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Above-ground biomass recovery following logging and thinning over 46 years in an Australian tropical forest

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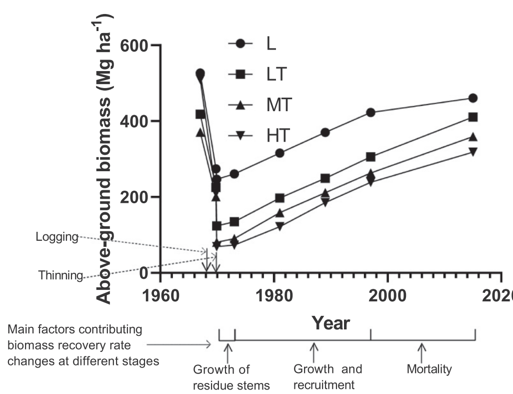
HIGHLIGHTS

- AGB recovery rates could be explained by the densities of residual stems.
- Initial biomass recovery after logging was largely contributed from residual stems.
- Biomass recovery rates decreased at a later stage mainly due to mortality.
- Selectively logged forests still have high carbon sink potential.
- Biomass recovery of forests after logging and thinning takes at least 50 years.

GRAPHICAL ABSTRACT



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ABSTRACT

Managed tropical forests are a globally important carbon pool, but the effects of logging and thinning intensities on long-term biomass dynamics are poorly known. We investigated the demographic mechanisms of above-ground biomass recovery over 48 years in an Australian tropical forest following four silvicultural treatments: selective logging only as a control and selective logging followed by low-, medium- and high-intensity thinning. Initial biomass recovery rates following thinning were poor predictors of the long-term changes. Initial biomass recovery from 1969 to 1973 was slow and was largely concentrated on an increase in the biomass of residual stems. From 1973 to 1997, above ground biomass (AGB) increased almost linearly, with a similar slope for all sites. From 1997 to 2015, the rate of biomass accumulation slowed, especially for the L treatment. All thinning treatments stimulated more recruitment and regrowth of non-harvested remaining trees compared to the untreated control. Biomass at both the low and medium intensity treatments has almost fully recovered to 98% and 97% of pre-logging biomass levels respectively. The predicted times of complete above-ground biomass recovery for the logging only and high intensity treatments are 55 and 77 years respectively. The slower biomass recovery at the logging only site was largely due to increased mortality in the last measurement period. The slower recovery of the high intensity site was due to a combination of a higher initial reduction in biomass from thinning and the increased mortality in the last measurement period. The high mortality rates in the most recent measurement period are likely due to the impacts of two cyclones that impacted the study site. Our results suggest that it will take at

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least around 50 years for this site to recover to its pre-harvest biomass, much longer than many of the cutting cycles currently used in tropical forest management.

1. Introduction

Almost half of the world's primary tropical forests, up to 400 million ha, are managed for timber production (FAO, 2010; Blaser et al., 2011), as timber is an important economic resource in many tropical countries. To enhance the production of high-value commercial timber stocks as part of sustainable poly-cyclic harvesting, silvicultural treatments are sometimes applied following selective logging to remove non-commercial trees (Peña-Claros et al., 2008; Villegas et al., 2009; Gourlet-Fleury et al., 2013; de Avila et al., 2015, 2017). These silvicultural treatments are designed to increase the growth or regeneration of high-quality timber species by reducing competition from surrounding non-commercial trees. However, timber harvesting and subsequent thinning practices have immediate and potentially long-term impacts on the carbon stocks of tropical forests (de Avila et al., 2015). For example, biomass losses following logging have led to increased rates of global carbon emissions from tropical regions (Baccini et al., 2017). Understanding responses of biomass dynamics to management practices is important to implement sustainable forest management approaches. Yet, detailed information is lacking on the long-term effect of post-logging thinning intensity on the recovery trajectories of above ground biomass (AGB) stocks in logged tropical forests.

Although many studies have estimated recovery of tree biomass or carbon following clearance and disturbance in tropical forests (e.g. Blanc et al., 2009; Letcher and Chazdon, 2009; Huang and Asner, 2010; Martin et al., 2013; West et al., 2014; Rutishauser et al., 2015; Vidal et al., 2016; Roopsind et al., 2017, 2018), few studies have documented long-term trajectories of biomass recovery following logging and thinning. Disturbance intensities and many other factors, including climate, land use history, forest age, remnant forest structure, and environmental changes can greatly affect the recovery of AGB in tropical forests (e.g. Hughes et al., 1999; Caspersen et al., 2000; Johnson et al., 2000; Read and Lawrence, 2003; Chazdon et al., 2007; Lin et al., 2015; Poorter et al., 2015; Rozendaal et al., 2017). Logging intensity can also strongly influence forest biomass recovery time (e.g. Sist et al., 2012; Rutishauser et al., 2015; Vidal et al., 2016). Biomass recovery following logging can take from decades to over a hundred years (Sist et al., 2012; West et al., 2014; Rutishauser et al., 2015). However, few studies address the impacts of different intensities of thinning on long-term recovery of biomass stocks in tropical forests.

