A Forever Young Ecosystem: Light Gap Creation and Turnover of Subtropical Mangrove Forests in Moreton Bay, Southeast Queensland, Australia

Aldrie Amir[1,2] & Norman Duke[1]
[1]Centre for Marine Studies, University of Queensland, St. Lucia 4072, Queensland, Australia
[2]Institute for Environment and Development, Universiti Kebangsaan Malaysia, 43600 Selangor, Malaysia
a.amir@uq.edu.au

ABSTRACT
Light gaps act as important renewal agents in mangrove forests. Light gaps progress through a number of stages starting from the death of a patch of trees through to its infill and rejuvenation of forest. These define a process of mangrove regeneration where forests naturally replace themselves over time. Light gaps in Moreton Bay mangroves were assessed to develop a greater understanding of the physical characteristics and microclimate change with adjacent canopies. Historical aerial photographs from 1978 to 2007 were analysed to reveal the dynamic processes of these mangrove forests and the role of light gap creation. The annual average number of new light gaps and the annual average number of gaps in recovery phases were calculated and used to estimate forest turnover. The average size of gaps in Moreton Bay is 84.2 m^2. Average forest turnover based on gap creation decreased from 1987 to 2007. An increase in gap creation rate may be indicative of an increase in storm activity - a possible tangible effect of global climate change.

Keywords
Mangrove, light gap, forest dynamics, natural disturbance, natural regeneration, lightning strike

1. INTRODUCTION

1.1 Definition of Light Gaps
Numerous small gaps are a noticeable feature of mangrove forests around the world [1]. These gaps appear as randomly created when viewed from the air, both in distribution and age. These gaps are often referred to as canopy gaps, light gaps or lightning gaps by various researchers [1-4].

Clarke and Kerrigan [4] defined canopy gaps as areas where some pinpoint concentrated natural disturbance had caused the death of a small number of mature trees (minimum width of about 5 m). Disturbance, whether natural or man-made, play a significant role in the distribution and abundance of tree species in forests [5]. Subsequent processes progress through various stages starting with the decomposition of dead trees with the recruitment and survival of seedlings, to the infill of the gap to rejuvenate the forest. These stages define an important series of steps for mangrove regeneration providing a means whereby they might naturally replace themselves over time [1].

1.2 Canopy Disturbance & Gap Phases
Canopy disturbance creating light gaps has been seen as a natural mechanism in the dynamics of forest ecosystems throughout the world [2,5,6-12]. This phenomenon is also observed in mangrove forests [1,3,13-15]. Disturbances initiate a cycle designating forests as spatial mosaics of structural phases driven by the creation of gaps, the openings in the canopy [2].

Once a gap is created, the forest's ecological and physical processes will be altered. Naturally, the gap will adapt to the change and grow to restore itself back to the original forest condition [5]. Gap creation, growth and closure have important implications for tree regeneration and recruitment. These gaps change the physical and biological attributes of the forest with sudden change of light penetration to the forest floor with the deterioration of dead trees and growth of new trees [12]. Causes of gap creation have been the subject of discussions including natural and man-made [1].

Whitmore [11] recognizes three phases in gap succession in mature tropical forests: (a) gap-phase is an opening of the forest canopy and/or understory; (b) building-phase consisting of young trees, mostly shade-intolerant, growing rapidly to fill the gap and attain the canopy; (c) mature-phase formed by an intact canopy of large trees.

This was further elaborated by Duke [1] for light gaps in mangrove forests. Light gap in mangrove forests is characterised into six phases, commencing with a forest showing no gap, cycles through two creation phases (initiation and opening) and three recovery phases (recruitment, filling and closure), before returning to the original condition (Figure 1). Duke [1] also hypothesized that the creation and regeneration of these gaps prevent mangrove forests from reaching senescence stage, hence maintaining the youthful conditions of the forests.

1.3 Lightning: Cause of Gap Creation
The cause of most gap creation in mangroves is largely unknown. The common small and distinctive circular light gaps in mangroves are possibly caused by a number of factors, most likely to be lightning strikes. By understanding the cause of gap creation, we may be able to better model forest growth and development so we might better use these highly productive ecosystems. This is especially relevant where gap creation might be linked to storm disturbance and climate change.

