Mangroves and Climate Change: Past and Future

By J. H. Slob
Contact: J.H.Slob@gmail.com

MSc. Thesis
Programme: Environmental Biology, track Palaeoecology
August 23, 2012

Supervisor:
Dr. Friederieke Wagner-Cremer

Laboratory of Palaeobotany & Palynology
Faculty of Geosciences
Utrecht University

Contents:

Introduction

Mangroves built up intertidal forests growing on tropical and subtropical coasts. Mangroves represent approximately 3% of the tropical forests worldwide, approximately 180000 km^2 according to Spalding et al. (1997). Mangrove forests are important ecosystems for different reasons. They form a line of protection against hurricanes and their associated storm surges and their roots stabilize coastal sediments. Moreover they filter sediments and nutrients out of terrestrial runoff and prevent them from reaching more vulnerable ecosystems such as seagrass beds and coral reefs (Alongi & McKinnon, 2005). Mangroves have various uses for the local population as well, the most important ones being for timber and firewood as well as fishing grounds.

To date, however, mangroves are declining worldwide. Population increase has increased conversion of natural mangrove areas to other uses such as agricultural ground and aquacultural use such as shrimp ponds in Asia (Blasco *et al.*, 2001). In places like Florida there is a high demand for coastal property along the shorelines. Overharvesting for timber exceeds forest recovery rates in many places. Next to these direct impacts, there are changes in freshwater supply to riverine mangroves and also herbicides and eutrophication affecting current mangrove stands.

Besides the consequences of human activities, future climate change will have strong effects on the remaining (in some places degraded) mangrove forests. The most obvious climate related problem in the future for mangroves is sea level rise (SLR), as mangroves are restricted to intertidal areas. The potential consequences of rising temperature and atmospheric CO_2 concentrations and of possible changes in precipitation are far more obscure though.

Here I will present an overview of what is known so far from the past and expected for the future regarding mangroves and their response to climate change.

On mangroves

Mangroves are forests growing in an intertidal setting. The trees which grow here are adapted to being flooded regularly and to the salinity of the seawater in which they grow. Mangroves often dispose of salts through glands on their leaves or simply prevent salt from entering their roots. Their root systems are adapted to growing in the intertidal area as well, most species have lenticels in their trunk, prop roots or special upward projections known as pneumatophores. Lenticels are hydrophobic pores which are connected to canals that allow the plant to transport oxygen to its waterlogged roots.

Mangroves usually lack a true understory, which is most likely due to a combination of stresses, such as lower light conditions, soil salinity, hydrogen sulfide, anoxic soils and lack of nutrients (Krauss *et al.,* 2008). Snedaker and Lahmann (1988) argue that it’s almost impossible for plants to develop which can survive in the shade of mangroves because they simply can’t meet the energetic demands of the highly stressful environment. Frequency of inundation is the most important factor determining distribution of species in a mangrove forest, all the more because it also influences a lot of other factors, such as pore water salinity and waterlogging (Krauss *et al.,* 2008; Lugo & Snedaker, 1974).

The structure of mangrove forests depends strongly on their location. A study by Pool *et al.* (1977) showed that regular occurrence of hurricanes can limit the development of mangroves, while freshwater input with its increased nutrient input can increase forest complexity and production.

Forest types

Mangrove zonation was long thought to be linked to succession and as such it was thought that different zones replaced each other and were building outward into the sea. This idea was first developed in Florida, where many mangroves show a zonation from land to sea. Mangroves were believed to be a terraforming ecosystem which could claim land from the sea. The behavior of mangroves depends on the behavior of sea-level however, swiftly rising water will cause mangroves to lose area and show seaward zones on top of landward ones. Both prograding and retracting systems have been identified using palynology, some examples are a receding sequence from Florida and a prograding sequence from Australia (Woodroffe, 1990). The main types of mangrove forest (after Ewel *et al.*, 1998) are:

- Fringe forest, which occurs adjacent to the sea and is subject to daily tidal inundation, salinity is relatively constant here.
- Basin forest, which occurs inland and is inundated by tides less often. Bad drainage of these forests means they are flooded longer and that salinity increases due to evaporation.
- Riverine forest, which is located along estuaries also experiences tides, but at much lower salinities due to a freshwater input.

Distribution across the globe

Mangrove forests grow along coasts in tropical and subtropical climates. Mangrove forests worldwide are divided into two groups based on geography. The first group includes mangroves in Asia, Oceania and Eastern Africa, where they have the highest diversity with40 species of true mangrove listed (Tomlinson, 1986). The second includes the Americas and Western Africa and is much less diverse with only 8 species of true mangrove recognized (Tomlinson, 1986). The map in figure 1 shows the species richness of mangroves worldwide.

