logging. Immediately after conventional logging, the simulated quantity of detritus, coarse and small woody debris and fine litter was 92 Mg C ha^{-1}. The estimate of above-ground debris produced during logging of the conventional areas, based on stand inventory and logging damage data, was 74·5 Mg C ha^{-1} (Pinard & Putz 1996). Simulation of RIL logging (described in Pinard *et al.* 1995; Pinard & Putz 1996) generated 44 Mg C ha^{-1}, 7 Mg C ha^{-1} higher than the measured value.

The simulated value of coarse woody debris stores 6 years after conventional logging was 20 Mg C ha^{-1}, very similar to the observed mean value of 21 Mg C ha^{-1} (SD = 22; M.A. Pinard, unpublished data). From the field measurements, more coarse woody debris was present in logged forest 6 years after logging than was present in the study site before logging. If we assume that the 6-year-old logged site is a reasonable representation of conventionally logged sites 6 years after logging, the model appears to simulate coarse woody debris dynamics in a reasonable way over this period.

Results from simulations in which timber volumes extracted were varied indicate that, as volume extracted is increased from 0 to 75 m^3, mean carbon storage drops by 20–25% (Fig. 4). This decline is principally related to removal of biomass in trees felled. The slopes of the lines for the three time intervals are similar because, at these low extraction rates, canopy conditions remain relatively closed and hence, although trees from lower layers grow into upper layers to replace felled trees, total ecosystem carbon storage appears to be similar over 20, 40 and 60 years.

As timber extracted increased from 75 m^3 to 200 m^3, the amount of carbon stored in the forest was strongly affected by the time period considered. Mean carbon storage over 20 years dropped by 16% as timber extracted was increased from 75 m^3 to 200 m^3. For 40- and 60-year intervals, the rate of

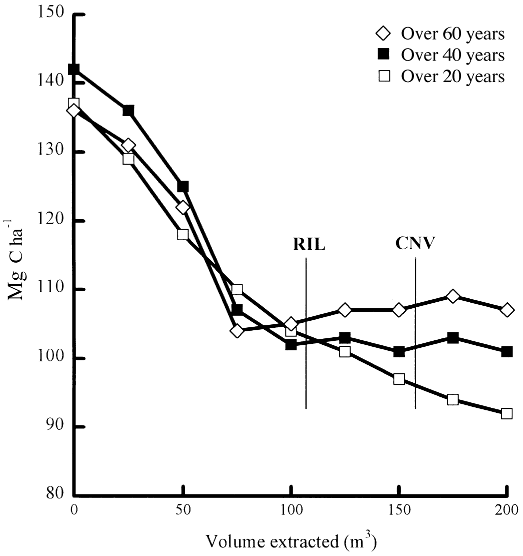

Fig. 4. Changes in mean carbon storage over 20, 40 and 60 years following logging as volume of timber extracted increases. Logging damage was held constant for all simulations (0% soil damage, 20% fatal damage, 20% other damage). The vertical lines mark the mean volume extracted in the study area in Sabah where reduced-impact logging (RIL) and conventional logging (CNV) methods were used.

change in mean carbon storage with increased volume extracted was less (Fig. 4). As volume extracted increased from 75 to 200 m^3, mean carbon storage changed only 3–6%. Because logging damage was held at a constant level for these simulations, sufficient numbers of lower canopy trees were available to replace harvested trees, regardless of the number felled and extracted. As more trees were felled, the resulting increase in upper layer canopy openness was associated with a positive growth response in trees in lower layers and, consequently, little difference in mean carbon storage resulted. The differences in the relationship between carbon storage and volume extracted for the three time intervals is related to recovery time (i.e. longer time intervals allow more recovery). Results from these simulations suggest that gains in growth compensate for the decrease in standing biomass related to higher levels of timber extraction. The increases in carbon storage over 40 and 60 years as volume extracted increases above 75 m^3 (Fig. 4) are an artefact of the assumption that logging damage was constant across the range of extraction levels. In practice, logging damage typically increases as volume of timber extracted increases.

