



Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems

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Abstract

Turnover within both mangrove and terrestrial forests is driven by stand development in conjunction with factors influencing tree death and replacement at various temporal and spatial scales. Development in terrestrial forests appears comparable with that in mangroves but turnover seems to differ considerably between these broad forest types. The most important difference is in the character of small forest gaps. Gaps are common in terrestrial forests but those in mangroves rarely involve falls of large older trees in the first instance. Instead, mangrove trees usually die standing in small clusters of mixed age cohorts. Identifying a common cause for gap creation in mangroves might be important towards understanding what drives forest turnover but there is a greater need to quantify this process. Small-scale disturbance in mangrove forests is poorly quantified but preliminary evidence implies that its importance may have been greatly under-estimated. Based on available observations, a conceptual model of mangrove forest development and gap regeneration is proposed. The model helps explain the peculiar characteristics and structure of mangrove forests and how these forests might respond to changing environmental conditions and disturbance at various landscape scales.

Introduction

Mangroves, like most forests, are dynamic, ever-growing, and constantly re-establishing and re-newing themselves. They differ from terrestrial forests chiefly because there are special conditions and requirements for survival in tidal locations. For instance, mangrove plants have a notable tolerance to saltwater tidal conditions, and they are highly dispersive plants with buoyant propagules often utilising vivipary (Tomlinson, 1986). By using such features and many others, mangrove plants have been able to occupy, dominate and stabilise exposed tidal foreshore environments. In such places, influenced much by severe hydrological and physico-chemical conditions, and faced with constant issues of change like sea level rise, it has been essential for mangrove plants to have regenerative processes which are adaptable, progressive, dynamic, and mostly successful. Situated at the sea edge, forested stands are subject to land and river runoff, as well as, the direct action of the sea itself. The mere presence

of species in this habitat implies that they must have successful regenerative strategies.

Mangrove habitats are therefore seen as dynamic but they are also seen as relatively stable ecosystems dominated by only a few species (Tomlinson, 1986; Smith, 1992; Ricklefs and Latham, 1993; Duke et al., 1998). A range of attributes and influencing factors including species associations, stand development and forest turnover have been considered (see the review by Smith, 1992), especially in view of their potential role in ecosystem function (Robertson et al., 1992) and the importance of mangrove forests to people (Field, 1995). Despite this attention, however, no strategy or model adequately explains the natural processes involved in forest turnover and how this is achieved and sustained in mangroves. It is the objective of this treatment to provide a conceptual model based on the distinctive features of mangrove forests, and to question some apparently entrenched misconceptions concerning forest dynamics and turnover in tidal

environments. This view is presented with the further intention of identifying and encouraging further quantification of forest turnover especially with respect to the numerous small gaps found commonly in mangrove sites around the world.

Factors influencing dynamics and turnover of mangrove stands

Dynamic processes in forests are ruled by two guiding factors. First, all forests are made up of individual trees with each contributing to the overall condition and character of the entire forest stand. Secondly, although each tree is a separate organism with a predictable life span, a forest may have an independent and possibly indefinite life span, depending on the success of its regenerative processes and replacement of individuals in the forest. When trees die they must be replaced if the forest habitat is to be maintained through time. It is this replacement process and the species with the most successful strategies to carry on this process which determine the character and composition of forests through time. As expected, this dynamic will differ in response to both internal factors and external influences acting at particular locations. Two factors are highlighted in this treatment including effects from different mangrove species and the greater physical exposure of sites to wind and water action.

Species effects

Growth strategies used by particular mangrove plant species must influence their success in particular locations and determine the kind of forest which will occupy these places. The effect of competing influential factors and the difficulties for plant species in accommodating to the tidal zone, especially in exposed locations, forces strong selection pressure on occupant genotypes. This is the reason why it is generally acknowledged that only around 70 taxa regularly occupy this zone worldwide (Duke et al., 1998) and why only a much smaller subset achieve dominance in the habitat.

One of the most conspicuous of the dominant mangrove genera is *Rhizophora*, a plant group with highly specialised morphological attributes ranging from stable above-ground root structures of looping sturdy prop roots to viviparous buoyant propagules. In most tropical locations, these plants are synonymous with the mangrove habitat. *Rhizophora* forests

have the same appearance worldwide, with dense canopies of glossy, tough green leaves covering numerous gnarled to erect stems emerging from an interconnected tangle of above-ground roots bedded in soft wet mud along the waters' edge of most tidal habitats and locations. The type of mangrove taxa at the edge zone also largely determines the success and stability of entire stands extending back to the high water mark as well as those extending upstream to the tidal limit. In exposed locations where protective front trees have been lost, there is often erosion and progressive collapse of inner mangrove zones.

Successful regeneration of *Rhizophora* forests occurs chiefly via a reproductive strategy involving propagule production, seedling establishment, and growth and competition with neighbouring seedlings (Duke et al., 1999). Vegetative regrowth appears less important in *Rhizophora* forests.

By contrast, regeneration in *Avicennia* forests occurs via a combination of reproduction and vegetative growth, and *Avicennia* may be favored over *Rhizophora* in areas of relatively frequent severe wind and hail damage. *Avicennia* represents a second dominant genus occupying the tidal zone worldwide. Their dominance is especially high in areas which are climatically more harsh than those where *Rhizophora* usually dominates, either in areas of extreme aridity (noting their dominance in the higher intertidal, and generally in seasonally dry locations; e.g., dry areas of Pacific Panama, north-western Australia and the Arabian Gulf) or in cooler temperate sites (noting higher latitude sites like New Zealand and southern Australia). But this genus appears to have an additional advantage over *Rhizophora* species where *Avicennia* is more tolerant of storm damage.

