



Review

# Environmental drivers in mangrove establishment and early development: A review

Ken W. Krauss<sup>a,\*</sup>, Catherine E. Lovelock<sup>b</sup>, Karen L. McKee<sup>a</sup>, Laura López-Hoffman<sup>c</sup>, Sharon M.L. Ewe<sup>d,1</sup>, Wayne P. Sousa<sup>e</sup>

<sup>a</sup>U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506, USA

<sup>b</sup>University of Queensland, Center for Marine Studies, School of Life Science, St Lucia, QLD 4072, Australia

<sup>c</sup>University of Arizona, Department of Geosciences, Tucson, AZ 85721, USA

<sup>d</sup>Southeast Environmental Research Center and Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

<sup>e</sup>University of California, Department of Integrative Biology, 3060 VLSB, Berkeley, CA 94720, USA

Received 28 February 2007; received in revised form 7 December 2007; accepted 20 December 2007

Available online 15 January 2008

## Abstract

Mangroves have a global distribution within coastal tropical and subtropical climates, and have even expanded to some temperate locales. Where they do occur, mangroves provide a plethora of goods and services, ranging from coastal protection from storms and erosion to direct income for human societies. The mangrove literature has become rather voluminous, prompting many subdisciplines within a field that earlier in the 20th century received little focus. Much of this research has become diffuse by sheer numbers, requiring detailed syntheses to make research results widely available to resource managers. In this review, we take an inclusive approach in focusing on eco-physiological and growth constraints to the establishment and early development of mangrove seedlings in the intertidal zone. This is a critical life stage for mangroves, i.e., the period between dispersal and recruitment to the sapling stage. We begin with some of the research that has set the precedent for seedling-level eco-physiological research in mangroves, and then we focus on recent advances (circa. 1995 to present) in our understanding of temperature, carbon dioxide, salinity, light, nutrient, flooding, and specific biotic influences on seedling survival and growth. As such, we take a new approach in describing seedling response to global factors (e.g., temperature) along with site-specific factors (e.g., salinity). All variables will strongly influence the future of seedling dynamics in ways perhaps not yet documented in mature forests. Furthermore, understanding how different mangrove species can respond to global factors and regional influences is useful for diagnosing observed mortality within mangrove wetlands, managed or natural. This review provides an updated eco-physiological knowledge base for future research and reforestation activity, and for understanding important links among climate change, local physico-chemical condition, and establishment and early growth of mangrove seedlings.

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**Keywords:** Biotic effect; CO<sub>2</sub>; Ecophysiology; Flooding; Global climate change; Growth; Light; Nutrient; Salinity; Sea-level rise; Temperature

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\* Corresponding author. Tel.: +1 337 266 8882; fax: +1 337 266 8586.

E-mail address: [kkrauss@usgs.gov](mailto:kkrauss@usgs.gov) (K.W. Krauss).

<sup>1</sup> Present address: Ecology and Environment, Inc., 1665 Palm Beach Lakes Boulevard, Suite 500, West Palm Beach, FL 33401, USA.

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## 1. Introduction

Globally, mangroves are generally undervalued, over-exploited, and poorly managed (Ewel et al., 1998a). Yet, their importance to humans, wildlife, and global carbon balance is paramount (Walters et al., 2008; Nagelkerken et al., 2008; Kristensen et al., 2008). Human activities have destroyed 35% of the world's mangrove forests over the last two decades (Valiela et al., 2001), and mangrove conservation and sustainable use as a zone of critical transition between land and sea needs to be better appreciated (Ewel et al., 2001; Saenger, 2002). Such human impacts and global change have prompted worldwide scientific interest in understanding the ecology and eco-physiological requirements of mangrove establishment, persistence, growth, and development (Robertson and Alongi, 1992; Kathiresan and Bingham, 2001; Saenger, 2002). The literature is vast, so an updated review of experimental studies may be the only effective way for coastal managers to understand how mangrove seedlings respond eco-physiologically to the many natural, anthropogenic, and global-change-induced factors worldwide.