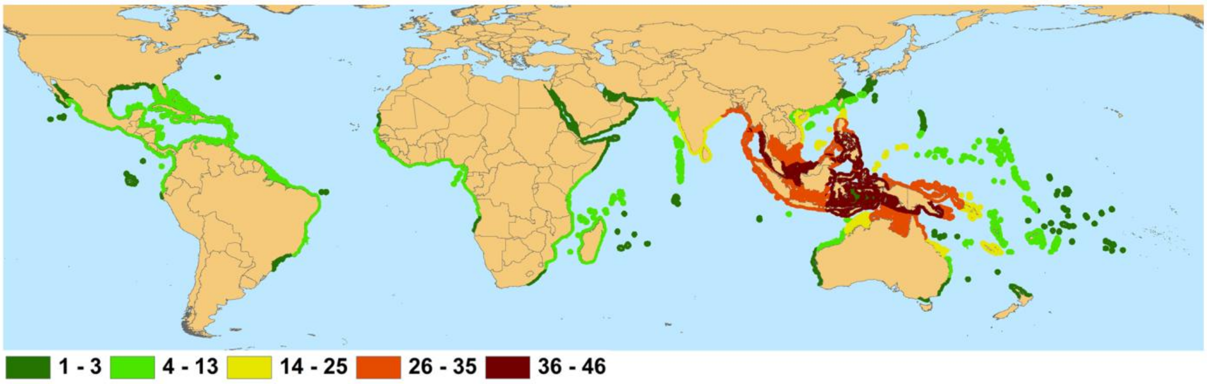

Figure 1 The species richness of mangroves worldwide (from Polidoro *et al.*, 2010)

The uses of mangrove forest

There are many direct and indirect benefits mangroves provide. First of all they are an important habitat to many different species of fish, crabs, birds and other animals (Nagelkerken *et al.*, 2008; Sasekumar *et al.*, 1992). The presence of mangroves has a strong effect on fishery yields (Aburto-Oropeza *et al.*, 2008), since they provide food to offshore systems through outwelling of carbon (Ong, 1993). One commonly stated benefit of mangrove ecosystems, it's function as a nursery habitat, is controversial though. Even if there are indications that there is such a function, it has never been truly shown (Sheridan & Hays, 2003).

Mangroves also provide protection against erosion of the coastlines on which they grow by reducing flow, locking sediment in place with their roots and promoting sedimentation (Thampanya *et al*., 2006). The presence of mangroves can even have a profound effect on erosion of nearby unvegetated parts of the coastline. Mazda *et al*. (2002) found that riverine mangrove forests on the floodplain of tidal channels can slow down tidal flow in the channels when the vegetation is dense enough to cause enough drag. The coastal erosion happens through eddies during the ebb tide, which are far less strong if the flow in the channels is slower. Mangroves filter sediments and nutrients out of runoff as well, keeping them from reaching more vulnerable ecosystems (Alongi & McKinnon, 2005). The presence of mangroves protects the hinterland area to some extent from the hazardous forces of nature, such as tsunamis and cyclones (Alongi, 2008; Das & Vincent, 2009). Another benefit of mangrove forests is that they are a carbon sink as they store organic carbon in the peat layers they form (Ong, 1993). This is especially useful now in the light of atmospheric CO_2 increase due to burning of fossil fuels and the development of the global carbon cycle.

Human threats

The worldwide mangrove area is threatened by human actions. The large losses are a cause of major concern (Duke *et al.*, 2007). Loss of area is likely to go hand in hand with declines of the number of species, since forest size and number of species are directly correlated. Species loss could subsequently be followed by loss of ecosystem functionality, as has been demonstrated in other ecosystems. The effects of species loss are likely to have an even bigger impact on mangrove forests since they are naturally species poor (Duke *et al.*, 2007).

A threat assessment was made for all mangrove species by Polidoro *et al.* (2010) using the criteria for the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species. Eleven species (16%) turned out to qualify for one of the 3 threatened categories, while another 7 (10%) only met the criteria partially and were therefore classified as Near Threatened. Two species turned out to be critically endangered, *Sonneratia griffithii* and *Bruguiera hainesii*, of both these species fewer than 500 mature individuals are known. The most threatened type of habitat are those located upriver in estuaries and the high intertidal areas as these areas are first to be cleared for other uses, 44% of the species occurring in these habitats is threatened. Due to coastal development and conversion to other land uses (such as fish ponds), 30% of fringe forest species are also threatened. The biggest threats to all mangroves are overexploitation and habitat destruction and removal of mangroves to convert the land for aquaculture, agriculture and urban development. Some species are globally of little concern, since they are widespread, but these species may be threatened locally or regionally at the same time. The region with the highest species diversity in mangroves, the Indo-Malay Philippine archipelago, is also the region where the highest loss of area occurred with a 30% reduction since 1980 (Polidoro *et al*., 2010). Central America has the highest proportion of threatened species, 4 out of 10, due to clearing for settlement, shrimp ponds and agriculture. The Caribbean region has the second highest loss rate at 24% due to clearing for multiple reasons, various types of pollution and storm and hurricane damage.

A study by Blasco *et al*. (2001) on the changes in mangrove forests in Continental Asia showed large losses. Satellite images from the not well accessible Myanmar showed large deforested areas which were recorded as mangroves 50 years ago and the areas cleared were one of the few habitats of the species *Heretiera fomes*, the status of which is currently unknown. In Thailand shrimp ponds are the main cause of losses and even some forests designated as reserves have disappeared. In Vietnam the mangroves of the Mekong delta had already suffered from conversion to agricultural land and been a target of herbicide use during the Vietnam War and are now the victim of conversions to shrimp ponds and changes in hydrology. The study shows that there hasn't been a great net loss of mangrove area at all and in some areas reforestation has been successful. A major problem however is that these reforested areas are nothing like the natural forest as they often have an artificial composition, while up to 40% of the total mangrove area is degraded due to hydrology changes and overexploitation. This shows that the loss of natural mangrove ecosystems is far greater than the loss in total mangrove area, which is non-existent here. Vulnerability to human interference is further increased by climate change.