The ability of *Avicennia* species to coppice and rapidly sprout from damaged stems seems to provide an important advantage for this genus growing in areas affected by frequent storms. In mixed stands, there is a factor acting in a converse way where *Avicennia* propagules are preferentially more heavily damaged by Grapsid crabs and boring insects than *Rhizophora* propagules (Smith, 1988). The net long term effect, depending on such influencing factors, may result in different proportions of *Rhizophora* and *Avicennia* species in different localities.

In Moreton Bay, south eastern Queensland in Australia, mangrove stands are dominated by *Avicennia* trees and while *Rhizophora* is present, it is only a minor component with occasional smaller trees under closed *Avicennia* canopies (personal observations).

This is not considered to be entirely due to a latitudinal affect (around 27°S) since *Rhizophora* trees dominate canopies nearby both to the north and south. Based on preliminary evidence of the severity of tree damage caused by hail storms in central Queensland (e.g., Houston, 1999) and in the bay area itself (personal observations), it is suggested that severe storms have influenced mangrove forest structure and species composition. If so, what frequency of hail storms might have tipped the balance in this effect? And, to what extent are the apparent advantages provided to *Rhizophora* species by Grapsid crabs, noted above, outweighed by the frequency and severity of local hail storms, and the more rapid recovery of storm-damaged *Avicennia* trees and forests? Furthermore, does the loss of Grapsid crabs and other infauna due to sediment pollution also contribute to the dominance of *Avicennia* in this bay, referring to a greater dominance of *Avicennia* adjacent to populated areas in the bay?

Exposure effects

Stand integrity largely depends on the character of trees along forest edges and site exposure. Edge trees of *Rhizophora* and *Avicennia* are characterised by gnarled and lateral structures with greater numbers of stems and lateral branches, as well as higher and more numerous root structures. Foliage also curves down on edge trees to form a protective mantel serving to deflect strong winds. Such trees provide valuable protection along exposed shorelines, a feature demonstrated in hydrological studies showing the influence of mangrove root structure on water flow and wave action (e.g., Mazda et al., 1997). But, how are these relatively exposed trees normally replaced?

In Bahia Las Minas, Panama, in Central America, large areas of *Rhizophora mangle* were lost in the long-term despite strong early recruitment of sites deforested by large oil spills in 1968 and 1986 (Duke et al., 1997a, 1999). The agent of damage in this example is perhaps unusual, but this instance identifies a question which is widely applicable and crucial toward understanding an essential limitation to mangrove forest turnover. In this instance, recruits re-established in deforested sites in the 5–6 years immediately following the spill incidents, demonstrating that oil in sediments did not appreciably inhibit early growth in this instance. After six years, however, seedlings growing in exposed locations suddenly died. This loss apparently had little to do with the original spill, and it was attributed to scouring of foreshore areas by drift logs

after the protective root structure of dead remnant trees had deteriorated. This occurrence was the same as that observed in a site near Cape Flattery, north eastern Queensland in Australia. In this case, a large area of foreshore mangroves dominated by *Rhizophora stylosa* was lost also in an oil spill incident (Duke and Burns, 1999). Once again, established recruits up to five or six years old were suddenly lost to driftwood scouring as trees killed by oil deteriorated and no longer provided protection for seedlings. In both instances, it had to be concluded that young seedlings were unable to achieve sufficient size and structure to protect themselves in exposed foreshore areas once occupied by mature trees of the same species. Recruitment was unsuccessful despite six years of plentiful re-establishment and early growth in the shelter of the dead trees. So, the crucial question is, how do mangrove forests replace themselves and continue to stabilise exposed shorelines in normal circumstances? Apparently, foreshore stands cannot afford to suffer collapse as seen following such deforestation incidents. It must be concluded that large-scale disturbance and ecosystem collapse and renewal is generally uncommon.

Forest development and replenishment

As mangrove forests clearly survive and flourish in exposed coastal environments around the world, they must have strategies allowing them to accommodate the full range of influencing factors. From the examples presented above, it seems in part at least that there must be a smooth and progressive strategy of forest turnover whilst at the same time differing degrees of disturbance will influence forest composition and structure. Based on the currently accepted model of mangrove forest development, however, it is difficult to understand how turnover might occur. The current model is based on an implied model of linear growth where the age of trees within stands is indicative of stand age. In order to understand replenishment and turnover in mangroves better it is appropriate to re-examine this model.