Long-term data on temporal trajectories of biomass recovery through assessment of tree demography (growth, recruitment and mortality) in tropical forests can provide important information for sustainable tropical forest management and for parameterizing mechanistic models of biomass recovery and carbon storage. Three demographic processes drive the dynamics of biomass recovery following disturbances i.e. the growth of remnant living trees, tree recruitment, and tree mortality (Carreño-Rocabado et al., 2012; Sist et al., 2012). The intensity and severity of disturbance influence recruitment, diameter growth and mortality through changing environmental conditions and competitive interactions. High-intensity disturbances typically leave behind fewer large and small trees, increase light penetration, and reduce competition between trees. The altered environmental conditions will subsequently increase recruitment and accelerate diameter increment growth (Sist et al., 2012). Changes in the rate of recruitment, mortality and growth of remnant trees can subsequently affect size-class distributions (Peña-Claros et al., 2008; Villegas et al., 2009). The growth of large trees plays a disproportionate role in biomass accumulation (Slik et al., 2013; Sist et al., 2014; Lutz et al., 2018; Bastin et al., 2018). For example, trees with a DBH > 60 cm represented only 9.3% of the total tree density but stored almost half of total AGB (Sist et al., 2014). Furthermore, the mortality of large trees also contributes disproportionately to AGB losses, relative to their abundance. However, few studies (e.g. Mazzei et al., 2010; Rozendaal and Chazdon, 2015; Rozendaal et al., 2017) have investigated how these demographic components in different size classes drive rates of AGB recovery following stand-level disturbances.

In 1967, the Queensland Department of Forestry (QDF) established a long-term study in a tropical rainforest in Atherton Tablelands, north Queensland, the original purpose being to assess the long-term impacts of different intensities of liberation thinning on commercial timber volume. The experiment covered 16 ha and comprised four adjacent 4-ha blocks. Following selective logging in 1968/69, three thinning treatments of different intensities were applied together with a 'control' treatment, which was left untouched after logging. The experiment was conducted without replicates and lacked an unlogged control, as the data were to be used internally for forest management purposes. Here, we use this rich source of temporally replicated data to gain insights into the demographic processes driving biomass recovery over 46 years following different intensity silvicultural treatments. First, we describe how AGB recovery rates vary over time following selective logging and thinning. Second, we assess the relative importance of recruitment, growth, and mortality as short- and long-term drivers of biomass changes in response to thinning.

In this paper, biomass recovery rates mean the rates of increase of above-ground biomass over specified time intervals during the long-term recovery process. We hypothesized that higher intensity thinning would facilitate the recruitment of new trees and increase the increment growth rates of new recruits and remnant trees. Thus, up to a threshold level of thinning, the biomass recovery rates would increase with treatment intensity. Above this threshold level, however, increasing thinning intensity would reduce the stem density of remnants dramatically. We hypothesized that growth and recruitment would be more important drivers of biomass recovery rates immediately following disturbance because of reduced competition. However, we expected mortality to increase in importance as a driver of biomass recovery rates at later stages because of more intense competition and the short lifespans of early successional tree species that recruit immediately following treatment.

2. Methods

2.1. Study site

The study was established in 1967 by QDF (Queensland Department of Forestry) in a wet tropical evergreen rainforest on the Atherton Tablelands, north Queensland, Australia (17° 17′ S, 145° 24′ E). The site is surrounded by natural tropical forests, which now form part of the larger Wet Tropics of Queensland World Heritage Area where logging was banned in 1987. The elevation is approximately 1150 m above sea level and the annual rainfall is approximately 1400 mm. The annual rainfall pattern is seasonal, with a pronounced maximum of about 250 mm per month during the wet season (December to March) and a minimum of about 50 mm per month during the dry season (May to September). The soil in this study site is grey brown clay loam derived from granite with some parts of the study site are rocky. Information contained in the original experiment commencement report prepared by Department of Forestry staff when the experiment was established indicated that the area was used as a practice artillery range during the 1935–1945 war years and that the presence of occasional cut stumps in surrounding forest suggested that a small quantity of timber was extracted when the surrounding area was opened up for agriculture. The forests in our study site were considered by the Department of Forestry to be in pristine condition prior to the experiment commencing.

In the study site, 223 species above 10 cm DBH were recorded in the sample plots over 48 years of investigation. The stem density and basal area in the sample plots before logging was 277 stems ha^{-1} and 55 m^2 ha^{-1}, respectively (Hu et al., 2018). The dominant species prior to logging in 1967 were *Flindersia pimenteliana* (F.Muell.), *Flindersia brayleyana* (F.Muell.), *Flindersia bourjotiana* (F.Muell.), *Ceratopetalum succirubrum* (C.T.White) and *Franciscodendron laurifolium* (F.Muell.). There are few woody lianas, but climbing palms (*Calamus muelleri* H. Wendl.) are abundant in the understory and subcanopy. Further information about the study site and changes in species composition over the 48 years can be found in Hu et al. (2018, 2020).

2.2. Experiment design and sampling

The experiment was established by the QDF in 1967. Following selective logging in 1968, four treatments were applied in September 1969. Thinning practices were originally designed to promote the proportion, recruitment and growth of commercial timber species, predominantly *Flindersia* species (Hu et al., 2020). The objective of different intensity thinning practices was to assess which thinning intensity would promote the highest commercial timber volume. These treatments were logging only (L) as a control, post-logging low-intensity thinning (LT), post-logging medium-intensity thinning (MT) and post-logging high-intensity thinning (HT). These silvicultural treatments varied in the levels of initial reduction of stand basal area and stem density and in the size and position of trees that were removed (Table A.1 and A.2). The logs were extracted using a bulldozer with a blade. The skid trails were scattered across the plots. The density of skid trails was 14.21% on average (calculated in area) across the eight 0.5-acre plots and the 40 0.1-acre plots (0.4 ha per treatment).