History of the mangrove ecosystem

Modern mangrove species must have come into existence some time after the evolution of angiosperms. There are some claims of earlier mangrove like ecosystems, but these are completely unrelated to the current mangroves and it's still uncertain whether these systems truly were intertidal (Plaziat *et al.*, 2001), so these will not be dealt with here. The largest problem by far with the identification of past mangrove species is of course evolution over time. Species can evolve from related species with different preferences, which could lead to a locality being wrongfully identified as a mangrove. Another possibility is that parts of the plant (e.g. pollen or seeds) had such different appearances in the past that fossils are simply not recognized as originating from mangroves. The best way to identify a true mangrove for what it is, is to look at the entire assemblage in which the presumed mangrove (micro)fossil is found. The presence of some species of gastropods and molluscs for example confirms a plant grew in tidal areas, which is an absolute requirement for a species to be designated as a mangrove. Assigning parts of which the appearance has changed over time to a certain species can often be done using other fossils of known origin which are consistently found in association with the presumed mangrove fossil.

Currently the mangroves of the world are divided into two distinct provinces, one which includes the Asian, Australian and East African mangroves, while the other includes the American and West African mangroves. Over time there have been several hypotheses which attempted to explain this distribution. Most of these used tectonic movement or continental drift to explain the split into two distinct ranges. The following account of the early history of mangroves up to the Pliocene is adapted from Plaziat et al. (2001). Plaziat et al. place the first appearance of mangroves at the start of the Tertiary, with *Nypa* (fig. 2), a stemless palm, occurring in the late Cretaceous already, associated with some possible but unconfirmed mangrove like pollen. The record during the Palaeocene is similarly poor, this is mostly due to a cooling period in the middle Palaeocene, though Sonneratiaceae first appear in the Late Palaeocene.

Figure 2 Nypa, a stemless palm.

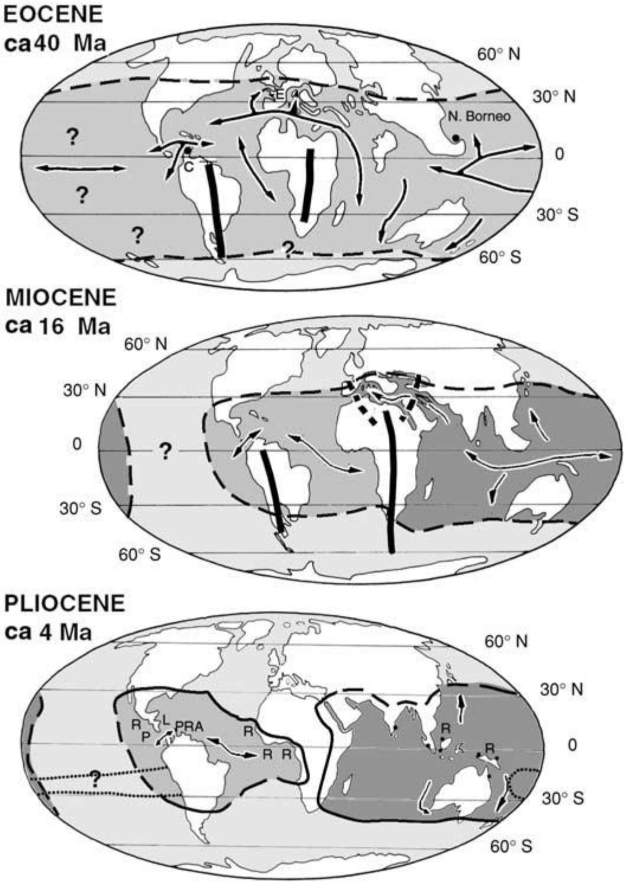

Figure 3 Changes in mangrove area during the Eocene, Miocene and Pliocene (from Plaziat *et al*., 2001). The marked areas show the mangrove distribution, the arrows show possible colonization routes. During the Eocene mangroves were widely distributed and could there were no barriers to colonization, during the miocene distribution was more restricted and parting into two areas was starting to take place, while during the Pliocene the current situation is already in place.