The development model

Stand development in mangroves has been described in a four stage model to explain observed differences in structural characteristics with expected differences in age (e.g., Jimenez et al., 1985; Fromard et al.,

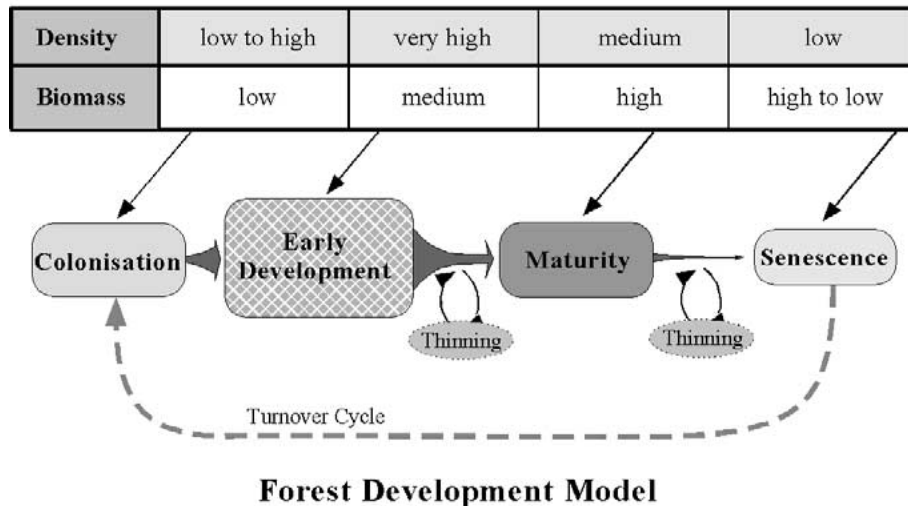


Figure 1. A preliminary model of stand development in mangroves. The schematic shows four stages described in terms of density and biomass of trees: colonisation, early development, maturity, and senescence. The cycle is driven by thinning post 'early development', and forest collapse with 'senescence' when the cycle resumes with re-'colonisation'.

1998). In this model, forests established during a colonization phase, progress through subsequent phases of early development, maturity, to end in senescence before recommencing with colonisation. The duration for a full cycle of this model was estimated to be around 80–100 years.

The development model is represented in the schematic diagram (Figure 1) where stem density levels are represented by different block sizes showing, from left to right (arrows), the phases as they occur from smaller to larger (= younger to older) trees. The four chief stages are redefined for this treatment in the context of field observations made in *Rhizophora* stands of Panama (Duke et al., 1993, 1999; Duke, 1996):

- a) **Colonisation** is the establishment phase when propagules take root on unoccupied or damaged tidal areas. Recruitment and subsequent growth is rapid. At this stage, thinning is minimal (if any), and seedling height growth is expected to be vigorous and largely unrestrained. Density is expected to increase through this phase. This stage lasts until canopy closure is largely achieved.
- b) **Early development** is the phase following canopy closure when seedling height growth continues to be rapid. Thinning is very active at this stage with a rapid decline in density, and the seedling bank is formed under the closed canopy. During this phase, gaps might be created by: driftwood scouring, flotsam smothering, and sed-

iment erosion or deposition. Towards the end of the phase, height growth is expected to slow as the canopy approaches 'site maximal canopy height'.

- c) **Maturity** is the phase commencing when the 'site maximal canopy height' is achieved. Plant growth is then largely based on increasing biomass of individual trees with a further, but slower, reduction in density by thinning. During this phase, gaps may be created by sediment erosion or deposition, lightning strikes, wind and hail storms, cyclones and hurricanes.
- d) **Senescence** is the phase when large individual trees begin to die standing, or they fall over and die when root support gives way, or trees are weighed down with epiphytes, or they die from deterioration and rot. Forest density is expected to be low, and there may also be considerable quantities of dead branches and stems on the forest floor in advanced stages. Thinning at this phase is expected to be quite minimal. Gaps might be created by the death of old trees, and sediment erosion or deposition. Storms are considered less important in this instance chiefly because the presence of old, larger, more fragile, individuals suggests that the frequency of such incidents would be very low (also see Ewel et al., 1998).

The transition between phases was considered to be universally progressive and generally un-interrupted; i.e., where tree age was taken to be indicative of stand age. For example, Fromard et al. (1998) used lay-

ering of sediments to estimate development duration of around 80 years for a senescent stand. This, and similar, deductions were apparently based on the assumption that forest development proceeded without interruption as expected in managed plantation stands. In the latter case, mangrove forest structure has often been linked with stand age (e.g., Walker, 1952; Noakes, 1955; Putz and Chan, 1986; Chong, 1988), and it seemed reasonable to assume that natural forests might behave similarly. Another assumption in applying this model was that individual trees observed in senescent stands were successful survivors of the original colonizing cohort. As such, the model might be assumed to represent the life span of successful individual plants from their establishment to old age.

From the early development phase, the model is largely driven by tree growth and thinning. Successful plants must have rapid height growth, and for this, they might rely heavily on shade intolerance as this would rapidly remove slower growing competitors. The early death of these neighbours not only reduces competition but it also creates additional space and releases vital nutrients. In view of these factors and the importance of establishment success for mangroves, it is proposed that shade intolerance has an evolutionary advantage for congeners in these environments (also see Snedaker and Lahmann, 1988). This idea might explain the common occurrence of shade intolerance in many species occupying mangrove habitats worldwide.

Loss due to shade intolerance was noted as rapid loss of intermediate cohorts between the seedling bank and the upper canopy, particularly for closed *Rhizophora* forests in Panama (Duke, 1996). In this case, the relationship between forest biomass accumulation and density, as used by Fromard et al. (1998), provided a useful basis for identifying early developmental stages of mangrove forest growth, but there are important limitations to this model.