The experiment used a nested block design, comprising four adjacent blocks measuring 200 m long and 200 m wide (i.e. of 4 ha each) in 1967 (Fig. S1). The L, LT and HT blocks faced south, whereas the MT block faced north. The slopes are 5 to 10° for the L, MT and HT blocks and 10–20° in the LT block. Ten 0.04-ha (20 m long and 20 m wide) plots were established in each of the four blocks prior to logging (1.6 ha in total) and data from these plots provided the pre-logging baseline data on species composition, size distributions, and basal areas. Data were collected in August 1967 (before logging) and in August 1969 (soon after logging) from those 40 plots. Due to the large cost of collecting data in such a large experiment, after silvicultural treatment in September 1969, two 0.2 ha rectangular sub-plots were established in each of the four blocks for future long-term data collection (100 m long and 20 m wide, see Fig. A.1). Data were subsequently collected from these eight 0.2 ha plots immediately after silvicultural treatments in September 1969 and again in 1973, 1981, 1989, 1997 and 2015. At the time of the first measurement, all trees above 10 cm DBH were identified to species level and their DBH was recorded. Each tree was assigned a unique identifying number which was painted on the bole along with a painted line indicating where the DBH had been measured. In subsequent measures, new recruits (i.e. those stems growing into 10 cm and greater but not previously recorded) were also identified, their DBH was measured and the tree marked in the same way as initially measured stems. Tree mortality was also recorded. The QDF adopted the convention that for trees with buttresses or deformities, DBH was measured just above these features. A new DBH measurement point (and associated paint mark) was established where a buttress extended past the previous measurement height. In these cases, the diameter at both the old and new measurement points (higher and lower DBH line) was recorded. The average DBH of both old and new measurement points was used to calculate AGB of buttressed trees with changes in DBH measurement points, (Lewis et al., 2009).

When the experiment was initiated in 1967, treatments were not replicated and only two plots were sampled within each treatment, as the QDF designed and conducted the experiment for their own use and did not intend to undertake statistical analyses that required replication. The lack of an unlogged natural forest control limited the analysis of changes, given that natural forests are also subject to changes over time. We recognize that pre-logging data do not completely substitute for long-term data collected in unlogged sites. However, the pre-logging data provide a reasonable baseline, as the changes related to natural processes would likely be relatively small compared to those induced from logging and subsequent silvicultural treatment.

2.3. Data analysis

Data from the two plots per treatment were pooled for analysis. We estimated above-ground tree biomass (AGB) using an allometric equation developed by Chave et al. (2014):

$\ln(\mathrm{AGB}) = -1.803\text{-}0.976 \times E + 0.976 \times \ln(\rho) + 2.673 \times \ln(\mathrm{DBH})\text{-}0.0299 \times \ln(\mathrm{DBH})^2$where AGB is the above-ground tree biomass (Kg of dry matter), ρ is the species-specific wood density (g cm^{-3}), E is a location-specific bioclimatic stress variable, which compounds indices of temperature variability, precipitation variability, and drought intensity. AGB was expressed as metric tonnes per ha (Mg ha^{-1}) in our study. Species-specific wood densities estimated from living tree biomass, were mainly obtained from a database published by Cause et al. (1989). Where local wood density values were not available, we used a genus-level wood density based on local measurements, from a database of Ilic et al. (2000). Genus-level wood density is generally a good proxy for species-level wood density (Chave et al., 2006).

The number of recruits growing into the 10 cm DBH class in each period was recorded. We compared the densities of trees in four size classes (10–19.9 cm, 20–39.9 cm, 40–59.9 cm, ≥60 cm) over time and between treatments. Recruitment was calculated as the density of recruits over a certain period. Tree mortality was calculated as the number of trees that died annually during each time interval. AGB recovery rates from stem increment growth rates, recruitment and mortality were also divided into four size classes in each measurement period. Average annual biomass recovery rates during each measurement period were calculated as the increase of biomass during a period divided by the number of years in each period. The data from the two plots in each treatment were combined to have one 0.4 ha plot per treatment. Above-ground biomass recovery in 2015 of each treatment was extrapolated to pre-logging levels using the biomass recovery rates from 1969 to 2015 as a linear regression to predict at which age biomass would recover fully to its pre-logging level for each treatment. We estimated the carbon fluxes of forests from logging in 1967 to 2015 due to logging, thinning, growth, recruitment and mortality of trees. We calculated biomass loss from logging, thinning, mortality and biomass gain from growth and recruitment. We assume that tropical forest carbon is half of dry biomass (Gibbs et al., 2007).

3. Results

3.1. Above-ground biomass dynamics following different silvicultural treatments

AGB for trees ≥10 cm diameter at breast height (DBH) increased over 46 years following thinning. Pre-logging biomass varied substantially among the four treatments, from 371 to 527 Mg ha^{-1}, and was higher in the logging only treatment (L) and high-intensity thinning (HT), compared to the low-intensity thinning (LT) and medium-intensity thinning (MT). However, post-logging biomass was similar across the treatments (201 to 274 Mg ha^{-1}) because of higher biomass removal by logging operations in L and HT (Table 1). As expected, biomass

Table 1
The above-ground biomass removed through logging and thinning. Numbers in the table are absolute values. For reductions through logging (the biomass of harvested logs), numbers in the brackets are percentages of biomass reductions through logging to pre-logging biomass. For the reductions through thinning, numbers in the brackets are percentages of biomass reductions through thinning to post-logging biomass. For post-thinning values, numbers in the brackets are percentages of post-thinning biomass to pre-logging biomass.

Variables (Mg ha^{-1})	L[a]	LT	MT	HT
Pre-logging biomass (1967)	527	418	371	510
Biomass lost through logging (May 1969)	280 (53%)	193 (46%)	170 (46%)	300 (59%)
Biomass reductions through thinning (1969)	0 (0%)	102 (45%)	120 (60%)	141 (67%)
Post-thinning biomass (August 1969)	247 (47%)	123 (29%)	81 (22%)	69 (14%)
Biomass gain 1969–2015	214	287	278	249
Net biomass loss through logging, thinning, recruitment, growth and mortality	(−66)	(−8)	(−12)	(−201)

[a] L: logging only without silvicultural treatment; LT: logging and light intensity treatment; MT: logging and medium intensity treatment; HT: logging and high intensity treatment.

reduction through thinning was lowest in LT (102 Mg ha^{-1}), moderate in MT (120 Mg ha^{-1} respectively), and highest in HT (141 Mg ha^{-1}), ranging from 45% to 67% of pre-treatment levels (Table 1). After thinning, L had the highest biomass, followed by LT, MT and HT (Fig. 1a). By 2015, treatment L still had the highest above-ground biomass (AGB), whereas HT had the lowest AGB (Fig. 1a). By 2015, the AGB in LT and MT almost completely recovered to their pre-logging levels (98% and 97%, respectively), but AGB in L and HT was 12.4% and 37.3% below their pre-logging levels, respectively (Fig. 1a).

