

Chapter 2

Impact of Extreme Events on Salt-Tolerant Forest Species of Andaman and Nicobar Islands (India)

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1 Introduction

Andaman and Nicobar Islands situated in the Bay of Bengal off the eastern coast of India (Fig. 2.1) are endowed with very dense forest exhibiting rich diversity of plant species. Luxuriant mangroves constitute one of the most important forest types that exist in these islands. Mangroves are the salt-tolerant plants that are found mainly in the tropical and sub-tropical intertidal regions of the world (www.mangroveindia.org). They are defined as tree or bushes growing between the level of high water of spring tide and level close to but above mean sea level (Macnae 1968) or type of coastal woody vegetation that fringes muddy saline shores and estuaries in tropical and sub-tropical regions (Blasco et al. 1975). Duke (1992) has defined a mangrove as “a tree, shrub, palm or ground fern, generally exceeding one-half metre in height, and which normally grows above mean sea level in the intertidal zone of marine coastal environment, or estuarine margins”. A term often used while describing mangroves is ‘mangal’. Macnae (1968) suggested using the term ‘mangal’ to refer the mangrove ecosystem and the term ‘mangrove’ for referring the individual plant species. The mangrove forest ecosystem comprises the intertidal flora and fauna in the tropics and sub-tropics and dominated by evergreen sclerophyllous broad-leaved trees with stilt roots or pneumatophores and viviparous seedlings (UNESCO 1973).

There have been different estimates on global distribution of mangroves. According to McGill (1959), mangroves cover approximately 75 % of the World’s tropical coastline between 25° N and 25° S latitude. There have been different estimates of area under mangroves in the world varying from 10 million ha to 24 million ha. It is estimated at 16.2 million ha by Saenger et al. (1983), 10 million ha by

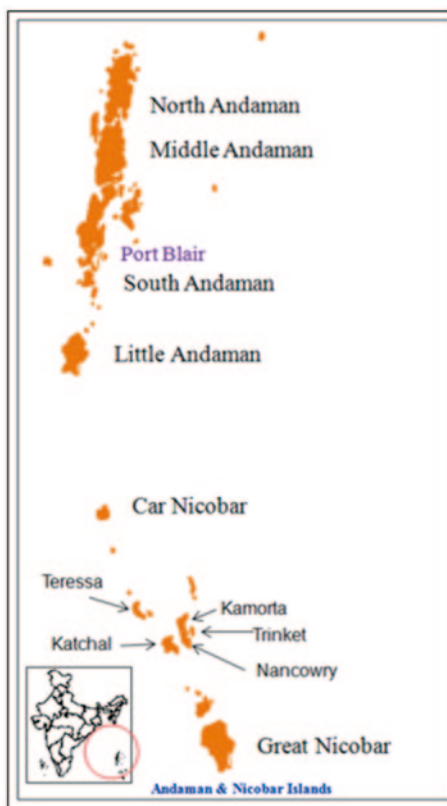
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Fig. 2.1 Location of Andaman and Nicobar Islands



Bunt (1992), 24 million ha by Twilley et al. (1992), 14–15 million ha by Schwamborn and Saint-Paul (1996) and above 18 million ha by Spalding (1997). The most recent estimate by Wilkie and Fortuna (2003) suggests that mangroves cover an area of about 14.65 million ha. In India, distribution of mangroves spreads across all the nine coastal states, Union Territories (UTs) of Pondicherry, Daman-Diu and Andaman and Nicobar Islands (ANI). Figure 2.2 shows State/UTs-wise mangrove availability in India. There have been different estimates of mangroves by different authors. Khan (1957) estimated area under mangroves of Indian coast as 0.55 million ha, Sidhu (1963) as 0.68 million ha and Blasco (1977) as 0.36 million ha. These estimates did not include mangroves of Daman-Diu, Goa, Karnataka, Kerala and Pondicherry. Forest Survey of India (FSI), an organisation under the Ministry of Environment and Forests, Government of India, is assessing the forest cover of the country including that of mangroves on biennial basis since 1987. These assessments are based on interpretation of satellite data followed by limited ground verification. According to the latest estimate of the FSI (2009), total area under mangrove vegetation in India is 4,639 km². Out of this, 615 km² area (i.e. 20 % of the total mangrove area of the Indian territory) is in ANI. In Andaman district, the area under mangroves is 612 km², while in Nicobar district mangroves occupy