The Early Eocene in contrast shows the appearance of many new taxa, such as *Pelliciera, Ceriops, Avicennia, Bruguiera, Barringtonia* and Rhizophoraceae. At this time mangroves appeared widely, ranging from palaeolatidudes of the 40˚ northern location of the London Clay deposit, and 40˚ to 65˚ south for deposits in Australia. By the end of the Eocene *Avicennia* and the Rhizophoraceae had expanded their range and were as widely present as *Nypa. Nypa* reached its widest distribution at the end of the Eocene as well, before collapsing and disappearing from Europe, West African and South American domains for reasons which remain unknown. The fact that the taxon remained successful across the Eastern Province makes it all the more odd and a climatic explanation unlikely. The wide range and radiation during the Eocene were due to a warming episode which started in the Late Palaeocene. Polar ice caps were probably absent at this time, which made higher temperatures at these high latitudes possible. The authors also hypothesize that the most important cause of this extreme poleward extension could be a lack of extreme winter weather, mangroves today don't seem to be sensitive to lower average temperatures nearly as much as to frost, which is often fatal even for shorter periods of time. A mid-latitude humid belt could explain the high diversity at these latitudes. The Atlantic and Indian ocean were connected at the time, facilitating colonization of the European, West African and American shores. Westward circulation along tropical coasts likely facilitated propagule transport.
During the Oligocene a cold event caused a crisis and mangrove range was much more restricted. The demise of *Nypa* in the western range may have been caused by this cooling event.
The Early Miocene was warmer and mangroves were without a doubt present in Europe, all the way up to 40˚ northern palaeolatitude in Hungary. On Honshu, Japan, high diversity mangroves developed as well, appearing as far as 42˚ north. Regional aridity likely prevented *Nypa*, which was abundant in Asian mangroves at the time, from re-colonizing the coasts of Europe and Western Africa. The situation in the southern hemisphere is unfortunately unclear due to lack of records from the time, but records from the northern hemisphere indicate the modern partition into two geographic ranges was already established at this time. *Avicennia* was recorded from the Mediterranean both before and after the Messinian salinity crisis, but these pollen are possibly reworked. If *Avicennia* truly was present, winter temperatures could not have been low enough to freeze buds. The low diversity of Mediterranean mangroves was either due to impoverishment of an

earlier richer ecosystem, or because the region had to be re-colonized. The authors concluded that the area was likely re-colonized from Asia, but this potential migration path faced barriers of different kinds, such as closure of straits and by the Middle Miocene increasing climatic barriers.
The first modern glaciation followed after a period of progressive cooling in the Late Miocene and Early Pliocene. Geographic obstacles to mangroves were mostly the same as now by the end of the Late Miocene, excluding the Panama Strait which closed during the Pliocene (around 3 million years ago according to Ellison, 2008).
During glacial times mangroves have been on the move a lot due to sea level change. Glaciations would cause water to drop up to hunderds of meters below the current level, while deglaciations would return all this water back into the oceans and make the water rise to it's previous level. The last deglaciation has for example left drowned coastal features from the Last Glacial Maximum over 100 meters below the current water level in Southern Florida (Woodroffe, 1990). Since the last Glacial Maximum water has risen, fast at first and later slowing down. Around 3000 years ago the rate of SLR was slow enough for mangroves to become widely established again. The ability of mangroves to survive such glacial cycles shows that these forests are able to adapt to rising sealevel, which is important in the light of future SLR due to climate change.

Sea level change

One of the major concerns when it comes to mangrove forests and climate change is the possibility of an increase in (SLR). There have been numerous studies from various localities which investigated past responses of mangroves to changes in sea level. The continued existence of mangrove localities depends on their ability to keep up with SLR in the future. The main constituent of mangrove peat is mangrove roots, but when forests are located in estuaries there can also be a substantial input of terrestrial material. Decomposition and compaction also have an influence on the peat accumulation rate. Elevation of the forest however is of course relative to sea level, which means rises in sea level and subsidence or other tectonic activities also have an influence on elevation. The combined result of all these factors determines whether mangroves can maintain their relative elevation and persist or lose elevation and retreat landward or even drown.
A study by McKee et al. (2007) focuses on oceanic mangroves with little to no input of terrestrial material. This enables the examination of the biological component of the peat accumulation in mangrove forests. The mangrove stand they studied at Twin Cays in Belize has some of the oldest and thickest deposits of mangrove peat on the Western Hemisphere, up to 10 m in places. Peat accumulation rates at the site followed the rates of SLR closely. Mangroves did not appear at Twin Cays when SLR was faster than 5 mm/y and established when SLR slowed to around 3.5 mm/y. Comparison of the different types of forest at the location showed that fringe forest is far more productive and can more easily keep up with SLR, it should be fine up to SLR rates of 4 mm/y. This study shows that mangroves can to some extent adjust to increased SLR, but not infinitely. Another possible response to SLR from mangroves is landward retreat, at the Twin Cays site a sand lens shows that at some point the forest retreated landward and the location was later reoccupied.
Another interesting location are the mangroves on Bermuda, which were studied by Ellison (1996). These mangroves are the most northerly in the world, they are able to persist thanks to the mild climate caused by the nearby Gulf stream. The study focused on a mangrove forest in Hungry Bay, which consists solely of *Avicennia germinans* and *Rhizophora mangle*. *Laguncularia racemosa* is absent due to the time it takes for a propagule to reach Bermuda, those from *L. racemosa* simply

don't last long enough. The mangrove forest at the site became established around 2100 yrs BP. Before 3000 yrs BP mangrove pollen are present, but only sporadically, indicating propagules were arriving and trees occasionally grew to maturity on the island, but no large mangrove stands were able to develop. This was due to the much faster SLR before 3000 yrs BP, which was about 2.6 mm/y, after 3000 yrs BP SLR dropped to 0.7 mm/y.