We divided biomass recovery trajectories into three distinct phases over 46 years following thinning: the first four years following thinning (1969–1973), the next 24 years (1973–1997) and the last 18 years (1997–2015). Over the first 4 years, AGB recovery rates in L, LT, MT, and HT were initially slow (i.e. 3.5, 2.86, 2.44 and 1.04 Mg ha^{-1} yr^{-1} respectively) (Table 2). In the second phase from 1973 to 1997, biomass recovery was rapid, and almost linear across each of the four sites, albeit with different starting points (Fig. 1a) with AGB recovery rates in the four treatments ranging from 6.48 to 8.52 Mg ha^{-1} yr^{-1}. Over the next 18 years (third phase), AGB recovery rates in the four treatments decreased, with the most dramatic decrease in L. The AGB recovery rates in L decreased to 2.12 Mg ha^{-1} yr^{-1}, while those in LT, MT and HT decreased to 5.84, 5.34 and 4.4 Mg ha^{-1} yr^{-1} respectively. Over 46 years, the average annual AGB recovery rate in L, LT, MT, and HT was 5.2, 6.0, 5.9 and 5.2 Mg ha^{-1} yr^{-1}, respectively (Table 2). The net biomass changes of forests from logging in 1967 to 2015 due to losses from logging, thinning, mortality and gains from growth and recruitment were highest in HT, with a biomass loss of 201 t/ha, while the other treatments only had biomass losses of 66, 8 and 12 t/ha in L, LT and MT, respectively (Table 1). We extrapolated the above-ground biomass recovery of each treatment to predict when biomass would fully recover to pre-logging levels in each treatment. The age for full recovery to pre-logging level in treatment L, LT, MT and HT is 55, 47, 47 and 77 years, respectively (Fig. 1b). We predicted that biomass in L and HT still needs another 9 and 31 years to recover fully to pre-logging levels after 2015 with biomass in LT and MT recovered fully one year after 2015.

3.2. Changes in growth, recruitment, mortality, and size class distributions

Over the 46 years, recruitment of new trees increased with thinning intensity, as predicted (Fig. 2a). When comparing the recruitment rates between treatments during each measurement, the recruitment rates from 1969 to 1973 in the thinning treatments (21, 16 and 18 stems ha^{-1} yr^{-1}, respectively in LT, MT and HT) were substantially higher than those in the logging only control (8 stems ha^{-1} yr^{-1}, Fig. 2a). Most tree recruitment took place between 1973 and 1981, with the highest recruitment rate in MT (56 stems ha^{-1} yr^{-1}). Recruitment rates in the four treatments decreased substantially from 1981 to 2015. By 2015, the recruitment rates in the four treatments were similar, approximately 10 to 11 trees ha^{-1} yr^{-1}. The density of recruits

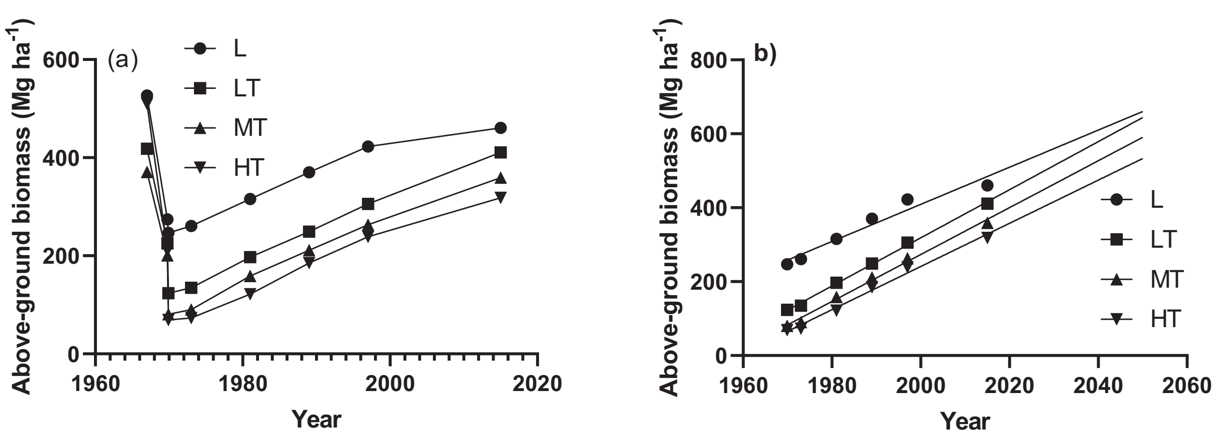

Fig. 1. (a) Above-ground biomass changes over years for trees ≥10 cm; (b) extrapolation of above-ground biomass recovery from 2015 biomass to pre-logging levels based on the biomass recovery rate from 1969 to 2015 as a linear regression. L: logging only; LT: logging with low-intensity thinning; MT: logging with medium-intensity thinning; HT: logging with high-intensity thinning. Interventions of selective logging (1968) and thinning (1969) are shown by downward arrows above the time axis.

Table 2
Average rate of net biomass gain in each measurement period for each treatment.