Re-assessment of the development model

The importance of the development model used alone must be questioned since it is based on several unsubstantiated assumptions. For one, tree age does not necessarily approximate stand age. Second, trees at any phase of growth, particularly in senescent stands, may not have been present during the initial colonisation phase. And thirdly, tree death does not appear to be dependant on tree age. For such reasons, it is not possible to classify forests by age of cohorts, and

forest age cannot be based on the developmental stage of the forest. Where tree/cohort age is taken to be stand age, and forests progress through the developmental stages, then at some point the trees might die of old age in senescence.

The cycling of the growth model also implies that turnover of mangrove stands takes place through a sequence of colonisation and growth, followed by senescence and apparent ecosystem collapse before it is re-colonised. There are some reported instances of stands in senescent decline (e.g., Fromard et al., 1998; Ewel et al., 1998), but in general, evidence of a 'colonisation-collapse' cycle in progress are rare. This is especially notable for mangrove stands which currently occupy particularly exposed locations, and where they appear to have done so for thousands of years (e.g. see; Duke, 1997). This being the case, it is difficult to understand how this turnover strategy alone might promote stand longevity, especially where stands deforested by oil spills (Duke et al., 1997a) or cleared for access and views (Duke et al., 1997b) never recover and are lost forever when left to natural processes, even when they are planted with new recruits (Duke, 1996).

As noted, there are few reports of senescent stands of mangroves. This might be argued on the basis of expected low frequency of occurrence and reporting. However, a more compelling argument against the development model presented is the frequent and common occurrence of small light gaps in most mangrove forests (see Smith, 1992). The presence of these gaps implied their substantial influence on the development model, and this effect might vary widely depending of the incidence and frequency of gap creating incidents. Therefore, a more effective model must incorporate gap regeneration. The lack of such a model clearly implies that the influence of gaps on forest turnover has largely been under-estimated in studies of mangrove forests. This view is supported by a corresponding lack of data on gap frequency, and there has been virtually no quantification of the extent, or proportion, of forest area in gap regeneration. In the remaining sections of this treatment, I review observations of gap occurrence and processes, and present a revised model which incorporates gap regeneration with stand development.

Light gaps in mangrove forests

Forest gaps are common amongst terrestrial forests, and the processes of gap restoration form an integral part in the turnover of standing biomass (e.g., Maberley, 1983; Hubbell and Foster, 1986; Denslow, 1987; Brokaw and Scheiner, 1989; Whitmore, 1989). In many ways, these same processes occur in mangrove forests (e.g., Duke, 1992; Ricklefs and Latham, 1993; Duke et al., 1999). However, despite ancestral links with terrestrial trees, the success of mangroves in tidal wetlands has required the evolution of different strategies to accomplish comparable ecological outcomes. For instance, mangroves make use of regular tidal flooding with their production of buoyant propagules which are distributed widely by coastal and oceanic currents, as well as more locally in surrounding tidal forests. Since most mangroves have buoyant propagules (Duke et al., 1998), this strategy is considered fundamental to the evolution of mangrove species, and in their survival and dominance of tidal habitats worldwide.

Special characteristics of mangrove gaps

The causes of tree death and forest damage in mangroves range from episodic events such as violent wind storms (Craighead, 1964; Putz et al., 1984; Smith et al., 1994), frost damage (Lugo and Patterson-Zucca, 1977), hail damage (Houston, 1999; personal observations); plant pathogens (Pegg et al., 1980; Wesre et al., 1991), wood-boring insects (Feller and McKee, 1999), lightning strikes (Paijmans and Rollet, 1977), single tree falls (Ewel et al., 1998), to slow and progressive changes such as changes in sea level (Ellison and Stoddart, 1991), water courses (Breen and Hill, 1969; Ward et al., 1986; Gordon, 1988), deposition and erosion (Fromard et al., 1998), and seasonal flooding or drought. The scale of damage caused by these disturbances varies considerably from the vast areas destroyed by Hurricane Andrew in Florida (Smith et al., 1994) to single tree incidents. However, the most common gaps in mangroves are small gaps comprising around 10–20 trees and reputedly caused by lightning (also see, Craighead, 1971). Although the cause has not been demonstrated, it seems likely that a surge of electricity striking a central tree might affect those in the immediate vicinity, especially as root grafting is common and the trees grow in saturated sediments.

The small gaps in mangroves however, differ from those in terrestrial tropical forests where individual living trees fall and leave elliptical gaps. By contrast, mangrove trees rarely fall green, and light gaps in mangrove forests are not often created by the death of large ancient trees. It is more common to see gaps comprised of small circular clusters of up to 20 dead trees of various age classes (e.g., Golley et al., 1962; 1975; Doyen, 1986). A number of these 'pot-hole' impressions form a broad mosaic of small regeneration patches reflecting various ages and stages of canopy recovery. Below the canopy, different stages of gap recovery are apparent for several reasons. When a gap is young, considerable extra light enters the gap, often illuminating patches of vigorous young plants in an otherwise sparse undercanopy. In older closed gaps, groupings of younger trees are notable in the forest because of their slender stems and greater density.

In general, gap recovery depends on a combination of two chief processes, namely the establishment and growth of new recruits (reproductive processes), and the sprouting and lateral spreading of surrounding trees (vegetative processes). The balance between these regenerative processes is expected to effect forest structure and composition since different species are known to respond differently to damage. For instance, forest gaps may take several decades to recover through reproduction favoured by some species, like *Rhizophora*, while others, like *Avicennia*, respond more rapidly with vegetative regeneration. But, in many instances, the two competing processes probably complement each other by acting simultaneously to fill gaps. At this time, any changes in influencing factors affecting species recruitment and survival would be expected to alter forest species composition and structure.