Mangrove occurrence in India



Fig. 2.2 Locations of availability of mangroves in India

only 3 km². Area wise, mangrove cover in ANI ranks third in the country after West Bengal and Gujarat, but as far as density and growth are concerned mangroves in the ANI are perhaps the best in the country (Fig. 2.3). It is evident by the fact that approximately 89 % of the mangrove cover in ANI falls under the category of either very dense mangroves (with more than 70 % canopy density) or moderately dense mangroves (with canopy density between 40 and 70 %). As many as 34 exclusive

Fig. 2.3 Luxuriant mangroves of Austin Creek, North Andaman



species distributed among 17 genera and 13 families are reported from ANI (Dagar et al. 1991). Mangroves in these islands mostly fringe the creeks, backwaters and muddy shores. Luxuriant mangroves are seen in Shoal Bay in South Andaman, Yerrata in Middle Andaman and Austin Creek, Kalighat Creek and Cadell Bay in North Andaman (Dam Roy 2003).

Mangrove ecosystem consists of mostly unrelated salt-tolerant trees and shrubs which show similar physiogamy and physiological characteristics and structural adaptations to the habitat (Yanney-Ewusie 1980). The environmental and ecological factors that affect the mangroves are the drying effects of the sun and wind, osmotic imbalance caused by the high salinity of seawater in which it is immersed, and growth in salty, oxygen deficient, and waterlogged soils, the action of tides, exposure to freshwater, destruction effects of storm surges and the diurnal and seasonal fluctuations of temperature. Nature has therefore endowed mangroves with a series of remarkable adaptations which enable them to flourish in an environment characterized by high temperatures, wide fluctuating salinities and shifting of anaerobic substrates. They are adapted to high water stress, exhibit mechanisms that permit water uptake against a gradient and have xerophytic adaptations, extensive and specialized root system (Dawes 1981).

2 Adaptations in Mangroves

According to Warming (1883), the mangroves have adapted to their environment through:

1. Mechanical fixation in loose soil.
2. Respiratory roots and aerating devices.
3. Vivipary.
4. Specialized means of dispersal and
5. Development of xerophytic structures in relation to soil salinity.