SENSITIVITY ANALYSES

Simulation results over 60 years without logging were most sensitive to parameters describing tree allometric relationships and physiological capacities (Table 6). In general, biomass in trees > 45 cm d.b.h. at 60 years was most sensitive to small changes in input variables, constants or parameters. For the other response variables examined, no change greater than 15% was observed with an increase of

Table 6. Results from sensitivity analyses. Variables were increased by 15%, and response variables were reported if the value changed by 5% or more. Percentage change from base run (unlogged scenario, logging scenario for final three variables) are presented. For the response variables, subscripts symbolize the number of years over which the simulation was run, Bio refers to above-ground biomass, C refers to carbon stored in above-ground biomass and necromass (soil organic matter, coarse woody debris, small woody debris and fine litter), and end B45 refers to above-ground biomass in the upper layer (i.e. trees > 45 cm d.b.h.) during the final year of the simulation. Numerical subscripts used for input variables refer to canopy layer

	Response variables							
Input variable	mean C_{20}	mean Bio_{20}	end Bio_{20}	mean C_{40}	mean Bio_{40}	mean C_{60}	end $B45_{60}$	$Pioneers_{20}$
B_{25} (initial biomass layer 2)							−31%	
LAI_{45} (leaf are index layer 1)							+5·3%	
LAI_{25} (leaf area index layer 2)							−25%	
TR (stemwood fraction)			−11%		−11%	−5%	+26%	
CD (crown diameter ratio)			−14%		−10%		−39%	
I (full sun illumination)							−30%	
K_{45} (light extinction coefficient)			−9·4%	−5·1%	−5·1%	−6·4%		
$P_{\max}$ (maximum photosynthetic rate)				+5·6%			23%	
M (slope of light response curve)							−30%	
C (conversion Ps to organic matter)	+7%	+6·3%		+7·5%		+5·5%	−21%	
PR (leaf energy use efficiency)	+7%	+6·3%		6·1%			−21%	
R (stem respiration)			−11%	−5·6%	−5·8%	−6·4%		+9·6%
LAI_P (leaf area index pioneers)								+14%
$P_{\max P}$ (maximum rate for pioneers)								−14%
mc_{45} (crowding mortality rate layer 1)								

15% in any one input variable, constant or parameter.

The model's sensitivity to changes in stemwood fraction and crown area/stem diameter ratio is probably due to the influence of these variables on each layer's leaf area. Leaf area sets the upper limit for carbon gain in photosynthesis and is also used to determine whether conditions are crowded or not, thus setting mortality rates. The allometric statistics used in the model were developed from the destructive harvesting of 150 trees in west Malaysia (Kato, Tadaki & Ogawa 1978). The model's reliance on one set of allometric statistics to describe all non-pioneer tree species simplifies forest development processes and does not allow for varying stature, architecture or wood densities.

The selected response variables were sensitive to small increases in physiological parameters, specifically the light extinction coefficient for the top layer (K_{45}), stem respiration rate (R), rate of photosynthesis at light saturation ($P_{\max}$), the slope of the light response curve (M), leaf energy use efficiency (PR), conversion factor for photosynthetic gain to organic matter production (C) and leaf area index for layer 2 (LAI_{25}). The model's sensitivity to upper layers' leaf area indices and light attenuation factors suggest that woody biomass accumulation could be affected by invasion of the stand by vines.

The selected response variables were insensitive to small changes in initial amounts of detritus, conversion factors (organic matter to carbon) and mortality rates. The response variables changed little with a 15% increase in initial layer biomass. One exception was biomass in the subcanopy tree layer (25–45 cm d.b.h.); the ending biomass in the canopy layer was 31% less when initial conditions were raised from 48·5 to 56 Mg o.d.m. ha^{-1} (Table 6). This increase changed little with a 15% increase in initial layer biomass. One exception was biomass in the subcanopy tree layer (25–45 cm d.b.h.); the end biomass in the canopy layer was 31% less when initial conditions were raised from 48·5 to 56 Mg o.d.m. ha^{-1} (Table 6). This increase caused subcanopy tree mortality rates to shift from normal to crowded conditions, so fewer trees made the transition into the canopy layer during the 60-year run. The observed decline in canopy tree biomass at year 60 associated with an increase in LAI_{25} is related to a similar phenomenon of increased growth rates in the subcanopy layer leading to crowded conditions, increased mortality rates and fewer trees moving into the canopy layer.