Treatment	Average rate of net biomass gain (Mg Ha^{-1} year^{-1})					
	1969–1973	1973–1981	1981–1989	1989–1997	1997–2015	1969–2015
L	3.50	6.82	6.86	6.52	2.12	5.16
LT	2.86	7.79	6.50	7.05	5.84	6.01
MT	2.44	8.52	6.58	6.49	5.33	5.87
HT	1.04	6.09	7.90	6.72	4.40	5.23

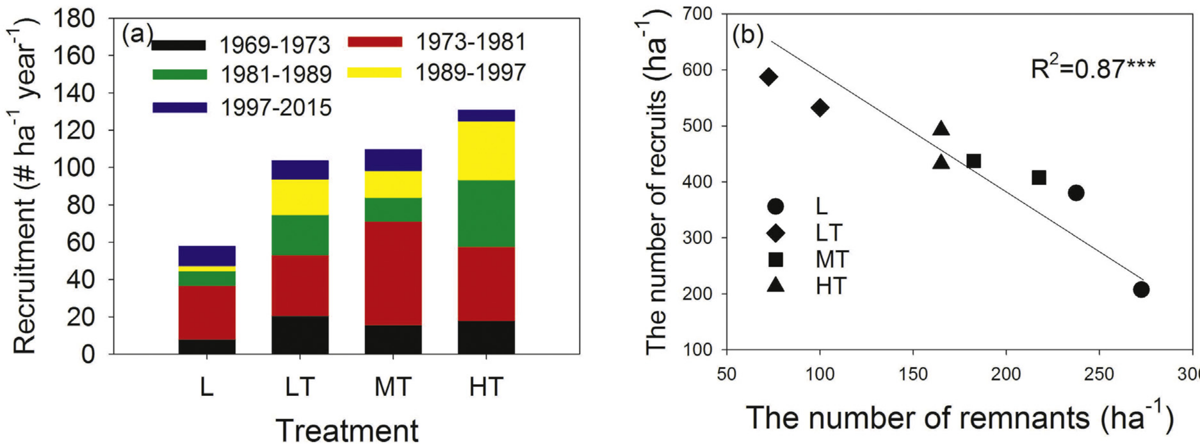

Fig. 2. (a) Densities of recruits in each period for each treatment. (b) The relationship between the density of remnants (≥10 cm) post-treatment to the density of recruits over 46 years in each treatment. Two dots for each treatment indicates two plots in each treatment. L: logging only; LT: logging with low-intensity thinning; MT: logging with medium-intensity thinning; HT: logging with high-intensity thinning.

over 46 years decreased as a linear function of the density of remnants across the four treatments ($R^2 = 0.86$, $p < .05$; Fig. 2b).

The absolute number of stems (≥10 cm) that died in each treatment (0.4 ha) increased over time (Table 3). During the first four years following thinning, only two trees died; a small tree (10–19.9 cm DBH) in LT and a large tree (40–50 cm DBH) in HT (Table 3). From 1973 to 1981, few trees in the 10–19.9 cm and 20–39.9 cm DBH classes died, with no mortality of trees in the ≥40 cm DBH class. From 1981 to 2015, the number of dead trees in the 10–19.9 cm DBH and 20–39.9 cm DBH classes increased compared to the previous periods. Tree mortality was concentrated in the 10–19.9 cm DBH class. The number of dead trees in L was higher than those in the thinning treatments (Table 3). Three of the five species with the highest mortality rates were early successional species: *Alphitonia whitei* Braid, *Polyscias murrayi* (F.Muell.) Harms and *Litsea leefeana* (F.Merrill.) Merr. (Table A.3).

Before logging, the tree size distributions were similar for all four treatments (Fig. 3). However, thinning dramatically reduced the stem densities in all size classes, with the decreases being progressively more marked as the level of thinning intensity increased (Fig. 3). Over 46 years, the stem densities in different size classes increased in the thinning treatments. By 2015, the tree size class distribution in the three thinning treatments had recovered to pre-logging conditions (Fig. 3).

Table 3
The observed number of trees that died over 46 years in different size classes for each treatment (0.4 ha per treatment).

Periods	Size classes	L	LT	MT	HT
1969–1973	10–19.9 cm	0	1	0	0
	20–39.9 cm	0	0	0	0
	40–59.9 cm	0	0	0	1
	≥60 cm	0	0	0	0
1973–1981	10–19.9 cm	3	9	0	2
	20–39.9 cm	0	1	0	2
	40–59.9 cm	0	0	0	0
	≥60 cm	0	0	0	
1981–1989	10–19.9 cm	17	11	26	8
	20–39.9 cm	3	3	1	1
	40–59.9 cm	1	1	1	1
	≥60 cm	0	0	0	0
1989–1997	10–19.9 cm	22	19	14	23
	20–39.9 cm	5	3	2	2
	40–59.9 cm	1	1	0	0
	≥60 cm	0	0	0	0
1997–2015	10–19.9 cm	38	25	45	33
	20–39.9 cm	22	14	26	9
	40–59.9 cm	4	0	1	1
	≥60 cm	1	1	0	1

Note: The mortality may include a few of the poisoned trees that may die only after many years' thinning. However, this was not recorded in the historic data. Therefore, we could not tell whether this is the case.

3.3. Above-ground biomass changes from recruitment, growth and mortality

AGB changes from growth, recruitment and mortality varied in different size classes, and over time. Biomass gain from recruitment peaked from 1973 to 1981 and then declined (Fig. 4). Biomass gain from increment growth was highest from 1981 to 1997 (Fig. 4). Biomass loss from tree mortality increased dramatically from 1997 to 2015. The biomass gains of existing trees varied between different size classes (Fig. 4). Trees in the medium size DBH classes (20–39.9 cm and 40–59.9 cm) contributed most to AGB changes from 1997 to 2015, compared to trees in the other size classes (Fig. 4). Over the 46 years following thinning, the AGB accumulation rates were higher in medium-size trees (20–39.9 cm DBH and 40–59.9 cm DBH, Fig. 4). The biomass gain from trees above 60 cm DBH was low in all treatments. Among size classes, the mortality of large trees (≥60 cm DBH) and medium-size trees (20–39.9 cm DBH) contributed most to the biomass loss.