Lightning is seen as the most likely common cause of mangrove gaps from a number of likely causes including hail, wind, insects, pathogens and toxic chemicals [1]. According to Smith [3], storm disturbances are frequent in tropical mangrove forests of northern Australia and form gaps at scales from a few square metres to hectares. But, these are very patchy in distribution.

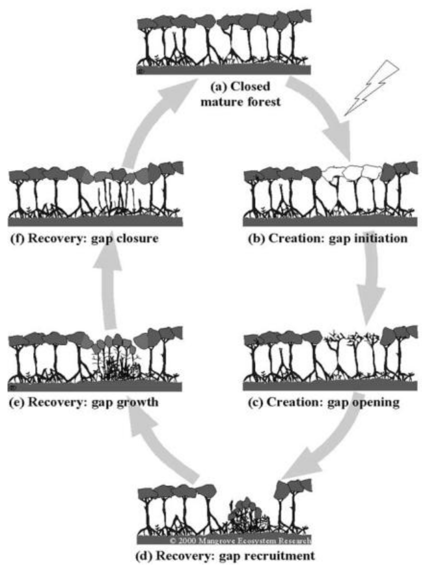


Figure 1. Six phases in a mangrove forest light gap creation and recovery cycle as described by Duke [1]

Lightning is reportedly a common disturbance agent in many terrestrial forests and plantations, for example in Malaysia [16], Papua New Guinea [17], including mangroves in Australia [3], Panama [3] and Florida [18]. Duke [1] proposed that lightning strikes within the mangrove canopy might create a relatively circular to elliptical clearing from the top to the bottom of the forest canopy and the trees remain standing dead for several years. This contrasts for the most part with gaps in terrestrial forests. Lightning strikes, often followed by treefalls, create large gaps in terrestrial forests, >500 m^2 [3], 20-705 m^2 [8], 63-88 m^2 [6].

According to Rakov & Uman [19], lightning can cause structural damage to terrestrial trees without burning them. Schmitz & Taylor [20] found that majority of trees recovered from lightning damage, though many were weakened and died after being attacked by insects or diseases. Rakov & Uman [19] also found that single lightning can sometimes kill a group of trees instantly with damage often seen on one or two trees, normally towards the centre. They also suggest that lightning may play a hidden role by reducing the natural resilience and resistance of trees leading to attack by the insects and pathogens.

1.4 Objective

The objective of this study was to determine the role of light gaps in natural regeneration of mangrove forest. It is hypothesised that with increase of storm activity (increased amount of lightning strikes) will cause a corresponding increase in the creation of light gaps which in turn will increase mangrove forest turnover rate.

2. MATERIALS & METHOD

2.1 Site Description and Species

Studies of light gap characteristics were carried out in four sites around Moreton Bay area in Southeast Queensland, namely Luggage Point, Boondall Wetlands, Fisherman Island and Whyte Island. Figure 2 shows the location of the research sites.

Moreton Bay mangroves are dominated by *Avicennia marina* with saltmarsh and saltpan fringing inland. There are some occasional presence of *Aegiceras corniculatum*, *Rhizophora stylosa*, *Ceriops australis*, *Bruguiera gymnorhiza* and *Excoecaria agallocha*.

Moreton Bay region is classified as subtropical, experiencing moderate temperatures all year round. The mean annual maximum temperature of the area is 24°C, the highest maximum 36°C and a lowest minimum of 0°C [21]. Water temperatures around Moreton Bay ranged from 19˚C during the cooler months (August-September) to 26˚C during the warmer months (November-April) [22].

Rainfall in this region is intermittent, with short intense rainfall interspersed with long periods of dry conditions, where the highest rainfall events are associated with monsoonal depressions during summer (December-February), annual average of 1200 mm [23].

2.2 Field Investigation

Field studies were carried out in selected light gaps of various phases in mangrove forests around Moreton Bay, Brisbane. Coordinates of these gaps were pre-recorded using Google Earth. Field surveys were carried out for verification, field sampling and measurement. In the centre of each light gap, the coordinates were recorded. North, south, east and west corners of the gaps were marked.

Two transects were laid across each gap, with one being north-south transect and the other east-west. Transects start and end outside the gap from and into the adjacent forest and data were sampled from nine plots in each gaps (Figure 3). The distance from each edge into the canopy were of equal distance with gap length. The rationale behind this is to see the maximum effect of light (penetration) towards gap's and canopy's microenvironment.