For the logging scenario, the response variables changed little with a 15% increase in the selected input variables of the model (Table 6). Pioneer tree biomass at 20 years was sensitive to a change in maximum leaf area index for the pioneers (LAI_P), maximum photosynthetic rate ($P_{\max P}$) and crowding mortality rate for pioneers in layer 1 (mc_{45}). Mean carbon storage over 20, 40 and 60 years appeared to be insensitive to small changes in variables, constants and parameters within the model.

LOGGING DAMAGE AND CARBON STORAGE – FATAL DAMAGE

In general, as fatal stand damage increases, mean carbon storage in above-ground biomass decreases and mean carbon storage in necromass increases (Fig. 5a–c). The relationship between fatal damage and mean carbon storage in biomass is not linear; an inflection point is apparent at about 50–60% stand damage for all three time intervals examined. The inflection point marks the level of damage associated with decreased importance of biomass storage and increased importance of necromass storage. If more than 50% of the forest is damaged, standing biomass stores are low, regardless of the time interval considered. When less than 40% of the stand is killed, mean forest biomass increases with longer time intervals.

Necromass produced from trees killed during logging does not disappear immediately. Because of this delay, the three time intervals considered, 20, 40 and 60 years, are associated with slightly different patterns of change in carbon storage as incidence of

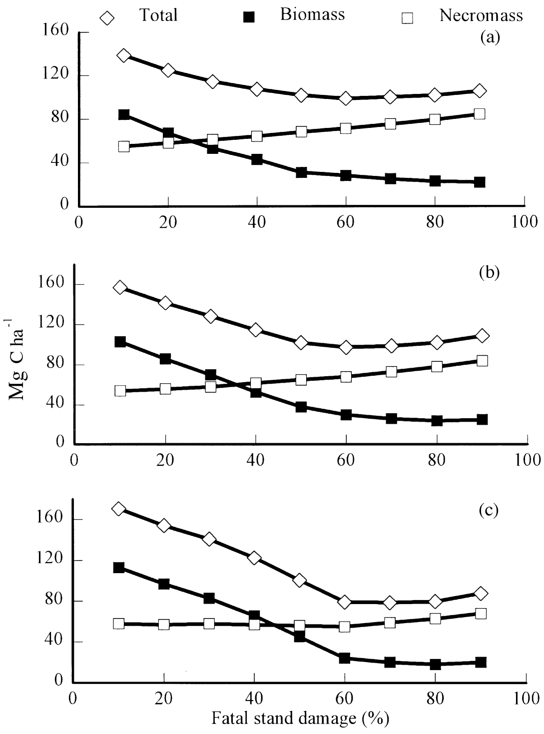

Fig. 5. Results of simulations in which the proportion of the stand receiving fatal damage was systematically increased in 10% increments. Mean carbon storage in biomass and necromass was calculated over (a) 20-, (b) 40- and (c) 60-year periods following logging.

fatal damage increases. As the time interval considered decreases, the reduction in mean carbon storage associated with an increase in fatal damage is less (Fig. 5a–c).

LOGGING DAMAGE AND CARBON STORAGE – NON-FATAL DAMAGE

Increasing postlogging mortality, either the duration of elevated rates or the rate itself, caused a decline in mean carbon storage up to 30% (Fig. 6). Increased duration of a relatively high mortality (1% year^{-1}), was associated with an approximately linear decline in mean carbon storage; increasing mortality from 1% to 5% caused a 12% decline in mean carbon storage over 60 years. In growth and yield plot studies in dipterocarp forest, mortality appears, on average, to remain relatively high for about 5 years (Wan Razali 1989). If mortality rates are high for only 1 year rather than 5 years, mean carbon storage over 40 or 60 years is 10% higher. If elevated mortality rates last 10 years rather than 5 years, the mean carbon storage over a 60-year period drops by 11%.