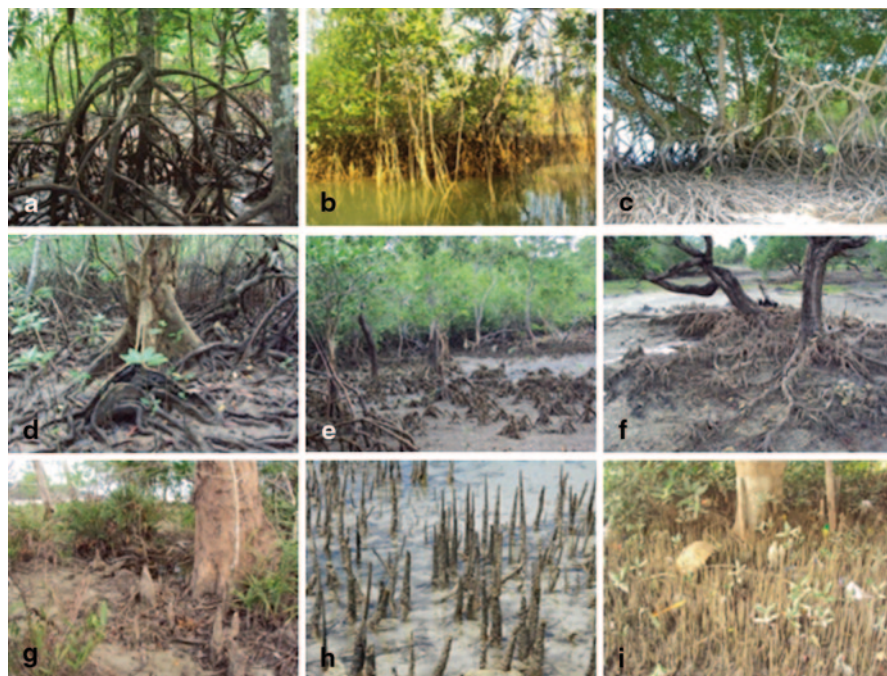


Fig. 2.4 Root systems in mangroves. **a** Stilt root of *Rhizophora* sp., **b** Prop root of *Rhizophora* sp., **c** Stilt root of *Rhizophora* hybrid, **d** Planks root of *Xylocarpus*, **e** Knee roots of *Bruguiera* sp., **f** Above ground root of *Lumnitzera* sp., **g** Above ground root of *Xylocarpus moluccensis*, **h** Pneumatophores of *Sonneratia*, **i** Pneumatophores of *Avicennia*

Macnae (1968) has described adaptations of mangroves considering their growth in ill-consolidated mud, specialization of stems and leaves, relationship between root and shoot systems and vivipary.

2.1 Morphological Adaptations

These include various types of aerial roots for proper exchange of gases and support of plant body, leathery shiny glaucous leaves with water storage tissue and viviparous germination in many species.

Mangroves have shallow root systems but they have adapted in a remarkable way to withstand the conditions of the nutrition, absorption of water and oxygen in anaerobic muddy soil and for anchorage on an unstable substratum. A variety of root systems exists in mangroves such as aerial roots, knee roots, stilt roots, tangle roots and pneumatophores or respiratory roots (Fig. 2.4). The aerial roots are highly developed and very extensive, forming intricate tangle making the movement in it very difficult. They help in allowing the atmospheric gases to reach the underground roots which lie in anaerobic soils. The strut and stilt roots in *Rhi-*

zophora species produce lateral roots from the base of the stems which form arch and re-arch before reaching substratum. Prop roots in *Rhizophora* species produce numerous thin unbranched roots at different heights. At ground level, they produce innumerable fibrous roots which help in absorption of water and nutrients. *Avicennia* and *Sonneratia* possess specialized finger like respiratory roots called pneumatophores with lenticels for passive diffusion of oxygen. Oxygen may pass through non-lenticellular part of the pneumatophores as well. Knee roots found in *Bruguiera*, *Ceriops*, *Lumnitzera*, etc., are lateral roots that bend upwards and come above the ground where they make knee-like curve before entering into soil again (Dagar et al. 1991). Lenticels are common on the knee roots and they are also considered to help in gas exchange.

2.2 Physiological Adaptations

Existence of high osmotic and diffusion pressure deficit (DPD) of cell sap, ultra-filtration mechanism of ions and salt-secreting glands are some of the physiological adaptations. Salt tolerance-related physiological adaptations are dealt subsequently in this chapter.

2.3 Anatomical Adaptations

Leaves have thick-walled epidermis with thick layer of cuticle and adequate tissue. Palisade tissue is well developed; water stomata are present in some cases, for example *Aegiceras corniculatum*; Mucilage cells occur in some species such as *Sonneratia*, *Rhizophora*, etc. The aerial roots on reaching the ground show short elongation zone and almost non-existent secondary growth. Like in aquatic plants, there are no root hairs in true mangroves and the endodermis acts as an effective absorbing layer (Tomlinson 1986). Mangrove woods exhibit unique anatomical features that enable the plants to withstand the high osmotic potential and the transpiration caused by high temperature (Tomlinson 1986). A number of vessels run through the wood and helps in developing high tension in the xylem (Scholander et al. 1964, 1965; Tomlinson 1986).