Woodroffe (1990) looks at mangrove systems which do have sediment inputs of external origin. He divides mangroves into three different main groups based on the setting in which they grow to examine the responses of mangroves to SLR. The three types he distinguishes are river-dominated, tidal-dominated and carbonate settings. River-dominated estuaries have mangroves which are located in river deltas where there is an abundant supply of terrigenous material being washed in from upriver. These systems are located in microtidal areas. Salt wedges prevent mangroves from establishing far upriver, and the most extensive mangrove forests are on the seaward edge and abandoned parts of the delta plain. Tide dominated estuaries can also support mangroves. These systems are in macrotidal areas. Flow in channels is often bidirectional due to the tides. These systems often have an extensive low-gradient plains suitable for mangroves. Carbonate settings have a very low input of terrestrial sediment and include locations on oceanic islands. Mangrove forests here either develop on a carbonate substrate or on mangrove peat. These settings usually occur in areas with low tidal ranges. River and tidal dominated estuaries have a steady input of allochtonous sediments which allows mangroves to accumulate sediments at much higher rates. Therefore these estuarine systems should be able to support mangrove systems at much higher rates of SLR (Woodroffe, 1990).

One of the problems with landward displacement of mangrove forests are possible barriers. These could have been present in the past as well, but currently anthropogenic barriers have increased this problem a lot. In many places the areas directly adjacent to mangroves has been developed and this could block landward migration of mangroves (Woodroffe, 1990). Especially if as sea level rises, measures are taken to preserve these properties, for instance by creating dykes and the like.

The 2007 IPCC report (IPCC, 2007) predicts that by the year 2100 the sea will have risen between 19 and 58 cm. Mangroves of the type studied by McKee *et al.* (2007) should be able to keep up with SLR in most of this range except for the uppermost part, which is clearly a faster than 5 mm/year. A more recent review by Donoghue (2011) however casts doubt on the accuracy of these estimates and cites numerous studies which have found that the estimates by the IPCC are probably too low, with several of them having lowest estimates higher than the high estimate by the IPCC. The IPCC itself admits that SLR may be higher. If these newer predictions are true it is likely many mangrove localities will be threatened in the future, localities with low sediment input even more so. Furthermore there are other influences that modify the tide, such as the nodal cycle, which may exacerbate the problem. The nodal cycle results from changes in the orbit of the moon and sun and has a periodicity of 18.6 years. Gratiot *et al.* (2008) found that this cycle has a large influence on the coastal mudflats between the Amazon and Orinoco. The cycle modulates mean high water by 3% and this was enough to cause the shoreline to retreat 90 m because of the gentle slope of the coast. Together with global warming the nodal cycle explained 90% of the shifts. This cycle poses an additional problem to mangroves in affected areas, because it increases mean high water level for multiple years and when added to the SLR caused by global warming it is bound to increase stress on mangroves.

Woodroffe (1990) notes that microtidal areas will be affected most strongly by changes in sea level, since in these areas the rise of sea level will be a much larger proportion of the total tidal range and will therefore cause larger stress and displacement.

Polidoro *et al.* (2010) indicate that SLR poses an unequal threat to different species of mangrove and types of mangrove. The mangroves most threatened by SLR are those growing on the landward edge of the forest, because these are the ones whose movement is most likely to be blocked by obstacles, both natural and manmade. Faster growing species will also be able to cope better than slow growing species.

Tropical storms, hurricanes and peat collapse

Hurricanes have a profound effect on mangrove forests. Mangroves are the first to be hit due to their coastal location. They are influenced by hurricanes to such an extent that mangrove in areas with more frequent hurricane activity have a very different structure. The trees in these forests have a lower canopy, a smaller diameter on average and the forests are structurally far less complex (Pool *et al.,* 1977). Smith et al. (2009) studied the mangroves in the Florida Everglades which were affected by hurricane 'Andrew'. Hurricanes cause damage to mangroves through high windspeeds and stormsurges, which both can strip the trees of leaves, break branches and uproot them. Another less obvious way in which hurricanes cause damage is through sediment deposition, if these deposits are thick enough they can block lenticels and suffocate the tree's roots, effectively killing the tree. They give examples of occasions where damage by hurricanes has led to shifts in vegetation type, mainly from mangrove forest to mudflats with salt marsh vegetation. This shift is caused by the near complete removal of mangrove forest, after which the peat under the mangrove loses elevation due to decay and the lack of new roots. This can cause a drop in elevation to the point where a locality is no longer suitable for mangroves. Cahoon et al. (2003) measured an elevation loss of 11 mm per year in a basin mangrove forest in Honduras, after near complete destruction of the forest by hurricane 'Mitch'. The effect of such a loss of elevation will be even more severe if the speed of SLR increases in the future as is expected. Even if extant mangroves will be able to keep up with the SLR, re-colonization of area lost due to hurricanes becomes far more unlikely since if re-colonization does not happen fast, the water is often too deep for easy establishment of propagules. There are also indications that soil chemistry changes after the removal of mangrove forest can make localities altogether unsuitable for re-colonization. High sulphide concentrations and lack of oxygen in the soils combined with the elevation change would make it difficult to impossible for propagules to establish in these areas.