If non-fatal damage merely reduces individual tree crown areas, results from simulations indicate that mean carbon storage is affected very little. Increasing the proportion of trees with non-fatal damage from 0% to 80% changed mean carbon storage over 20, 40 and 60 years by less than 2%. Increasing the proportion of the crown removed due to non-fatal damage from 25% to 80% also had little effect on mean carbon or mean biomass storage over time. However, little is known about the effects of wounding on dipterocarp growth and survival. Wounding that does not cause death may cause deformities or rots that will reduce the quality of the timber produced (Basham 1978). Certain species of dipterocarps appear to be particularly vulnerable to heart rots (Burgess 1966).

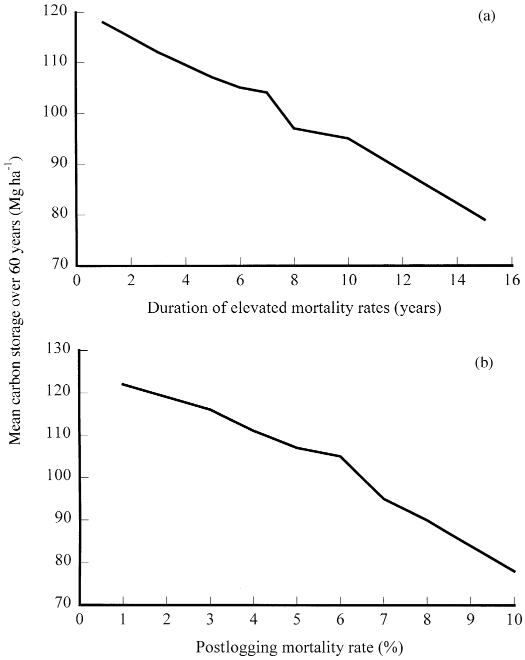

Fig. 6. Results from simulations in which annual postlogging mortality rates were systematically increased. Mean carbon storage over a 60-year period with (a) changes in the number of years mortality rates were held at 1% of individuals ha^{-1}, and (b) changes in the mortality rate for the first 5 years following logging.

PIONEER TREES

Site occupancy by pioneer trees, as represented in the model, is associated with reductions in total mean biomass over time. Results from simulations suggest that when 20–50% of the stand is killed during logging, as was the case in this study (Pinard & Putz 1996), replacing persistent forest species with pioneer tree species can reduce the site's potential for carbon storage by 15–26% over 40–60 years. When the sites are heavily damaged, as when more than 70% of the stand is fatally damaged, pioneer tree invasion is not associated with significant increases in mean biomass storage over 40 or 60 years. In simulations, the establishment of persistent tree species under pioneers is limited by a lack of seedlings when stand damage exceeds 40%. At levels of stand damage less than 40%, seedling densities approach prelogging stem densities and biomass within 40 years; the growth of persistent tree species to upper layers is only limited by physiological constraints.

CONVENTIONAL AND REDUCED-IMPACT LOGGING

Results from simulations indicate that the amount of carbon stored in the forest following reduced-impact logging was between 20 and 40 Mg ha^{-1} higher than that following conventional logging (Fig. 7; mean difference over 20 years, 29 Mg C ha^{-1}; mean difference over 60 years, 36 Mg C ha^{-1}). Part of the variation in the magnitude of the difference between the two methods was related to a pulse of carbon storage in pioneer trees following conventional logging. Carbon stored in necromass over time was less in the conventional logging simulation than the reduced-impact logging simulation. Although the input of logging debris at year 0 was greater following conventional than reduced-impact logging, the coarse woody debris that entered the pool over time was less and decline in soil carbon was greater in conventional than reduced-impact logging (Fig. 7). Biomass stabilized at approximately 120 Mg C ha^{-1} after year 30 following reduced-impact logging, whereas it stabilized at approxi-