The effect of gap size and shape towards the amount of light received by the gap and its surrounding is observed by measuring the amount of light received, which then used to illustrate the light regime across light gaps and the adjacent canopy. Light meter and hemispherical view camera were used to measure the level of light penetration. Hemispherical view images from each plot were taken using a fish-eye lens on Nikon Coolpix 4500 at half a metre height from the ground.

A series of historical aerial photographs of mangrove forests around Moreton Bay were obtained from the Queensland's Department of Natural Resources and Water and then analysed. Recent light gaps in selected sites on each photograph were marked and compared retrospectively to determine the trend of gap frequency.

2.3 Analysis of Data

The size of each gap was calculated using the circle area formula (for circular gaps), ∏r^2, or ellipse area formula (for ellipse shape gaps), ∏ * (north-south length ÷ 2) * (east-west length ÷ 2). The shape of each gap was measured by the ratio between length and width of the gap (gap size eccentricity). These measurements were done on georeferenced images and data verification was done on selected gaps at site. Images captured using the fish-eye lens camera were then analysed using Hemiview software to calculate the amount of light received in each plot.

2.4 Forest Turnover: Formula and Calculation

Lewis et al. [24] measured stem turnover as the mean of mortality and recruitment rates for a forest stand. They used the instantaneous rate measure, λ, calculated as:

$$\lambda = \frac{\ln(n_0) - \ln(n_t)}{t}$$

Where n_0 and n_t are the number of stems in the original population, and the number of stems surviving to time t respectively. The time between the two stem censuses is t.

Stephenson & van Mantgem [25] argued rather than analysing mortality and recruitment rates separately (which in theory would yield identical results), they simplified their presentations by analysing turnover rate as the average of mortality and recruitment rates.

In this study, turnover rate is calculated as the average of new light gaps created with gaps in recovery stages in an area in a monitored time frame.

$$\lambda_g = \frac{g_n - g_0}{t}$$

where;

λ_g = forest turnover rate based on series of light gap creation

g_n = frequency of light gaps * average size of light gaps in the *n* sequence of aerial photograph

g_0 = frequency of light gaps * average size of light gaps in the *0* sequence of aerial photograph

t = time difference between *n* and *0* aerial photographs

The turnover of the forest will then be measured by dividing the specified forest area with the turnover rate by the average size of gap.

$$T_f = \frac{A_f}{\lambda_g}$$

where;

T_f = forest turnover based on gap dynamics

A_f = forest area

λ_g = forest turnover rate based on series of light gap creation

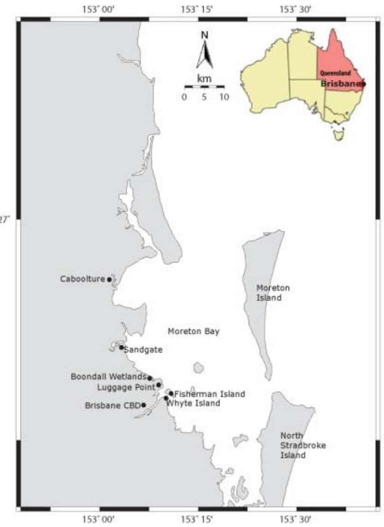


Figure 2. Location of research sites in Luggage Point, Boondall Wetlands, Fisherman Island and Whyte Island in Moreton Bay, Southeast Queensland.

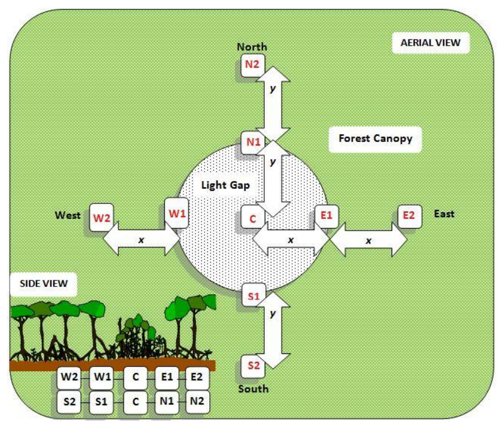


Figure 3. Sampling plots in each light gap.
Shaded area represents the gap, outside shaded area is the closed canopy. Plot C is in the centre of the gap. N1 is on the northern gap edge, E1 eastern gap edge, S1 southern gap edge and W1 western gap edge. N2 is in the northern canopy, E2 eastern canopy, S2 southern canopy and W2 western canopy.