Light gap regeneration phases

Light gap recovery in mangrove forests is characterised by six phases shown in Figure 2. In the proposed schematic, processes active at the time and some physical attributes are used to characterise each phase. These phases are based on *Rhizophora* dominated forests but most attributes are shared with other common mangrove genera, including *Bruguiera*, *Laguncularia* and *Avicennia*. This occurs despite remarkable differences in life history and growth architecture between the different plant types in the common mangrove habitats. The six phases commence with a forest showing no gap, and cycles through two creation

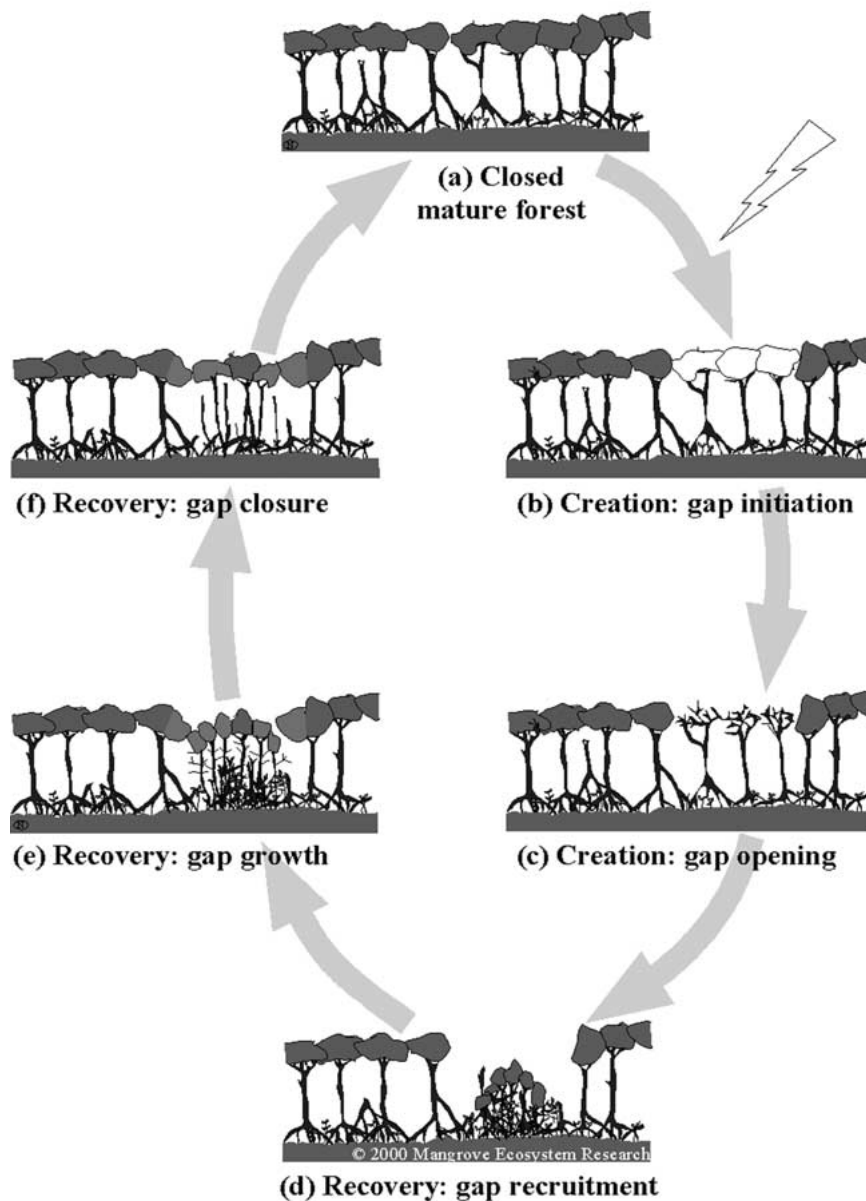


Figure 2. A schematic showing six stages of gap creation and recovery observed in common mangrove gaps: mature forest, gap initiation, gap opening, gap recruitment, gap growth and gap closure. The scheme is based on a *Rhizophora* forest, around 7–8 m tall. Gap creation is most likely to be caused by lightning strikes (see text). Also note the even stand height ('site maximal canopy height'), stem density, undercanopy seedlings ('seedling bank'), canopy sprouting of edge trees (vegetative regeneration), and wood breakdown.

phases, and three recovery phases, before returning to the 'unaltered' state. Each of the phases are described in the following scenario:

- a) *Closed mature forest.* A mature forest with no obvious indications of gap presence. The canopy is closed and it has roughly even height at, or near, the 'site maximal canopy height'. The stems are tall and near equally slender and erect. There are

few, if any, under canopy saplings and young trees. However, there is a 'seedling bank' of 2–3 year old seedlings often hidden amongst the above ground root structure.

- b) *Gap initiation.* A gap is first evident when leaves yellow on a small cluster of standing trees. Trees losing their leaves in this way usually die (NOTE: this occurrence should not be confused with the

annual leafing of deciduous mangrove species like *Xylocarpus mekongensis* and *Excoecaria agallocha*). While lightning seems a likely common cause of small gaps, other possible causes of gaps include: hail, wind, insects, pathogens and pollutants. However, each of these are less likely to result in small circular patches, around 50m² each, which tend to be characteristic.