2.4 Reproductive Strategies

Four methods of reproduction in mangroves have been described by Bhosale and Mulik (1991). These are:

1. Vivipary
2. Cryptovivipary



Fig. 2.5 Vivipary in mangroves (propagules). **a** *Rhizophora stylosa*, **b** *R. mucronata*

3. Normal germination
4. Vegetative propagation.

Among these four means of reproduction, vivipary is the most significant. Vivipary (Macnae 1968; Gill and Tomlinson 1969) means continuous development of the embryo after fertilization while attached to the parent without any intermediate resting or dormant period. Therefore, the term ‘propagule’ is used for these embryos instead of the term ‘seed’ (Fig. 2.5). The development of embryo continues during the dispersal by water (Van der Pijl 1972). It is argued that vivipary represents a precondition for increasing salt resistance in the seedling thereby facilitating survival, when detached, in a substrate of high salinity (Dagar et al. 1991). In some mangrove species such as *Aegiceras*, *Avicennia*, *Nypa* and *Pellicera*, a more advance state of vivipary known as ‘cryptovivipary’ is found where the embryo emerges from the seed coat but not the fruit before it abscises (Carey 1934). The advantages of vivipary are obvious for such plants which grow on the fringes of sea. After falling from the tree, the propagules float and remain viable for considerably long period of time. Mangroves have little or no capacity of vegetative propagation but some species such as *Avicennia* and *Excoecaria* have the capacity to coppice and could persist in western India in spite of over-exploitation (Blasco 1977).

3 Salt Stress Regulation Mechanisms

Presence of salt water is not a physical requirement of mangroves (Bowman 1917; Rosevear 1947; Egler 1948). Mangroves are facultative halophytes occurring in tidal areas where fresh water plants, which are intolerant to salt, cannot live. Most mangroves are capable of growing in fresh water (Teas 1979) but mangrove ecosystems are not found in strictly fresh water environment, probably due to the fact that mangroves are not good competitors and the salinity is important in reducing competition from fresh water and terrestrial vascular plants (Kuenzler 1974). Man-



Fig. 2.6 Succulent leaves in *Lumnitzera* and *Excoecaria* species

groves thrive best in muddy coastal plains where adequate fresh water supplies from river discharge with ample nutrients are available.

Each mangrove species is associated with an optimum salinity (Snedaker 1978). Each species occupies the salinity zone to which it is best suited and is best adapted physiologically. There are mainly two mechanisms of salt regulation (Scholander 1968).

3.1 Salt Exclusion

Rhizophora and other members of family Rhizophoraceae have a well-developed mechanism of ultra-filtration in their roots enabling only selective absorption of ions while extracting water from the soil. They may retain a low internal salinity by means of salt-excluding mechanisms in the roots.

3.2 Salt Excretion

Avicennia sp., *Aegiceras* sp., and several other species have salt glands on their leaves which secrete salt. *Lumnitzera* and *Conocarpus* have analogous structure to salt glands. Sodium chloride concentration in the xylem sap of these species is about 10 times greater than that in exclusion type. The ions which are excreted by these glands are mostly sodium and chloride. Though salt-excreting species allow more salt into the xylem than the non-salt-excreting species, but still they exclude about 90 % of the salt (Scholander et al. 1962; Azocar et al. 1992). Salt excretion is an active process as evidenced by ATPase activity in the plasmalemma of the excretory cell (Drennan et al. 1992).

Salt accumulation is also another salt-regulatory mechanism found in species of *Lumnitzera* and *Excoecaria* which accumulate salts in leaf vacuoles and become succulent (Fig. 2.6). In some species, salt concentration can also be reduced by