3. RESULTS

Gap characteristics are described based on observations carried out in 42 light gaps of various recovery phases in Moreton Bay mangroves (Table 1). Number of dead trees in each light gap ranges from 3 to 27 trees.

482 light gaps of different age, size, shape and growth phase were spotted and measured using Google Earth. ArcGIS was used to analyse historical aerial photographs to estimate gap's age. Figure 4 shows frequency distribution of light gaps by size class. Length/width of gaps ranges from 3.36 m to 36.33 m. Gap size ranges from 20.11 m^2 to 652.16 m^2. The average size of the total 482 light gaps is 84.2 m^2.

57% of all gaps are circular in shape with the eccentricity of length and width is between 0.75-1.25. Figure 5 shows the distribution of the eccentricity of gap area. Value 1.0 indicates circular gap formation (marked by solid line) and gaps with area eccentricity bigger than 1.25 and smaller than 0.75 are elliptic (limits marked by the dotted lines). 275 (57%) of the gaps are in the circular shape range. Gaps with eccentricity bigger than 1.25 are North-South elliptic, while smaller than 0.75 are West-East elliptic.

Light level is significantly higher in the centre of gaps compared to the edge and under the canopy. Figures 6 (a and b) show average light level in centre of gaps, gap edge and under the canopy across north-south and east west transects (light gap light regime).

The frequency of the creation of new light gaps increased through time, and the trends are almost similar in all four plots near Moreton Bay (Table 2). The average forest turnover became faster from 1987 (1561.56±354.82 years [excludes Luggage Point]) to 1414.52±434.05 years (1997) and to 1401.64±424.05 years in 2007.

Table 1. Gap phases, characteristics and estimated age observed in mangroves around Moreton Bay, Southeast Queensland

Gap Phase	Gap Characteristics	Estimated Age
Closed Canopy	No gap presence.	-
Initiation	Leaves yellow-brown-fall, trees dying-dead.	<1-2 years
Opening	Bare branches and twigs, dead trees standing. Almost similar seedling height in and outside gap.	2-5 years
Recruitment	Dead stumps still apparent. Fallen branches on gap floor. Seedlings height are different between in and outside the gap	5-10 years
Growth	Seedlings height are different in the gap, taller in the most-lit area. Seedlings transform into saplings.	10-30 years
Closure	Trees in gap approaching site maximal canopy height.	>30 years

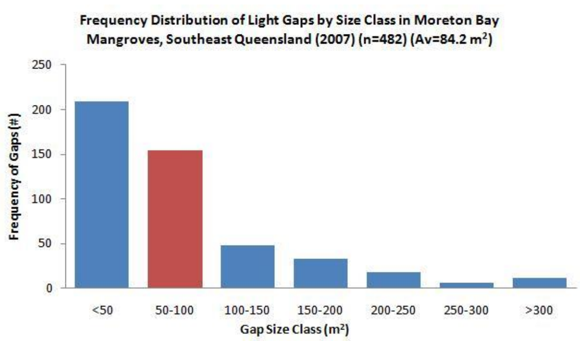


Figure 4. Size-class distribution of 482 light gaps in Moreton Bay mangroves, southeast Queensland

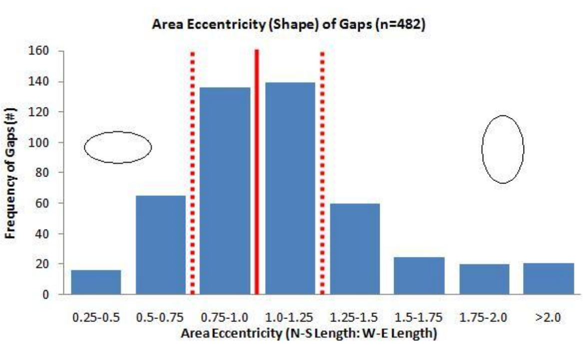
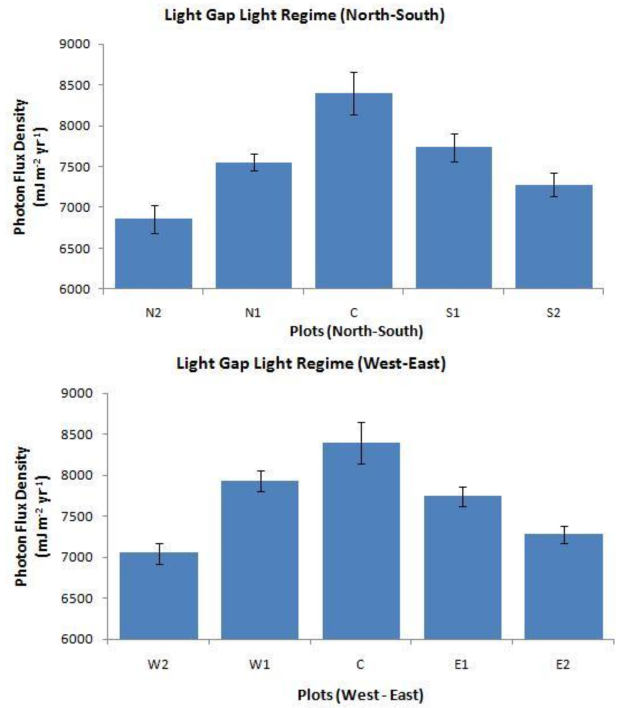