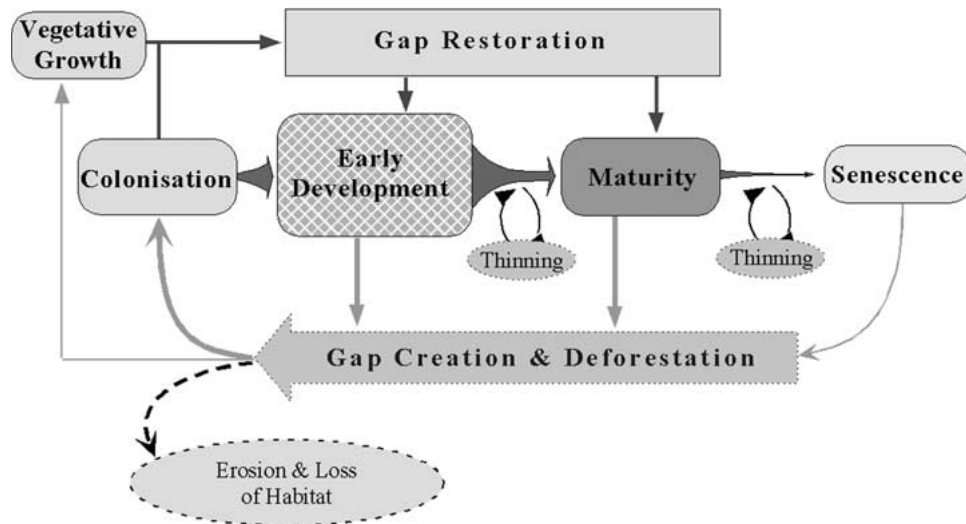
- c) *Gap opening*. Gaps at this stage are recognised by bare branches and twigs of standing dead trees. No leaves remain on these trees. Seedlings in the seedling bank are exposed to full sunlight, at least for part of the day, mostly around midday. This is the situation after approximately one year.
- d) *Gap recruitment*. This phase is the most notable and recognisable gap phase largely due to its maximal opening during this stage. At this interim phase, the gap is characterised by advanced degradation of dead trees and early recruitment of young seedlings. Dead trees are reduced to standing stumps surrounded by remnants of rotting logs of fallen branches and stems. Amongst the fallen timber, early recovery is characterised by a domed cluster of vigorously growing seedlings exceeding the height of the 'seedling bank' surrounding the gap. From within the forest, this phase allows great quantities of light to enter beneath the canopy, illuminating patches of forest floor. Viewed from above, such gaps are readily seen as small, deep circular holes in the dense canopy, with patches of dark mud of the forest floor often still visible. This is the situation after approximately five years.
- e) *Gap filling*. In this phase, the canopy of young recruits has closed and this largely covers the floor of the gap along with the remains of dead timber. Under the elevated canopy of young plants the seedling bank has reformed and it is comparable with that beyond the gap. Self pruning of lower limbs and thinning loss of less vigorous seedlings is quite high during this phase. An often less notable feature is the sprouting foliage from trees bordering the gap. It is thought that extension of surrounding canopy may contribute significantly to gap closure in some instances. This is the situation after approximately ten years.
- f) *Gap closure*. This advanced stage is the least recognisable gap phase since the canopy of recruits is near the 'site maximal canopy height', closely matching the height of undamaged forest. The canopy of surviving recruits has closed with the spreading edge of bordering trees. The gap

is effectively closed, and the 'seedling bank' is no different from that under the surrounding forest. From above, this phase is very difficult to identify. However, from beneath the canopy, the distinguishing features include: a relatively dense cluster of narrow stem trees; and, remnants of recently dead trees indicate the advanced extent of thinning and self-pruning. By this stage, there are few, if any, remnants of the original trees which previously occupied the gap. This is the situation after approximately fifteen years.

A model combining stand development and gap regeneration

The importance of gap regeneration can be assessed from a model which incorporates gap recovery in combination with stand development. This revised model of forest turnover processes is presented in Figure 3. The four developmental stages, described above, are shown across the page from left to right; stem density increases rapidly from colonization to early development, after which they decline rapidly until maturity, and then more slowly until senescence. As noted earlier, this decline in density is driven by tree growth and thinning. By comparison, the regenerative cycles are driven by gap creation incidents which act on the linear stand development process following canopy closure.

Gap creation may only affect a small portion of the forest at any time, but over time the effect on the forest is expected to be uniform since gap locations are apparently random within particular areas. Assuming trees are replaced randomly and systematically overall, the resulting effect would be to slow overall development of the stand. This would place greater importance on knowing the variability, frequency and severity of gap creation incidents on forest turnover. This is expected to be highly variable. By contrast, effects of plant growth and thinning appear relatively constant since they occur progressively in normal forest development. Therefore, in situations where gap creation frequency is high, regenerative turnover might feasibly overwhelm progress in stand development. In such circumstances, forest growth could be reversed resulting in forests become relatively younger, as more and more older trees are removed. This occurrence is clearly unsustainable, although, so too is the situation where stands approach senescence. In either case, forest turnover will be char-



Combined Regeneration and Development Model

Figure 3. The combined model of stand development and regenerative processes in mangroves. While growth and thinning drive development, gap creation and restoration determine the overall rate of development. Regenerative processes include reproductive and vegetative strategies. Where turnover of trees via gap creation exceeds turnover via development progress then stand development is expected to be stalled and reversed (see Figure 4b). If disturbance is severe and frequent, then the forest will collapse (see text).

acterised chiefly by factors influencing gap creation. It also seems that some intermediate level of gap creation may be optimal for long-term stand stability.