transferring the salts into senescent leaves or by storing them in the bark or the wood (Tomlinson 1986). With increase in water salinity, some species restrict their water use in order to achieve greater tolerance (Ball and Passioura 1993). In addition to these direct regulatory mechanisms, mangroves may also accumulate or synthesize other solutes to regulate and maintain osmotic balance (Werner and Stelzer 1990; Popp et al. 1993). Some species such as *Aegiceras corniculatum*, *Aegialitis annulata* and *Laguncularia racemosa* store mannitol and proline (Polania 1990), *Avicennia marina* stores glycine betaine, asparagines and stychyose (Ashihara et al. 1997) and *Sonneratia alba* synthesizes purine nucleotides that facilitates tolerance to salt load of 100 mM sodium chloride (Akatsu et al. 1996). Scholander et al. (1964) have demonstrated that in order to facilitate water flow from roots to leaves, the water potential at the leaves is held lower (−2.5 to −6.0 MPa) than in the roots (−2.5 MPa). Recent studies also show that mangroves can restrict cytosolic salt contents not only by ultra-filtration (Zheng et al. 1999; Wang et al. 2002; Aziz et al. 2001; Khan et al. 2001), but also by other means such as salt accumulation and ion sequestration (Mimura et al. 2003; Kura-Hotta et al. 2001). Salt-controlling strategies in mangroves are similar to those in glycophytes, but probably mangroves could exclude or sequester salt ions more efficiently (Shan et al. 2008). Many mangrove species (e.g. *Kandelia obovata*, *Avicennia marina* (Zhao et al. 1999; Suarez et al. 2006)) can accumulate inorganic ions and use them as osmolytes to maintain osmotic and water potential. This characteristic confers a survival advantage to these species in a saline environment (Tomlinson 1986). Shan et al. (2008) have shown that while sequestering excessive ions into vacuoles, mangroves could also accumulate organic osmolytes in cytoplasm to get osmotic equilibrium across the tonoplast. Organic osmolytes of mangroves mainly include hydroxyl compounds, free amino acids (especially Proline), polysaccharide (e.g. starch), etc. Oku et al. (2003) studied the relevance of lipid composition to salt tolerance in propagules of *Kandelia candel* and *Bruguiera gymnorhiza* planted with varied salt concentrations. This study result shows that salt stress specifically modulated the terpenoid concentrations in mangroves, whereas phospholipid and fatty acid compositions in both species are not changed with respect to varying salinity.

Salinity increases biosynthesis and accumulation of ABA, which modulates physiological reactions in plant response to salinity (Zhao et al. 1991; Montero et al. 1997; Gomez-Cadenas et al. 1998). It has been documented that ABA induces the expression of antioxidant genes encoding Cu/Zn-superoxide dismutase (Cu/Zn-SOD) (Guan and Scandalios 1998). Calmodulin (CaM), a ubiquitous calcium-binding protein, regulates the activity of a variety of enzymes and proteins that confers salt tolerance (Li et al. 2009). Yang and Poovaiah (2002) demonstrated the role of CaM in regulating H_2O_2 homeostasis, i.e. CaM down-regulated H_2O_2 levels in plants by stimulating the catalytic activity of catalase. Li et al. (2009) recently studied the correlation between ABA, CaM and antioxidant defense in *Bruguiera gymnorhiza* and *Kandelia candel* and found that elevated ABA and CaM concentration under short-term and long-term salt treatment may up-regulate the activity of antioxidant enzymes in the two mangrove species, thus avoiding excess ROS pro-

duction and the subsequent oxidative stress. ABA and CaM likely restricted root-to-shoot salt transport by reducing water flow (Li et al. 2009).

There is experimental evidence that salt stress affects the integrity of cellular membranes, activities of enzymes and the functioning of the plant photosynthetic apparatus (Serrano et al. 1999). An important cause of this damage is the production of reactive oxygen species (ROS; Smirnoff 1993). Oxidative stress generates ROS such as superoxide, hydroxyl and peroxy radicals and the balance between antioxidantation and oxidation is believed to be a critical concept for maintaining a healthy biological system (Jithesh et al. 2006b).

A number of reviews have concentrated on the link between salt stress and antioxidant pathways in plants (Bohnert and Jensen 1996; Dat et al. 2000; Van Breusegem et al. 2001; Arora et al. 2002; Borsani et al. 2003). The plant antioxidant stress pathway comprises two components, the non-enzymatic and the enzymatic components. The non-enzymatic component consists of antioxidants such as tocopherol, carotenoids, ascorbate and glutathione that are free-radical-scavenging molecules (Salin 1987). The enzymatic component consists of enzymes such as superoxide dismutase, catalase, ascorbate peroxidase, monohydroascorbate reductase, dehydroascorbate reductase and glutathione reductase (Salin 1987). Apart from these, an iron-storage protein, ferritin, is also involved in the reactive oxygen-scavenging network (Morel and Barouki 1999; Mittler et al. 2004).