4. Discussion

4.1. Biomass recovery dynamics

The long-term patterns of biomass recovery observed over 46 years following four different levels of disturbance provide important insights into the dynamics of biomass recovery processes and effects of silvicultural treatments, albeit that methodological limitations restricted statistical analyses and generalization. The change in above ground biomass (AGB) recovery rate in each treatment varied (Table 2), with AGB recovery rates in the four treatments increasing during the first 12 years, and then declining. These patterns indicate that initial AGB recovery rates following thinning are not good predictors of long-term change. Within each treatment, the biomass recovery was slow in the initial years, followed by almost linear increases over an extended period and then a slowing of recovery rates in the last measurement period. The precise pattern varied between the treatments, with the slowing in the last measurement period being much more pronounced in the logging only (least disturbed) site (Fig. 1a). Strikingly, the linear increase in biomass at all site follows almost exactly parallel trajectories, albeit from different starting points. Biomass did not completely recover to pre-disturbance levels in all treatments. This pattern, combined with the slowing in recovery rates in the last measurement period, means that

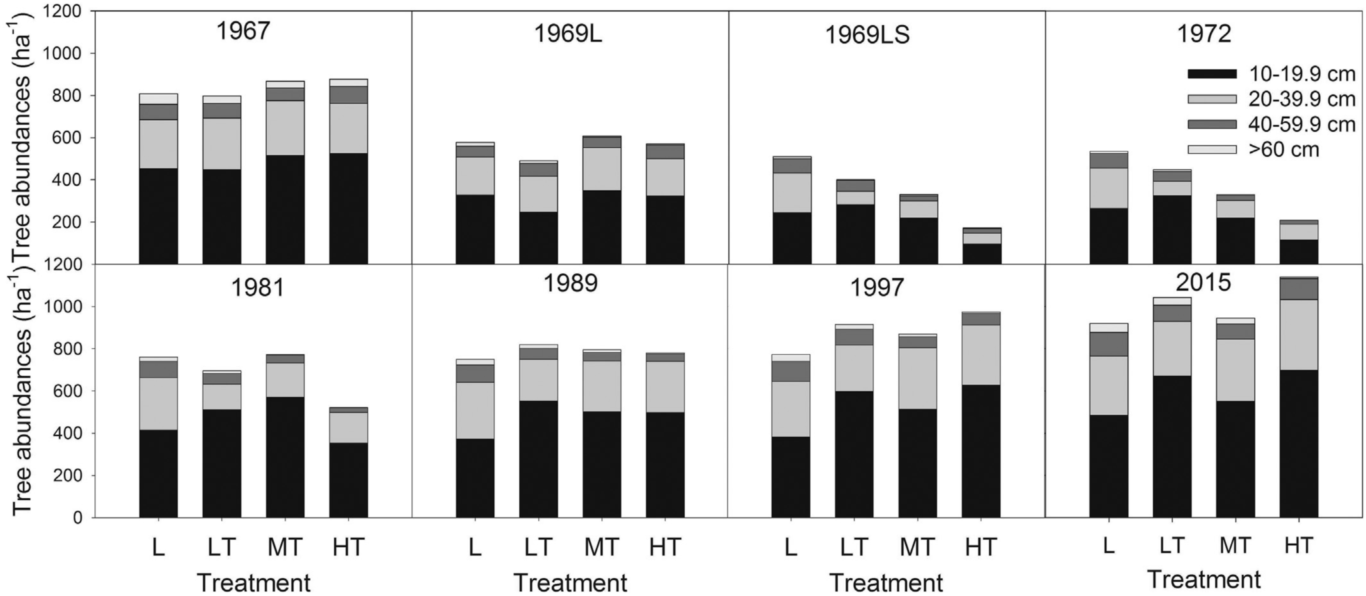

Fig. 3. The distribution of stem densities in different size classes in diameter at breast height over years. Trees were divided into four size categories (10–19.9 cm, 20–39.9 cm, 40–59.9 cm, and ≥ 60 cm). 1969 L means year 1969 after logging. 1969LS means year 1969 after thinning. L: logging only; L: logging only; LT: logging with low-intensity thinning; MT: logging with medium-intensity thinning; HT: logging with high-intensity thinning.

the 46-year period of our study is not long enough to completely recover to pre-distance levels.

The trends of AGB recovery rates changes over time can be explained through the size class distribution of trees remaining after treatment, the growth rates, recruitment, and mortality of trees. The slow AGB recovery rates in the first phase (i.e. first four years) were due to the small number of recruits and the predominance of small trees, as many large trees were removed through thinning. The lag in tree recruitment was similar to that observed by Kariuki et al. (2006). This lag is likely in part due to only trees ≥10 cm DBH being sampled and the time required for any pre-existing trees smaller than 10 cm DBH to grow up into the ≥10 cm DBH tree community.