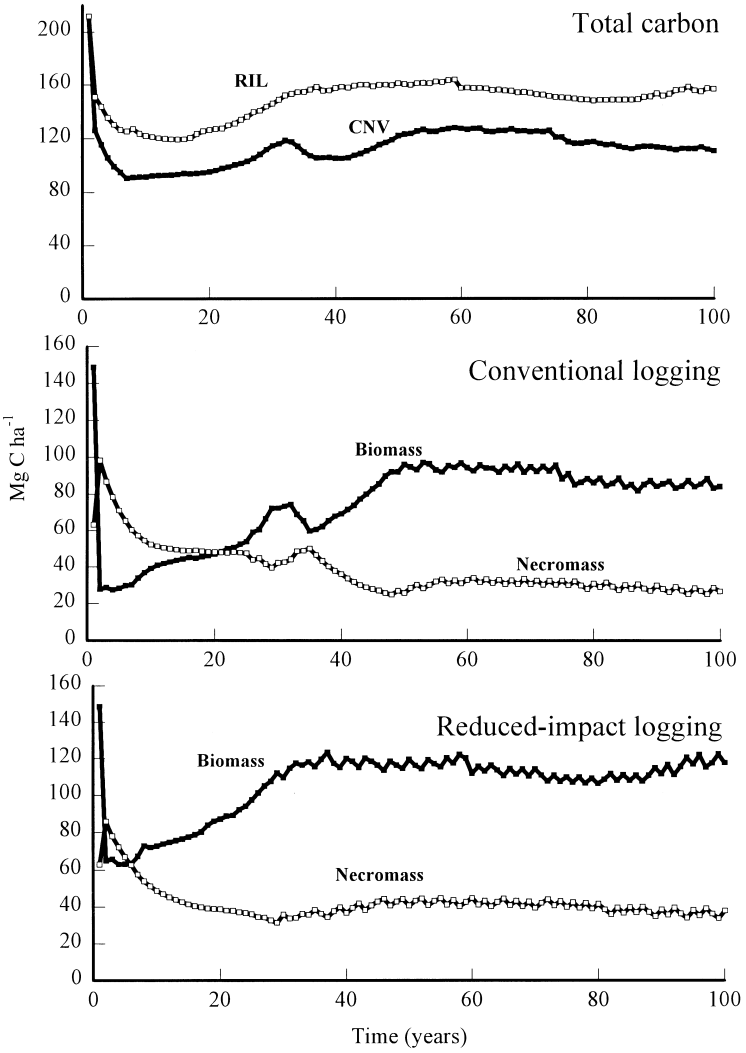

Fig. 7. Results from simulations for conventional logging (CNV; 154 m^3 ha^{-1}, 16·6% area with soil disturbance, 40% stand with fatal damage, 20% stand with minor damage) and reduced-impact logging (RIL; 104 m^3 ha^{-1}, 6·8% area with soil disturbance, 20% stand with fatal damage, 20% stand with minor damage). Total carbon includes biomass and necromass. Logging occurred in year 0.

mately 85 Mg C ha^{-1} after year 50 following conventional logging. The difference in time to reach stabilization was related to re-establishment of the canopy layer. During the first 40 years following conventional logging, relatively little biomass existed in the canopy layer (Fig. 8). Alternately, following reduced-impact logging, the canopy layer recovered to prelogging biomass levels after about 30 years.

Conclusions

Our model was developed as a tool for examining the effects of reductions in logging damage for ecosystem carbon storage over time. Simulation results indicate that the relationship between fatal stand damage and ecosystem carbon storage is not linear and that at 50–60% fatal stand damage, biomass recovery following logging is severely limited. This threshold damage level is often reached with conventional logging practices in Sabah. Reducing fatal damage from 40% to 20% and area with soil damage from 17% to 7%, as was the case in the reduced-impact logging project in Sabah (Pinard & Putz 1996), will be associated with an increase of 36 Mg C ha^{-1} in mean carbon storage over 60 years according to our model. The difference between the two harvesting methods is due to differences in stand damage rather than differences in timber volumes extracted.

Our model has several limitations, but perhaps the most important for simulating forest recovery from large-scale disturbances is that only two ecological groups of species are represented. The diversity of tree species that occurs in the dipterocarp forests