Most of the early studies in mangroves have dealt with the effects of salinity on photosynthesis (Ball and Farquhar 1984) and respiration (Burchett et al. 1989; Fukushima et al. 1997). However, recently, there has been a growing interest in the effect of salinity and its relation to antioxidant enzyme status in mangroves and their associates (Cherian et al. 1999; Takemura et al. 2000; Cherian and Reddy 2003; Parida et al. 2004; Jithesh et al. 2006a). Parida et al. (2004) assessed the activities of some antioxidant enzymes and levels of antioxidants in *Bruguiera parviflora* and suggested that under salinity stress plants are protected against activated oxygen species by the elevated levels of certain antioxidant enzymes, thus avoiding lipid peroxidation during salt exposure and differential changes in the levels of the isoforms due to NaCl treatment may be useful as markers for recognizing salt tolerance in mangroves.

The morphological, physiological and biochemical studies done in the past have not clearly explained the salt-adaptation mechanism and its evolution. Recently, some progresses have been achieved in understanding the mechanism of salt adaptation in mangroves on a molecular level. *Avicennia marina* is one of the well-studied mangroves because of its characters of salt secretion and high salt tolerance. *A. marina* deals with salt stress through accumulating betaine serving as an osmolyte. Hibino et al. (2001) first identified and cloned the *BADH* gene that is involved in betaine synthesis in *A. marina*. *BADH* was up-regulated under salt stress, and this tendency was consistent with the accumulation of betaine in *A. marina*. Two other genes, *AmT1* and *AmT2* (coding for Betaine/Proline transporter) were also isolated from *A. marina* later (Waditee et al. 2002). Jithesh et al. (2006a) reported that in *A. marina* high salinity did not lead to transcriptional change of gene *Sod1*, encoding enzyme Cu/Zn-SOD, but osmotic stress decreased transcript level of this gene and

under oxidative stress, its transcription was transiently up-regulated. *Cat1* was up-regulated by saline or oxidative stress but down-regulated by osmotic stress. *Fer1* was transcriptionally up-regulated by saline or oxidative stress but did not change under osmotic stress.

Aegiceras corniculatum is another species of high concern. Six hundred EST were obtained from the leaf SSH library of *A. corniculatum* under salt-stress (Fu et al. 2005). *P5CS*, which was related to osmotic regulation, and two aquaporin genes, which participate in water transport (Maurel et al. 2001) were up-regulated in *A. corniculatum* by salt stress (Fu et al. 2005). Expression patterns of these two aquaporins also indicated that *A. corniculatum* could recover from long-term salt stress and adapt to saline environment (Maurel et al. 2001).

Bruguiera gymnorhiza is a well-studied non-secreting true mangrove. Studies on its response to high salinity have been conducted recently at both the gene and genomic levels (Sugihara et al. 2000; Miyama et al. 2006; Miyama et al. 2007; Banzai et al. 2002a; Banzai et al. 2002b; Takemura et al. 2002). For example, in *B. gymnorhiza* oxygen-evolving enhancer protein 1 (OEE1), the protein was initially isolated and its corresponding gene was also obtained (Sugihara et al. 2000). Currently, there are also ongoing genomic studies of *B. gymnorhiza*. Miyama et al. (2006) established the first *B. gymnorhiza* EST library, which collected 14,842 ESTs from leaves and roots after high salinity or hormone treatments. Another non-secreting true mangrove species *Ceriops tagal* has also been of concern recently. More than 5,000 EST clones have been obtained from its root cDNA library and leaf SSH library of *Ceriops tagal* (Liang 2007).

4 Climate Change and Mangroves

Global climate change is considered to have significant adverse effects on mangroves. Global climate change and concomitant effects such as changes in temperature and CO₂, changes in precipitation patterns, storminess, and eustatic sea-level rise as observed over recent decades, are mainly due to anthropogenic activities. Increase in the Greenhouse gas (GHG) concentration in the atmosphere has been the main cause for the observed warming over the last 50 years (Houghton et al. 2001). Following account is based on the IUCN report by Elizabeth and Rodney (2006).

4.1 Temperature

The increase in the Earth's temperature in the past 100 years has been more than 0.6 °C and it is projected to be 2–6 °C by 2100 mostly due to the anthropogenic activities (Houghton et al. 2001). The impact of the projected increases in sea

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