In this review, we focus on eco-physiological and growth constraints to the establishment and early development of mangrove seedlings. We thus describe a critical life stage for mangroves. Our focus generally assumes that reproductive propagules have escaped losses from pre-dispersal herbivory and dispersal, and that once a seedling becomes rooted, survives, and develops to the sapling stage (approx. 1 m tall), that it has successfully established. We begin with some of the past research that has set the precedent for seedling-level, eco-physiological theory in mangroves that is not specifically addressed in subsequent sections, and then we focus on recent advances (circa. 1995) in our understanding of how temperature, carbon dioxide (CO<sub>2</sub>), salinity, light, nutrients, flooding, and specific biotic entities affect early seedling establishment, growth, and eco-physiological proficiency.

## 2. Eco-physiological paradigms

Explaining potential eco-physiological responses of mangroves to salinity, flooding, and light were important

contributions of past reviews (Ball, 1986, 1988a, 1998; Smith et al., 1989; Popp et al., 1993). In fact, many hypotheses have developed directly from those reviews and are still being tested by contemporary science programs. For this reason, we begin this review by summarizing five central paradigms that will not be discussed specifically in subsequent sections, but that are often used to interpret experimental results of studies on mangrove seedlings during establishment and early developmental phases.

### 2.1. *The lack of a functional understory in many mangrove forests*

The mangrove forest floor is often covered with seedlings and saplings of overstory species; however, there is a notable lack of herbaceous, shrub, and vine species in many forests. Chapman (1976) and Janzen (1985) made official note of this phenomenon and were puzzled that mangrove trees evolved to persist in the intertidal zone along multiple taxonomic lineages, yet herbs, shrubs, and vines had not. Janzen (1985) suggested that the most probable reason for this might simply be that plants were not able to garner enough carbohydrates from photosynthesis while being shaded to meet the metabolic demands of reproduction in saline soils.

Lugo (1986) argued that a functional understory does exist in high rainfall mangroves, and cited Chapman (1976) who listed many species of vines, herbs, ferns, and palms that occur in landward edge mangrove forests. These species begin to appear when soil salinity decreases. Lugo also suggested a modification of Janzen's ideas to include other stressors such as hydrogen sulfide, low oxygen, and low nutrients, which might be as important as light. Generally, however, Janzen (1985) and Lugo (1986) both agreed that the combination of stressors is prohibitive to reproduction in the mangrove understory.

Corlett (1986) suggested that tidal flooding, not salt, caused some freshwater forested wetlands at similar latitudes to lack an understory. Finally, Snedaker and Lahmann (1988) agreed with Lugo (1986) in suggesting that some factor other than salinity and light must be responsible, but that where the understory did exist along a landward edge, for example, circumstances were atypical. This discussion ends with the notion that “the intertidal environment has largely precluded the evolution of: (1) intertidal-halophytic adaptations in shade-tolerant terrestrial or freshwater aquatic species, (2) true shade-tolerance in intertidal halophytes, or (3) both characteristics in shade-intolerant plants” (p. 313, Snedaker and Lahmann, 1988).

### 2.2. *Inundation classifications*

Much of the literature on establishment and early development of mangroves have either ignored the effects of tidal flooding within laboratory settings or have failed to quantify tidal inundation in the field. However, Watson (1928) defined the importance of tidal flooding in mangroves many years prior to most experimental investigations. In a general sense, inundation classes were useful for describing the distribution patterns of 17 mangrove species in Malaysia. Classifications

included forests with inundation by all high tides, inundation by medium high tides, inundation by normal high tides, inundation by spring tides, and occasional inundation by exceptional or equinoctial tides (Watson, 1928). Different species of mangroves tended to grow among distinctive zones, and although these zones have characteristic hydroperiods, many mangrove species are capable of colonizing a range of inundation frequencies. What was important, however, was that segregation by flood state did occur naturally.

Chapman later applied this classification to south Florida mangroves where species diversity is considerably lower (Chapman, 1976). There, *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus* tended to transgress the continuum from inundation by spring tides to inundation by exceptional events in that respective order (Chapman, 1976). Explanations for these distributional patterns, or “zonation”, have since developed into a hypothesis rich debate, but many proposed factors are intricately linked to the depth, duration, and frequency of tidal flooding inherent to Watson's classifications.