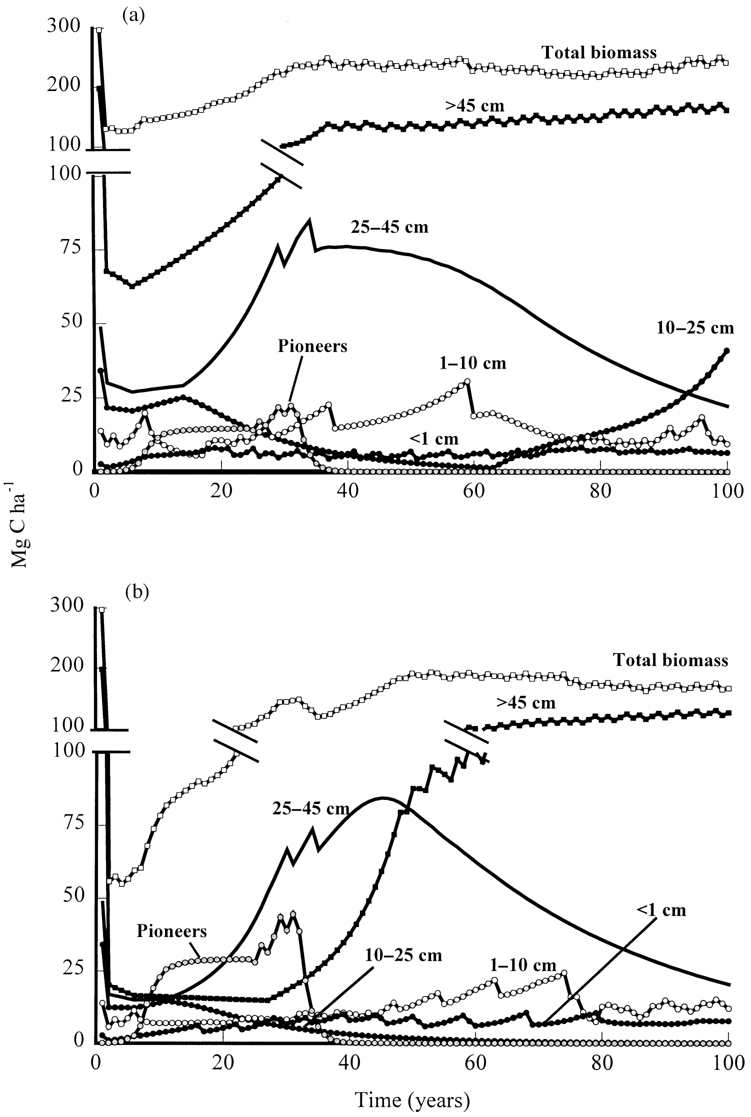

Fig. 8. Biomass by canopy layer (d.b.h. class) for simulations of (a) reduced-impact and (b) conventional logging. See descriptions of the two logging methods in the legend for Fig. 7.

of Sabah includes a broad range of tree allometries, architectures, canopy heights, reproductive phenologies and physiologies. Simulation results are sensitive to small changes in many of these parameters. If heavy logging damage causes a shift in tree species composition or results in a proliferation of vines, describing the recovering forest with a set of parameters appropriate for the prelogging composition may not be satisfactory. A more complex model, however, would be difficult to parameterize due to a lack of data, simulations could be computationally intensive, and evaluation would be more problematic.

In some old-growth temperate forests, polycyclic timber harvesting is associated with a substantial decrease in ecosystem carbon storage due to the erosion of necromass stores (Harmon, Ferrell & Franklin 1990). In unlogged dipterocarp forests, only about 25% of ecosystem carbon storage is in necromass (litter and soil), and results from simulations suggest that necromass stores recover to prelogging levels within a 60-year cutting cycle. Carbon storage in dipterocarp forest is principally in standing biomass. Harvesting activities that influence biomass recovery, for example by affecting site quality, species composition and vulnerability to fire, are of consequence to carbon storage. In dipterocarp forests, managing the forest for timber is compatible with maximizing carbon storage if appropriate harvesting practices are used.

Acknowledgements

Pinard thanks Yayasan Sabah (Forestry Upstream Division), Danum Valley Management Committee, State Internal Affairs & Research Office of the Sabah Chief Minister's Department, and the Economic Planning Unit of the Prime Minister's Department for permission to conduct research in Danum Valley. The work benefited from discussions with J.J. Ewel, F.E. Putz and J. Tay. We thank J.J. Ewel, F.E. Putz, K. Williams for comments on an earlier version of the manuscript.

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Received 13 October 1998; revision received 20 November 1999