It is possible that due to rises in temperature atmospheric circulation patterns will change in such a way that typhoons and hurricanes will increase in strength, occur more often or both. Liu and Fearn (2000) found large differences in hurricane activity during the last half of the Holocene. They used sand layers washed into a coastal lake by storm surges of large hurricanes to reconstruct hurricane landfall frequencies. Landfall frequencies turned out to be lower from 5000 to 3400 ka BP and from 1000 ka BP to present. In between these two relatively quiet periods was a hyperactive period from 3400 to 1000 ka BP with landfall chances five times those of the current, more quiet situation. According to the authors this period was most likely caused by changes in atmospheric circulation caused by higher temperatures. An article by Chan and Liu (2004) shows that recently higher sea surface temperatures in the equatorial Eastern Pacific or El-Niño conditions have been correlated to higher typhoon activities. Climate predictions expect an overall rise in temperature in the future, so an increase in hurricane occurrences seems likely. In fact Webster *et al*. (2005) found that hurricanes have already been increasing in strength, during the 35 years examined in the study the number of hurricanes decreased, but the number and proportion of category 4 and 5 hurricanes increased.

Temperature

Mangroves are highly vulnerable to freezing and their current distribution is largely determined by the absence of winter freezing. Increases in temperature in the future due to climate change may allow mangrove forests to expand their range northward. Especially less occurrences of frost will allow mangroves to expand their range, as they did during the Eocene when they appeared at very high latitudes compared to today (Plaziat *et al.*, 2010).

Concerning the effects of high temperatures on mangroves many aspects are unclear. Currently mangroves are mainly limited by low temperatures and therefore not much research has been conducted regarding high temperatures. Nevertheless it seems likely mangroves will be able to cope with projected temperature increases. Studies by Canoy and Banus (cited in Ellison, 2010) on the effects of temperature stress, e.g. due to thermal pollution by power plants, on mangroves has shown that mangroves are capable of surviving much higher temperatures than those predicted to occur due to climate change.

Precipitation

Precipitation influences mangroves mainly through runoff, which means the influence of changes in precipitation are largest for mangroves located in estuaries. Mangroves can show an increase in productivity when growing in less saline waters, and growth is further promoted by nutrients provided by runoff. Pool *et al.* (1977) found that riverine forests had both a higher complexity and relatively high canopy. Decreases in precipitation on the other hand increase salinity and could therefore increase stress and decrease growth. Another possible response is migration of zones up river or if this is impossible the loss of assemblages typical to upriver situations. This is yet another blow to these mangrove types, as the ones appearing upriver are also the ones suffering most from human intervention (Polidoro *et al*., 2010). Projected changes in precipitation differ by area and therefore each location should be considered separately.

Atmospheric CO_2 increase

All plants need CO_2 to survive, it is to them what oxygen is to us. Plants grow by converting water, CO_2 and energy from sunlight through photosynthesis into high energy carbon compounds and oxygen. The amount of CO_2 in the atmosphere has risen considerably since the Industrial Revolution and will continue to rise in the foreseeable future due to our use of fossil fuels. A rise in CO_2 can promote growth, but consequences of truly high concentrations are hardly studied, yet. So far economically important crops have been the main focus of research into the responses of plants to increased CO_2. Most research into the responses of halophytes to increased CO_2 have been performed on temperate salt marshes, which were shown to act as a carbon sink. Farnsworth *et al.* (1996) looked into the response of seedlings of the mangrove *Rhizophora mangle*. They found that seedlings grown under CO_2 concentrations of 700 ppmv grew much faster than those which were put at 350 ppmv. The additional CO_2 didn’t enhance height growth much, but promoted branching instead. Increased branching might increase mechanical stress from tides and drag, but this may not be a problem, since earlier lignification also made these seedlings much sturdier. A surprising result was that the high CO_2 plants also started flowering much earlier and, despite the first flowering not producing any propagules, another a few months later did produce viable propagules, this is almost two years earlier than is normally observed. The plants initially had a much higher production, but this decreased after a year for unclear reasons. Some possible explanations being down regulation and shortage of nutrients. Nitrogen concentrations in the leaves from the plants were lower for the high CO_2 plants, which may also indicate shortage of nutrients. The high CO_2 plants also had less stomata per unit leaf area, which was mainly due to greater expansion of the epidermal cells on their leaves.

Photosynthesis is often CO_2 limited in halophytes since they are under high water stress and therefore can only keep their stomata open for a certain amount of time. This means that a higher CO_2 concentration is likely to increase production, but the extent of the increase is uncertain and will differ between different species. The extent of the increase will also likely be limited by salinity and vapor pressure deficit. Salinity limits the uptake of water, while high vapor pressure deficit (the difference between the amount of vapor the air can hold and the amount it actually contains) will cause increased water loss from the stomata. Therefore if either or both of these are high the plant is more likely to close its stomata early. Evidence supporting this was found by Clough & Sim (1989) who found that stomatal conductance and CO_2 assimilation rate were far more strongly correlated for mangroves exposed to high salinity and water pressure deficit. This closer correlation than for less stressful sites indicated the plant's stomatal conductance is far more strictly regulated to limit water loss. The inability to take up much water may limit the ability of these plants to exploit the increased CO_2 concentrations. Despite this an increase in production to some extent seems likely, since the same volume of exchanged gas will provide the plant with more CO_2.

So the overall influence of increased CO_2 seems to be beneficial, due to the stimulation of growth. In the case of *Rhizophora mangle* the plant also reproduces earlier, which may be a benefit as well, since plants are less likely to be harmed by SLR before they mature. It's surprises like that which makes it necessary to conduct more research into the reaction of mangroves to CO_2, because different species may react in different ways.