### 2.3. *Salinity tolerance, zonation, and biomass allocation*

Interrelatedness of tidal flooding with salinity, fertility, and soil saturation influences zonation in mangroves on a site-specific basis (Ball, 1988a). Indeed, mangrove forests often segregate as distinctive bands of species (Saenger et al., 1977). From an eco-physiological perspective, species may overlap considerably in their range of tolerances to environmental factors, flooding or otherwise (Ball, 1988a).

Ball (1988a) described this overlap by first making the observation that mangrove species vary widely in their abilities to cope with salinity and rarely partition within a narrow functional niche. Because the mangrove environment is so dynamic, natural selection has affected extensions in the ranges of species tolerance as opposed to fine-tuning this response (Ball, 1988a). What is left in many mangrove environments are species with slower growth rates under a wide range of conditions, thus maximizing coexistence under moderate stress levels (Fig. 1).

Zonation theory in mangroves has a rich experimental history (Smith, 1992; but see Ellison et al., 2000), and includes hypotheses ranging from tidal sorting (Rabinowitz, 1978a,b; but see Sousa et al., 2007) to differential predation by crabs (Smith, 1987a,b,c; and more recently Sousa and Mitchell, 1999; Allen et al., 2003; Dahdouh-Guebas et al., 2002, 2004, among others). Ball (1988a), however, focuses on the evolutionary tolerance of established seedlings, saplings, and trees, which serves to explain many situations where zonation does appear.

### 2.4. *Interrelatedness of nutrient enrichment, growth, and herbivory*

Slow growth is often characteristic of plants in resource-limited environments as a potential tradeoff to anti-herbivore defense (Chapin et al., 1987). Small trees in stunted *R. mangle* forests on Caribbean islands and elsewhere have characteristics

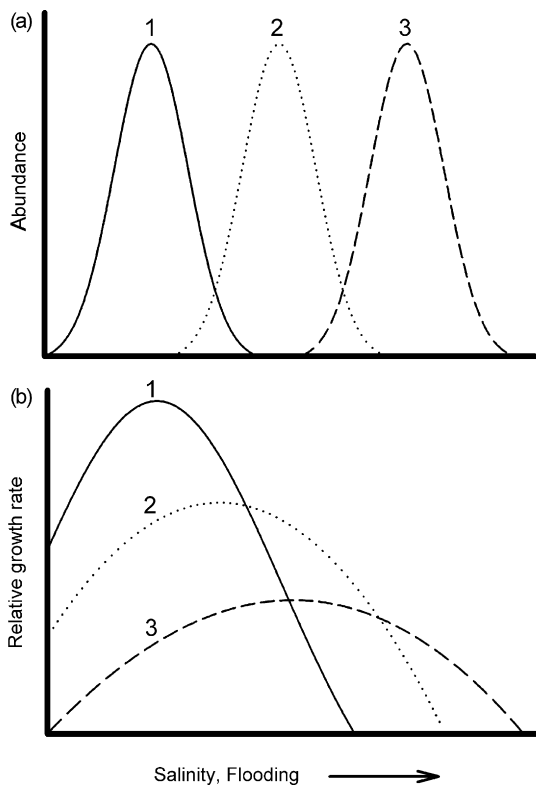


Fig. 1. Hypothetical response of three co-occurring mangrove species varying in salinity and flood tolerance (after Ball, 1988a). The top graph (a) depicts relative species abundance at a particular salinity or flood regime, while the bottom graph (b) indicates idealized ranges of physiological growth optima for species 1, 2, and 3 at specific salinity or flood regimes.

associated with resource limitation, including a small stature and sclerophyllous leaves. However, these sites, and many others globally, have additional stress gradients to consider. How, for example, does herbivory affect the host plant's condition along different nutrient, flood, and salinity gradients, and how are rates of herbivory affected by the host plant's condition?