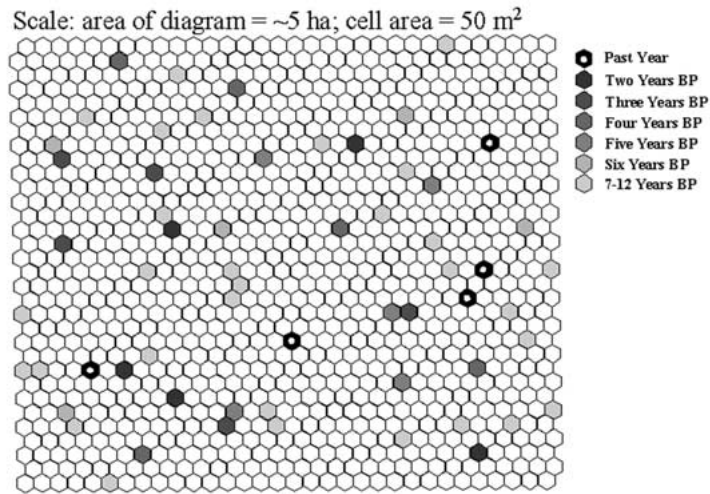
The importance of gap creation on forest turnover can be explored further using the relationship between area of gaps formed in a given time and the rate of gap recovery. The derived estimates can also be compared with rates of turnover in the absence of gaps. The difference in turnover rates represents the net rate, and quantifies the overall progress of development for particular forest stands.

Simple calculations are used to broadly quantify these estimates and relationships, shown schematically in Figure 4a. Since mean gap size is around 50 m² (Smith, 1992), this implies that forests with trees living up to 200 years might have the same rate of turnover from one light gap per hectare per year as would be achieved through stand development in the absence of gaps. In Figure 4b, the hypothetical relationship shown in the graph begins on the left with unimpeded stand development. For forests subject to gap creation, however, the rate of development is expected to be reduced substantially with increased frequency of gap creation. The graph also identifies a point at which development might be expected to stall. The frequency of gap creation at this turning point

would be around one gap per hectare per year, depending on the species and its growth conditions. In this situation, where regenerative turnover equals forest growth turnover indefinitely, it is therefore feasible for forest development to be stalled indefinitely also. Such an occurrence would help explain why some mangrove forests appear unchanging and stable, and why there are so few forests in advanced stages of senescence.

Verification of this proposal is difficult because few data are available from which to estimate gap occurrence in mangrove stands. However, in one reported case, Smith (1992) observed that the Murray River estuary in tropical north-eastern Australia had around 4–15% of its mangrove forests in some stage of gap recovery. *Rhizophora* trees in Panama took around fifteen years to achieve early gap closure (Duke et al., 1993, 1999) and their growth appears similar to *Rhizophora* stands of the Hinchinbrook area in Australia (personal observation). If so, the annual rate of gap formation would be around 0.3–1.0%, or 0.5–2.0 gaps per hectare per year. Since these estimates are around one gap per hectare per year, it suggests that the mangrove community in the Murray River estuary may be an example where developmental progress is more or less stalled. Assuming this is correct, turnover in these forests might occur entirely via gap forma-

(a) Total Area of Gaps for Year Classes



(b) Gap Creation and Stand Development

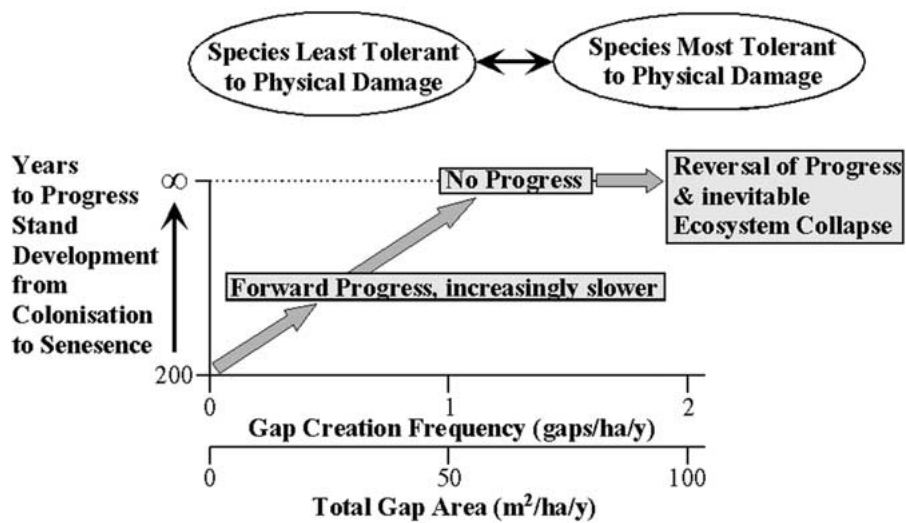


Figure 4. a) Diagrammatic depiction of above-canopy view of a mangrove forest with gaps at various stages of recovery (also see Figure 2). Expected gap size based on estimates of: mean area of gaps, around 50 m² each (shown as six-sided polygons); gap frequency, ~1 gap/ha/y; and, recovery time, around 15 y (see text). b) The proposed relationship (block arrows) in the model links gap creation in mangroves with progress through stand development. The ‘no disturbance’ scenario is shown where gap frequency is zero. At this point development time equals the maximal life span of individual trees, proposed to be around 200 years for this model. The dashed horizontal line shows the point where development is stalled indefinitely. Development is presumably reversed at greater levels of disturbance (see text). Differences in degrees of physical disturbance and gap creation are further proposed to influence species composition and dominance, epitomised in this article by comparisons of *Avicennia* and *Rhizophora* dominated mangrove forests.