Combined effects of different influences

The major problem with current climate change is that it's not like a controlled experiment, where only one variable changes at a time. Climate change is causing all the factors discussed before to change at the same time, causing complex interactions and feedbacks. When it comes to interactions with other environmental factors, hurricanes are most straightforward. Complete destruction of a forest by a hurricane and the peat collapse that accompanies this only cause a stronger negative effect when combined with SLR. SLR, changes in precipitation, temperature increase and the increase in atmospheric CO_2 on the other hand are all influencing the living mangrove ecosystem at the same time. These are all influencing the environment in which the plant is growing and some influence the same parameters. For example temperature increase can increase soil salinity by increased evaporation, while at the same time SLR will increase flooding and therefore flush away salts, the exact result of these interactions depends on the exact amount of change in each, which is impossible to predict. Another example is the positive influence of CO_2 on photosynthesis, which has been mentioned before, because when combined with an increase in temperature or decrease in precipitation increased water stress could prevent any benefit to the plant by forcing it to close its stomata to prevent further water loss. The fact that the exact extent of future changes are very uncertain makes it impossible to predict the exact effects of climate change on mangroves. The influence on mangrove forests will be different for each area as they depend on the exact changes in each of these parameters, which are different for each location.

The most problematic in the future will without a doubt be SLR though, as the effects of this are most profound and inland migration is likely to be hindered by both human and natural obstacles.

Conclusions

Mangroves have been around for a very long time, some can be traced back to the Late Cretaceous. Mangroves have adjusted to many changes, including changes in temperature during the Eocene and the recent glacials and the large changes in sea level associated with the glacial cycles. It is therefore highly unlikely that mangrove will go extinct altogether. Mangroves will be able to cope with future climate change like they have in the past. Several studies have shown that sediment accumulation in mangroves will be able to keep up with SLR to some extent. If SLR is too fast it will cause mangroves to be displaced landward together with the shoreline. A substantial decrease in mangrove area may be caused by this, however, as on many locations the landward mangroves cannot migrate inland, while erosion will happen at the seaward edge. Hurricanes also pose a threat which will increase in the future. Hurricanes damage mangroves by removing leaves and branches and even toppling complete trees. If a mangrove forest is killed (almost) completely it may not return if the location is not re-colonized fast enough, this is caused by decomposition of the peat, which causes the area to sink. Peat collapse is a big problem in combination with SLR, because the elevation change relative to sea level will be larger and therefore re-colonization will be even more unlikely. Expected increases in CO_2 and temperature seem to have mainly positive effects on mangrove ecosystems, as the one promotes growth and the other allows colonization of areas which are currently too cold during winter. However, much is still unclear regarding the effects of CO_2 and temperature increase. Again the mangrove habitat is unlikely to go extinct altogether, but the effects of loss of mangrove area can have negative effects all the same. Naturally populations of species which are to some extent dependent upon mangroves will decrease, which will also affect fishery in many places. Other ecosystem services, such as protection from tsunamis and storm surges, prevention of coastal erosion and filtering of terrestrial runoff will also be lost or reduced.   A way to protect mangroves from great losses due to climate change is by making sure that the remainder is at the very least left intact and degraded mangrove area is restored, as larger healthier ecosystems can cope with climate change much better.

References

Aburto-Oropeza O., Ezcurra E., Danemann G., Valdez V., Murray J. & Sala E. (2008) Mangroves in the Gulf of California increase fishery yields. *PNAS* **105:30**, 10456-10459

Alongi D. M. (2008) Mangrove forests: Resilience, protection from tsunamis and responses to global climate change *Estuarine, Coastal and Shelf Science* **76**, 1-13

Alongi D. M. & McKinnon A. D. (2005) The cycling and fate of terrestrially-derived sediments and nutrients in the coastal zone of the Great Barrier Reef shelf. *Marine Pollution Bulletin* **51**, 239-252

Blasco F., Aizpuru M. & Gers C. (2001) Depletion of the mangroves of Continental Asia. *Wetlands Ecology and Management* **9**, 245-256

Cahoon D.R., Hensel P., Rybczyk J., McKee K.L., Proffitt C.E. & Perez B.C. (2003) Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology* **91**, 1093-1105

Chan J. C. L. & Liu K. S. (2004) Global Warming and Western North Pacific Typhoon Activity from an Observational Perspective. *Journal of Climate* **17**, 4590-4602

Clough B. F. & Sim R. G. (1989) Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. *Oecologia* **79**, 38-44

Das S. & Vincent J. R. (2009) Mangroves protected villages and reduced death toll during Indian super cyclone. *PNAS* **106:18**, 7357-7360
Donoghue J. F. (2011) Sea level history of the northern Gulf of Mexico coast and sea level rise scenarios for the near future. *Climatic Change* **107**, 17-33

Duke N. C., Meynecke J.-O., Dittmann S., Ellison A. M., Anger K., Berger U., Cannici S., Diele K., Ewel K. C., Field C. D., Koedam N., Lee S. Y., Marchand C., Nordhaus I. & Dahdouh-Geubas F. (2007) A World Without Mangroves? *Science* **317**, 41-42

Ellison J. C. (1996) Pollen evidence of Late Holocene Mangrove Development in Bermuda. *Global Ecology and Biogeography Letters* **5:6**, 315-326

Ellison J. C. (2008) Long-term retrospection on mangrove development using sediment cores and pollen analysis: A review. *Aquatic Botany* **89**, 93-104

Ellison, J.C. (2010). Proceedings of the ASEAN Conference on Biodiversity, Singapore, 21-23 October 2009. ASEAN Centre for Biodiversity, Laguna Philippines.