Over the second phase (1973–1997), AGB accumulation rates increased dramatically. First, fewer remnants in the thinning treatments stimulated high rates of recruitment, especially in the second measurement (1973–1981) and these recruited trees made a substantial contribution to the AGB increment. Second, growth rates of existing trees were stimulated by reduced competition because of the thinning treatments. Third, small trees grew into medium-size trees or medium-size trees grew into large trees and larger trees had higher AGB

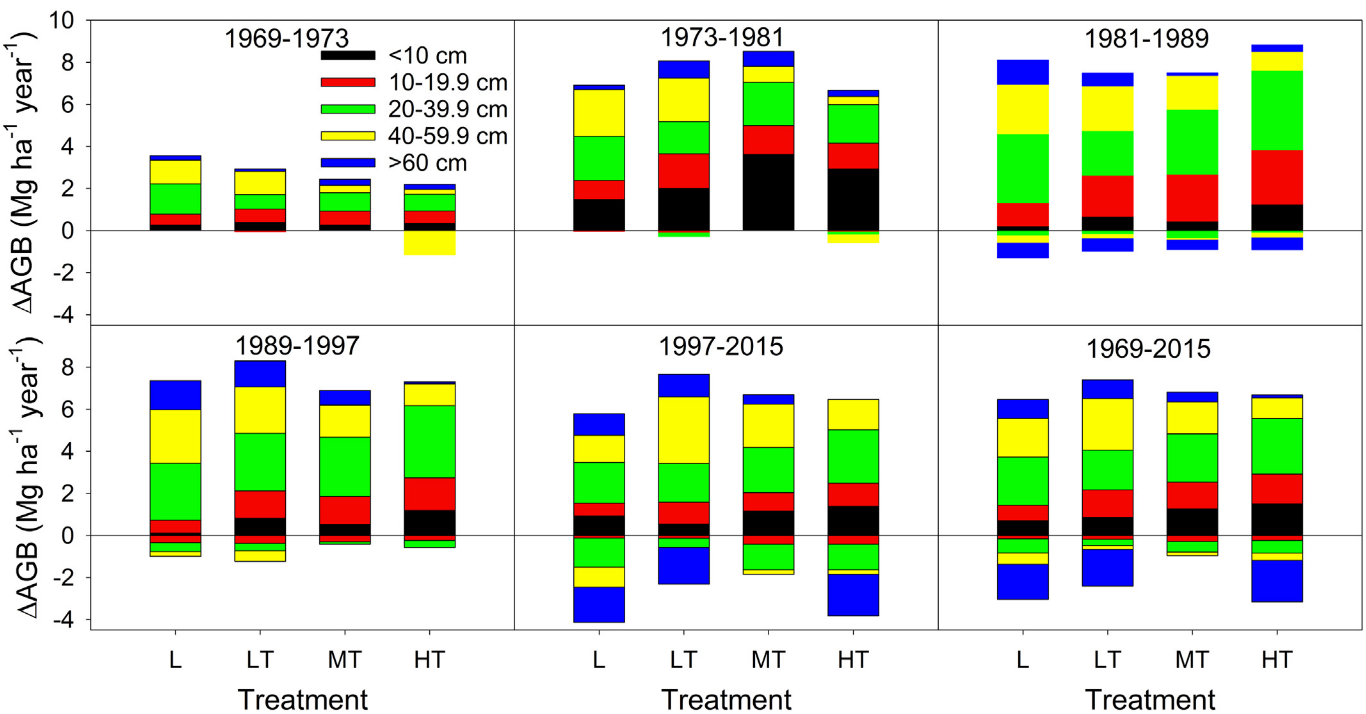

Fig. 4. Average annual above-ground changes rates (ΔAGB) of different size classes in each period. Positive values indicate biomass gain from recruitment and growth. Negative values indicate biomass loss from mortality. Biomass increase from recruits that grow into 10 cm DBH were indicated by black colour and the legend title of <10 cm. L: logging only; LT: logging with low-intensity thinning; MT: logging with medium-intensity thinning; HT: logging with high-intensity thinning.

accumulation rates (Fig. 2). Thus, the AGB recovery rates increased during 1973 to 1997 compared to 1969 to 1973. Many studies have found that thinning facilitated the recruitment and growth of trees considerably (Peña-Claros et al., 2008; Villegas et al., 2009; Gourlet-Fleury et al., 2013; de Avila et al., 2017).

In the third phase, the AGB recovery rates decreased due to increased mortality in all size classes, especially for the L site. In the last measurement period, the biomass recovery rate of L decreased dramatically to 2.12 Mg Ha^{-1} $year^{-1}$and was much lower than L, LT and MT (ranging from 4.4 to 5.84 Mg Ha^{-1} $year^{-1}$). The slower recovery in biomass at the logging only site in the last measurement period was largely due to the natural death of 22 trees in 20–39.9 cm DBH class and five trees >40 cm DBH (Table 3, Fig. 4). Fig. 4 also showed that the biomass gain contributed by the growth of trees in 20–39.9 cm in L decreased in the last measurement period and was less than the other three thinning treatments with a similar number of trees in 20–39.9 cm between four treatments (Fig. 3). At the high intensity thinning site, there were also two large trees >40 cm DBH died in the last measurement period, contributing to great biomass loss. It is very likely that the increased mortality in the final measurement period was due to the impacts of two large cyclones that impacted the site during this time. It was reported that Cyclone Larry, a Category 4 tropical crossed the north of Queensland in March 2006 and winds blew across Atherton Tablelands to the south side of the study site (Turton and Dale, 2007). Metcalfe et al. (2008) reported that the tropical Cyclone Larry brought community-level damage to the forests in the Wet Tropics region. Cyclone Yasi in February 2011 hit the Mission beach area at the south side of the study site as a category 5 cyclone (Negrón-Juárez et al., 2014). It also appears that the impacts of the cyclones had differential impacts, with the greatest impact being on the three more exposed south-facing sites (L, LT, and HT) and least impact on the north-facing site (MT) (Fig. 4). It is highly plausible that the destructive impacts of the two cyclones strongly contributed to reduced biomass accumulation rates.

The decreased biomass accumulation in four treatments in the third phase might also be partially attributed to the lower growth rates in the stand induced by increased competition. The decrease in biomass accumulation rates is in accord with other research showing that rates of biomass accumulation decrease through succession, in part due to increased mortality in larger size classes and the density induced decline in stand growth (Brown and Lugo, 1990; Silver et al., 2000; Feeley et al., 2007; Rozendaal and Chazdon, 2015; Rozendaal et al., 2017).