tion rather than via trees getting older. Such forests may never reach the senescence phase of stand development while gap creation remained constant. This means that these forests would never be subject to the 'colonisation-collapse' cycle, and this concurs with the apparent long-term stability of such stands.

Ecosystem collapse does occur however in response to both persistent and severe damage. For instance, mangroves struck by Hurricane Andrew in southern Florida were severely damaged over much of the 60,000 ha of mangroves in the area (Smith et al., 1994). In this rare, but important instance mangrove trees were both stripped of leaves, and trunks were snapped off over vast areas. These kinds of damage resulted in death of *Rhizophora* trees. Damage to *Avicennia* trees was significantly less, however, chiefly because they could regrow after defoliation, and from damaged trunks.

A further notable observation from the Hurricane Andrew incident however was the interaction between severe damage and light gaps. Seedlings growing in gaps at the time of the hurricane mostly survived and appeared set to lead any recovery of the larger area. Although not mentioned by Smith, seedlings in the previous undercanopy 'seedling bank' might also contribute to local forest recovery. This may provide an example where the 'seedling bank' had a demonstrable contribution toward ecosystem recovery (also see McKee, 1995). In this instance, however, the longer term problems related less to seedling availability and establishment, and more to deteriorating sediment conditions brought on by massive amounts of decomposing timber and absent fauna. The long term prognosis for these forests is not good.

Implications of the model

In summary, all mangrove forests have a combination of attributes and growth strategies which promote their survival, establishment and regeneration in small forest gaps, including: 1) abundant buoyant propagules; 2) self-planting strategies aided by the shape of propagules; 3) propagules holding large food reserves aiding dispersal and establishment; 4) rapid establishment growth of both roots and foliage; 5) an ability to sustain growth for around two-three years under closed canopies in a seedling bank; 6) shade intolerance which reduces resources taken by slower growing competitors; and 7) trophic links with

dependant benthic fauna which appear to promote greater height growth and standing woody biomass.

The proposed model (Figure 3) links stand development and regenerative processes with gap creation as the driving factor in concert with the various special attributes and growth strategies. The model explains why there are few senescent 'cemetery' stands in locations around the world and why mangrove forests have few single large tree gaps. It also provides a reason why forest structure is generally uniform in disparate global locations, and how mangroves have been largely stable habitats despite occupying exposed coastal locations influenced by regular changes in sea level through geological time. It appears that the response of mangroves to small-scale disturbance has been well-suited for their survival and proliferation in what appears to be a difficult and often harsh environment of the tidal zone.

The success of different mangrove stands growing under difficult conditions is explained also by the combined model. For instance, shade intolerance, which promotes thinning and stand development, is likely to have a significant advantage in forests dominated by small gap creation and recovery. It therefore seems no accident that most plants dominating mangrove canopies worldwide are shade intolerant.

In more exposed locations, however, mangroves are particularly vulnerable to factors influencing their turnover and regeneration. In these locations, species composition and forest structure needs to be maintained because sediments will be eroded rapidly without the continued stabilising influence of living tree roots. Erosion will de-stabilise deforested mangrove habitat leaving it unsuitable for re-establishment and vulnerable to ecosystem collapse. For such stands to remain stable over thousands of years, forest turnover and replenishment has had to be steady and regular, and always successful.

The successful strategies of mangrove habitats in the past, however, now appear to be seriously challenged in the face of an apparently increased frequency of large-scale pollution incidents, and predictions of increasing changes in global climate with rapid rises in sea level and increased severe storm activity. Such reported predictions in global climate change are also reasons for serious concern for the longer-term survival of mangrove habitat. The predicted changes are expected to affect mangrove environments worldwide and in each case the likely changes can be explained using the model.

With rising sea levels, forests need to migrate inland with subsequent die off along seaward margins. Such vegetation changes may already be taking place but the changes are very difficult to distinguish especially since few studies are focussed on this issue and the changes may only be slight at this early stage. However, since even conservative predictions indicate an acceleration in the rate of sea level rise then it is inevitable that the replenishment capability of seaward edge stands will be exhausted. The consequential loss of protective edge trees will be followed by a general collapse of mangrove stands in relatively exposed locations. Once the rate of small gap replenishment is exceeded by tree death from sea level encroachment then the stands are expected to collapse.

Similarly, an increased frequency of severe storm activity exceeding the rate of small gap creation and recovery is also expected to result in the collapse of large areas of mangrove forests. All these matters, emphasize the urgent need to monitor this threatening impact worldwide and to development and apply mitigation strategies where appropriate. The continuing assessment of forest gaps and the forces which create them is considered a vital area of research towards better understanding the role of biodiversity and ecosystem function in tidal wetlands worldwide.

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