A comprehensive, manipulative field experiment was designed in resource-limited settings to address these questions (Feller, 1995). Feller (1995) fertilized stunted trees with NPK, P, or N along a water depth and tidal elevation gradient and tracked many growth variables over two years. Growth was enhanced greatly by NPK and P fertilization, but was unaffected by N fertilization relative to controls for nearly all variables. Fertilization also enhanced the activity of specialist insects that feed on apical buds or bore into the stem, but had no effect on generalist folivores. Accordingly, leaf sclerophylly was found to be a strategy for coping with nutrient limitation in these environments rather than for herbivore defense. Fertilization of trees with NPK and P actually stimulated the production of less sclerophyllous leaves that were not nearly as tough as N-fertilized and control leaves after only 2 years (Feller, 1995).

Phosphorus has been described as a limiting nutrient controlling growth and productivity of many mangrove systems (Koch and Snedaker, 1997; Sherman et al., 1998; Chen and Twilley, 1999). Tradeoffs to herbivory may also be similar in

other mangrove forests worldwide, with the activities of specialist herbivores increasing proportional to site fertility and the activities of generalist folivores remaining constant at all canopy levels (Feller, 1995).

## 2.5. Geomorphological classification

Mangrove scientists have often been limited in their abilities to make comparisons among the incredible variety of geologic settings, hydrological fluxes, and geographical locations for which mangrove field studies are conducted. For south Florida, Lugo and Snedaker (1974) developed a common metric based upon the premise that geophysical processes and landscape position dictate the basic patterns of forest structure (Twilley, 1998), and proposed to separate mangroves into overwash islands, fringe, riverine, basin, hammock, and scrub forests. These ecological types differ predictably by soil type, salinity, and hydroperiod (Odum et al., 1982), and have been used to partition the functional description of many mangrove forests throughout the world.

However, there was a need to split these designations further in order to be more inclusive of global mangrove settings for which a more comprehensive ecogeomorphological classification scheme was needed (Woodroffe, 1992; Twilley et al., 1998). For this, segregation is first made by geomorphic type as delta, lagoon, delta/lagoon, or estuary mangroves based upon the degree of terrigenous input and position of the mangrove forest relative to this input (Fig. 2). The classification scheme predicts that forcing functions will act differentially based upon geomorphology and will lead to discrepancies in total energy

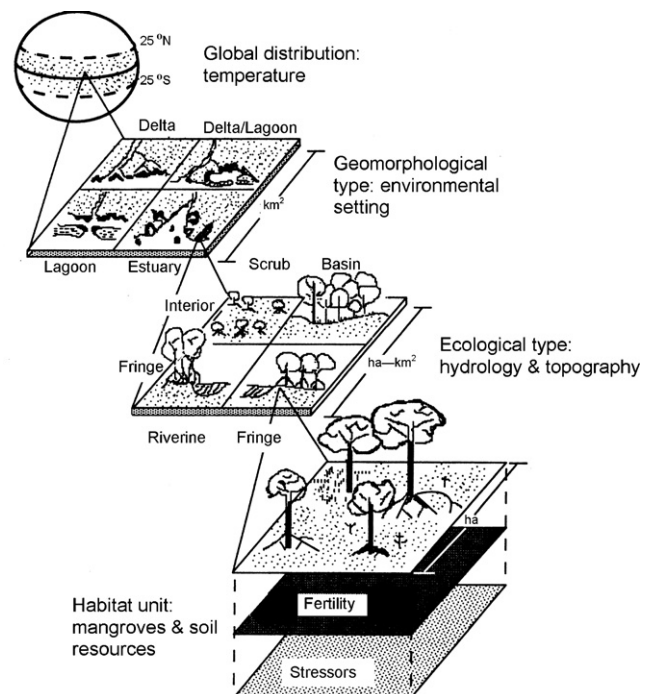


Fig. 2. Hierarchical classification system (ecogeomorphology) for use among different mangrove ecosystems worldwide, whereby function is based upon geomorphological development, ecological factors, site fertility, salinity gradients, and flood regimes (after Twilley et al., 1998).



flow potential for the specific mangrove location (Twilley, 1995). For example, this would explain why a fringe forest on a Micronesian island may respond differently to sea-level rise than a fringe forest in Panama even though latitudes may be similar. Ecological classifications (sensu Lugo and Snedaker, 1974) and a description of soil resources and stress gradients are then superimposed upon geomorphological setting to produce an overall classification scheme robust to the many conditions of mangrove forests globally (Fig. 2). The potential for mangrove seedling establishment and early development, hence, is similar within a given site ecogeomorphological class.