4.2. Potential of biomass recovery in logged and silviculturally treated forests

In our study site, logged and thinned tropical forests showed high levels of AGB recovery. AGB in low- and medium-intensity treatments showed almost complete recovery to their pre-logging levels within 46 years. However, HT requires more time (77 years totally as predicted) compared to LT and MT because of the greater removal of biomass through thinning (Fig. 1b). The AGB in L recover to 87.6% of its pre-logging level and as we predicted it needs another 9 years for full recovery (Fig. 1b). Compared to LT and MT, the longer biomass recovery time at the logging only site was largely due to the greater biomass loss from mortality and slower growth of trees in 20–39.9 cm DBH class in the last measurement period (Fig. 4). The pre-logging biomass in L was much higher than the other three treatments, which might reflect initial site differences, so more biomass was removed in L through logging to reach similar levels of post-logging biomass among the four treatments. This may partly also cause forests in treatment L take longer time to recover to pre-logging biomass level. The longer time required for full biomass recovery in the high intensity site a could be due to a combination of a higher initial reduction in biomass from thinning (Table 1), the initial slow biomass recovery during the first measurement period (1969–1973) due to a small number of remnants (Table 2 and Fig. 4) and the death of two large trees >40 cm DBH in the last measurement period (Table 3 and Fig. 4). Since the high mortality rates in the last measurement period are likely due to the impacts of two cyclones that impacted the study site, it appears that cyclones had a substantial negative impact on biomass recovery. This is important, at least for the tropical forests in region, as climate change modelling predicts that the intensity of cyclones crossing the north-eastern coast of Australia will increase. It also highlights that the natural process of biomass recovery can be substantially affected by climate change. From this perspective, increased intensity of cyclones predicted to occur as a result of climate change may also further slow biomass recovery. The impacts of climate changes including intense cyclones on forest biomass recovery could be further investigated in the future.

Although the AGB accumulation rates in the four treatments decreased from 1997 to 2015, the AGB in the silviculturally treated forests still showed an increasing trend after 46 years. The post-treatment biomass recovery trajectories over 46 years show that light to moderate thinning can increase above-ground biomass compared to the logged only forests over several decades. At this site, Hu et al. (2018) found that selective logging, low- and medium-intensity thinning did not alter the species composition of tropical forests greatly, and the species composition following high-intensity thinning recovered partially within 46 years.

The selectively logged and treated forests in our study still had high carbon sequestration and storage potential. With an average annual AGB recovery rate of 5.57 Mg ha^{-1} $year^{-1}$ over 46 years following logging and thinning, the carbon sequestration rates were higher than that of selectively logged Amazonian forests (1.33 Mg ha^{-1} $year^{-1}$) in which time of recovery was positively related to percentage of above-ground carbon lost through logging (Rutishauser et al., 2015). Based on analysis of biomass recovery data collected over much shorter time periods (ranging from 1 to 33 years after logging), Rutishauser et al. (2005), predicted that losses of 50% of initial above ground carbon stocks would require 75 years to recover in the forests in the Amazon region. In our study in which monitored recovery over 48 years, the biomass in the logging only treatment with initial biomass loss of 53% is predicted to recover fully in a further 9 years (i.e. 55 years in total). Although it must be noted that without the impact of cyclones on the site in the last measurement period, the recovery time in the logging only site would have been substantially reduced, evidenced by the full recovery of two of the three thinned sites after 47 years. The average annual AGB recovery rate in our study site is similar to that in secondary forests in Neotropics of 6.1 Mg ha^{-1} $year^{-1}$ over 20 years after clear-cut (Poorter et al., 2016). In that study biomass stocks took an average of 66 years to recover to 90% compared to 47 years for the LT and MT sites by measurement in our study and predicted age of 55 and 77 years, respectively for L and HT sites in our study.

According to Table 1, the above-ground carbon fluxes from logging, thinning, mortality, growth and recruitment were greatest in HT with carbon emission of around 100 t/ha, whereas only 33, 4 and 6 t/ha carbon was lost in L, LT and MT. However, much of the timber harvested from our study area was used to produce high-value products such as high-quality furniture, flooring and building construction, all of which have a residency time for carbon ranging from decades to centuries. Given that biomass has recovered to levels near to the original pre-logged forest, it is likely that there has been a net increase in carbon storage because of the carbon stored in the timber since the logging and the treatment of the forest until now. The net gains are likely to be lower in other forest types that yield a much higher proportion of 'disposable' products with a low carbon residency time (e.g. paper, low grade construction timber). From this perspective, our study also suggests that there is high potential of sustainably managed tropical secondary forests to act as substantial carbon sinks as well as reservoirs for forest biodiversity provided that there are sufficiently long logging rotation periods (Putz et al., 2012; Hu et al., 2018; Hu et al., 2020). Unfortunately, cutting cycles are often far too short (Dauber et al., 2005). Given that LT and MT require around 50 years for full biomass recovery, better practices and policies for forest management need to be developed for maintaining the balance between sufficiently long logging cycles for carbon recovery and balanced against the economic return from logging.

Authors' contributions

J. Hu and J. Herbohn conceived the ideas and designed methodology; J. Hu analysed the data and led the writing of the manuscript. All authors contributed critically to the data collection and manuscript preparation.

CRediT authorship contribution statement

Jing Hu: Conceptualization, Methodology, Formal analysis, Writing - original draft. **John Herbohn:** Conceptualization, Investigation, Resources, Writing - review & editing, Supervision. **Robin L. Chazdon:** Conceptualization, Investigation, Writing - review & editing, Supervision. **Jack Baynes:** Investigation, Writing - review & editing. **Jerry Vanclay:** Investigation, Writing - review & editing.

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Data availability statement

Data available from the UQ eSpace Repository https://doi.org/10.14264/uql.2017.640 (Hu et al., 2017).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.139098.

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