Figure 5. Frequency distribution of the eccentricity of gap area



Figures 6a & 6b. Average light level in plots in the centre of light gaps, gap edges and under the canopy across a) North-South transect and b) West – East transect

Table 2. Turnover rates and forest turnover estimations based on analyses of historical aerial photographs (1978-2007) in four different sites near Moreton Bay, Southeast Queensland

Sites	Year	Gap Frequency	Area in Gap Phase (%)	Turnover Rate (m^2/year)	Forest Turnover (years)
Luggage Point Plot Size = 40000 m^2 Mean Gap Size = 127.46 m^2	1978	2	0.64		
	1991	5	1.59	29.41	1359.92
	1997	6	1.91	26.83	1490.68
	2007	8	2.55	26.37	1516.84
Boondall Wetland Plot Size = 54400 m^2 Mean Gap Size = 91.53 m^2	1978	3	0.50		
	1987	7	1.18	40.68	1337.27
	1997	9	1.51	28.90	1882.08
	2007	12	2.02	28.41	1915.10
Whyte Island Plot Size = 62500 m^2 Mean Gap Size = 285.44 m^2	1978	2	0.91		
	1987	3	1.37	31.72	1970.63
	1997	7	3.20	75.12	832.04
	2007	9	4.11	68.90	907.11
Fisherman Island Plot Size = 32400 m^2 Mean Gap Size = 105.9 m^2	1978	2	0.65		
	1987	4	1.31	23.53	1376.77
	1997	6	1.96	22.29	1453.26
	2007	9	2.94	25.56	1267.50

4. DISCUSSION

Observations in Moreton Bay mangroves show that creation of light gaps is a natural phenomenon and happened randomly. This is supported by the fact that no cutting activity is taking place in this mangrove forest.

Based on the measurements on aerial imageries and verification in the field, the average size of canopy openings are almost similar as reported in previous reports for mangrove forests as well as other terrestrial ecosystems. Yamamoto [26] reviewed published figures and found out that total and average gap size are not significantly different between temperate and tropical forests. According to Yamamoto [26] also, gaps larger than 400 m^2 in area are rarely found. Smith [3] did identify light gaps of size larger than 500 m^2 in mangrove forests in North Queensland, however the number was extremely small.

The shape of the majority of light gaps in Moreton Bay mangroves are circular as the eccentricity of most of the gap area are close to 1.0. This could possibly be one of the strong indicator that these gaps were created by lightning strikes. Lightning strike as the cause of creation is yet to be proven, but for Moreton Bay mangroves, there was no physical evidence of treefall or insects attack in all light gaps that were surveyed.

The cyclical process of gap growth through various phases were clearly verified. As described in Table 1 and by Duke [1], these phases will be undergone by each light gap in mangrove forest around the world as part of the natural process of regeneration, provided no extensive interruption by any other kind of disturbance.

As predicted, significant difference between light received under the adjacent canopy and the centre of gap were observed. The extra exposure of light will influence the success of surviving seedlings as well as newly established seedlings to grow and renew the dead patch after canopy opening.

Increased of gap creation is believed to be a result of increased storm activity. This could be benificial to mangrove forests, as they accelerate natural regeneration and rejuvenate these forests. However, the important question is, to what extent can mangrove forests cope with the increasing pressure from this natural disturbance. If disturbance increases, is there a possibility of ecosystem collapse?

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