### 3. Temperature

Temperature is a major factor that varies greatly within forests, between forest types, and geographically across the distributional range of mangrove vegetation, and can therefore have tremendous impact on seedling establishment. Mangroves may encounter either high or low temperature extremes, although most work has emphasized the latter.

#### 3.1. Temperature extremes

Low temperature is widely regarded as the primary control on the latitudinal limits of mangroves globally (Lugo and Zucca, 1977; Tomlinson, 1986; Duke et al., 1998). Mangrove vegetation is essentially tropical and its distribution is constrained by sensitivity to freezing temperatures (Norman et al., 1984; Sherrod and McMillan, 1985; McMillan and Sherrod, 1986; Sherrod et al., 1986; Schaeffer-Novelli et al., 1990; Kao et al., 2004; Stevens et al., 2006; Stuart et al., 2007). The distributional limits of mangroves generally coincide with the 20 °C winter isotherm of seawater (Duke et al., 1998). Northernmost populations occur at ~32°N latitude (Bermuda, Japan) and southernmost populations occur at ~37–38°S latitude (Australia and New Zealand).

Reviews of physiological effects of chilling and freezing temperatures on plants (Larcher, 2001) provide a background for understanding effects on mangrove establishment and early development. In increasing order of impact to plants, low temperatures may: (1) increase the rigidity of biomembranes and increase the energy required for activating biochemical reactions, (2) cause chilling injury (as a consequence of lesions in biomembranes and interruption of energy supply to cells), or (3) freeze plant tissues, leading to vascular embolism, dehydration, or cellular rupture. The threshold temperature range for tropical trees (leaf tissue) is +5 to –2 °C.

Differential temperature sensitivity can be seen in mangroves. For example, *A. germinans* is widely regarded to be less sensitive to chilling temperatures than *R. mangle* (McMillan and Sherrod, 1986; Sherrod et al., 1986). Propagules of *R. mangle* that establish naturally or are planted in southern Texas cannot survive winter freezes, whereas *A. germinans* can (Sherrod et al., 1986). *Avicennia* spp. are typically found at the extreme latitudinal limits of mangrove distribution, e.g., *A. germinans* in North America (~32°N) (Sherrod and McMillan, 1985) and *A. marina* in Australia and New Zealand (~37°S

(Sakai and Wardle, 1978; Duke et al., 1998). Other work shows an exponential decrease in the numbers of mangrove species with decreasing air temperatures in northeastern Asia (Hsueh and Lee, 2000).

#### 3.2. Cold tolerance

Among the earliest studies to document freeze effects on mangroves was an investigation carried out at Seahorse Key, Florida (USA) on the Gulf of Mexico (29°08'N) (Lugo and Zucca, 1977). Inventories of frost damage to mature *A. germinans* were conducted following a record freeze (–2.7 °C), but also provided some qualitative observations for seedlings. Those seedlings growing in open areas were more negatively affected by frost than those growing intermixed with salt marsh, with the exception of mangroves that were taller than the salt marsh canopy. Also, seedlings growing under the mangrove canopy appeared to be unaffected.

Differences in cold tolerance among species are hypothesized to explain the more restricted distributions of *R. mangle* and *L. racemosa* in the Gulf of Mexico compared to *A. germinans* (Sherrod and McMillan, 1985). Early field and laboratory experiments support this hypothesis with respect to *R. mangle*. Seedlings transplanted from northern Florida to South Padre Island and Rio Grande, Texas (USA) could not survive sub-freezing temperatures at these locations (Sherrod et al., 1986). Field observations of *A. germinans* in Texas, Louisiana, and Florida indicated that this species can survive temperatures as low as –4 °C, but mature trees suffer near-total mortality at temperatures below –6.7 °C (Stevens et al., 2006). In New Zealand, *A. marina* (woody shoots) was unable to survive temperatures to –3 °C (Sakai and Wardle, 1978).