Ewel K. C., Bourgeois J. A., Cole T. G. & Zheng S. (1998) Variation in Environmental Characteristics and Vegetation in High-Rainfall Mangrove Forests, Kosrae, Micronesia. *Global Ecology and Biogeography Letters* **7:1**, 49-56

Farnsworth E. J., Ellison A. M. & Gong W. K. (1996) Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.) *Oecologia* **108**, 599-609

Gratiot N., Anthony E. J., Gardel A., Gaucherel C., Proisy C. & Wells J. T. (2008) Significant contribution of the 18.6 year tidal cycle to regional coastal changes. *Nature Geoscience* **1**, 169-172

IPCC (2007) Climate change 2007. *In*: Houghton J. T., Ding Y., Griggs D. L., Noguer M., van der Linden P. J., Dai X., Maskell K. & Johnson C. A. *The scientific basis: contribution of working group I to the third assessment report of the intergovernmental panel on climate change.* Cambridge University Press, Cambridge.

Krauss K. W., Lovelock C. E., McKee K. L., López-Hoffman L., Ewe S. M. L. & Sousa W. P. (2008) Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany* **89**, 105-127

Liu K. & Fearn M.L. (2000) Reconstruction of Prehistoric Landfall Frequencies of Catastrophic Hurricanes in Northwestern Florida from Lake Sediment Records. *Quaternary Research* **54**, 238-245

Lugo A. E. & Snedaker S. C. (1974) The Ecology of Mangroves. *Annual Review of Ecology and Systematics* **5**, 39-64

Mazda Y., Magi M., Nanao H., Kogo M., Miyagi T., Kanazawa N. & Kobashi D. (2002) Coastal erosion due to long-term human impact on mangrove forests. *Wetlands Ecology and Management* **10**, 1-9

McKee K. L., Cahoon D. R. & Feller I. C. (2007) Carribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Gloval Ecology and Biogeography* **16**, 545-556

Nagelkerken I., Blaber S. J. M., Bouillon S., Green P., Haywood M., Kirton L. G., Maynecke J.-O., Pawlik J., Penrose H. M., Sasekumar A. & Somerfield P. J. (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany* **89**, 155-185

Ong J. E. (1993) Mangroves – A Carbon Source and Sink. *Chemosphere* **27:6**, 1097-1107

Plaziat J.-C., Cavagnetto C., Koeniguer J.-C. & Baltzer F. (2001) History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management* **9**, 161-179

Polidoro B. A., Carpenter K. E., Collins L., Duke N. C., Ellison A. M., Ellison J. C., Farnsworth E. J., Fernando E. S., Kathiresan K., Koedam N. E., Livingstone S. R., Miyagi T., Moore G. E., Nam V. N., Ong J. E., Primavera J. H., Salmo S. G., Sanciangco J. C., Sukardjo S., Wang Y. & Yong J. W. H. (2010) The Loss of Species: Mangrove Extinction Risk and Geographic Areas of Global Concern. *PLoS ONE* **5:4**, e10095

Pool D. J., Snedaker S. C. & Lugo A. E. (1977) Structure of Mangrove Forests in Florida, Puerto Rico, Mexico, and Costa Rica. *Biotropica* **9:3**, 195-212

Sasekumar A., Chong V. C., Leh M. U. & D'Cruz R. (1992) Mangroves as a habitat for fish and prawns. *Hydrobiologia* **247**, 195-207

Sheridan P. & Hays C. (2003) Are mangroves nursery habitat for transient fishes and decapods? *Wetlands* **23:2**, 449-458

Smith T.J., Anderson G.H., Balentine K., Tiling G., Ward G.E. & Whelan K.R.T (2009) Cumulative Impacts of Hurricanes on Florida Mangrove Ecosystems: Sediment Deposition, Storm Surges and Vegetation. *Wetlands* **29:1**, 24-34

Snedaker S. C. & Lahmann E. J. (1988) Mangrove Understorey Absence: A Consequence of Evolution? *Journal of Tropical Ecology* **4:3**, 311-314

Spalding M., Blasco F. and Field C. (1997) World Mangrove Atlas. ISME, Okinawa.

Thampanya U., Vermaat J. E., Sinsakul S. & Panapitukkul N. (2006) Coastal erosion and mangrove progradation of Southern Thailand. *Estuarine, Coastal and Shelf Science* **68**, 75-85

Tomlinson P. B. (1986) The Botany of Mangroves. *Press Syndicate of the University of Cambridge*, Cambridge. 419 p

Webster P. J., Holland G. J., Curry J. A. & Chang H.-R. (2005) Changes in Tropical Cyclone Number, Duration and Intensity in a Warming Environment. *Science* **309**, 1844

Woodroffe C. D. (1990) The impact of sea-level rise on mangrove shorelines. *Progress in Physical Geography* **14**, 483-520