Other work focused on within-species variation in chilling sensitivity of mangroves (Markley et al., 1982; Norman et al., 1984; McMillan and Sherrod, 1986; Sherrod et al., 1986). Rooting of *A. germinans* from the coast of Texas was examined in the greenhouse over a range of temperatures, and seedlings at or below 15 °C failed to root (McMillan, 1971). Propagules and rooted seedlings of *A. germinans*, *R. mangle*, and *L. racemosa* collected over a latitudinal range from 17°45'N to 27°50'N were subjected to chilling temperatures (2–4 °C for 3–6 days) in the laboratory (Markley et al., 1982). Chilling tolerance of all three species appeared to vary with latitude, with material of more tropical origin showing greater sensitivity to low temperature. Seedlings and older specimens of *R. mangle* from more northern latitudes exhibited less physiological dysfunction (Sherrod et al., 1986).

The results of several chilling experiments (Markley et al., 1982; McMillan and Sherrod, 1986; Sherrod et al., 1986) were combined and analyzed statistically to determine if chilling sensitivity of propagules or seedlings of *A. germinans*, *L. racemosa*, and *R. mangle* varied significantly with latitude of the source material. Percent mortality of propagules and percent of rooted seedlings exhibiting leaf injury increased with decreasing latitude of source material, but the pattern did not differ among species (no species by latitude interaction ( $P > 0.05$ )) (Fig. 3). However, mortality of propagules differed

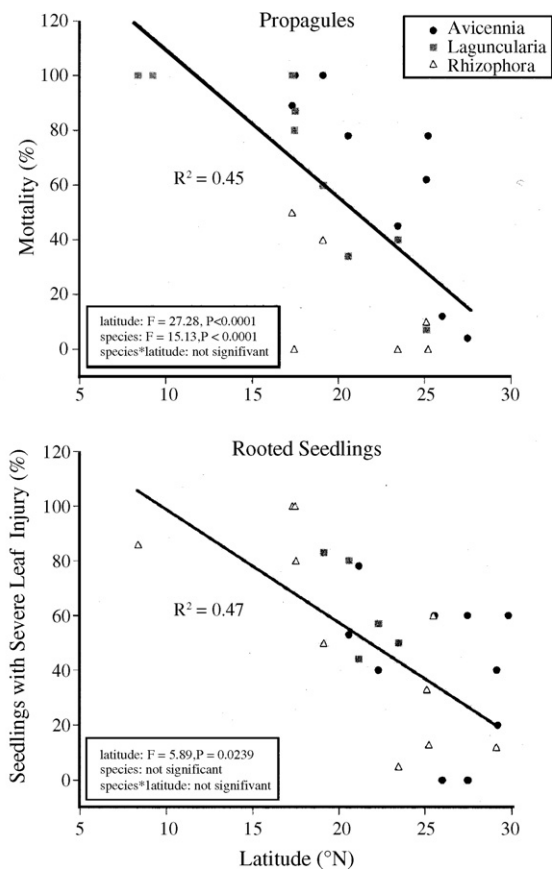


Fig. 3. Effects of mangrove species and geographic source on propagule mortality (upper panel) and percentage of rooted seedlings with severe leaf injury (lower panel) after exposure to chilling temperatures (2–4 °C for 5–6 days). Data from Markley et al. (1982), McMillan and Sherrod (1986), and Sherrod et al. (1986).

significantly among species, averaged across latitude: *A. germinans* (67%), *L. racemosa* (68%), and *R. mangle* (17%). These results indicate differences with latitudinal source, but cannot distinguish whether this variation is due to phenotypic plasticity or to genetic differences among mangrove populations.

### 3.3. Heat tolerance

Although less well studied, high temperatures can greatly influence the survival and growth of mangrove seedlings. Solar radiation varies spatially across mangrove forests, e.g., with degree of canopy development or disturbance frequency and severity. Incident light affects soil and water temperatures, which may greatly increase plant respiration or cause direct damage to sensitive tissues. High temperatures may cause one or more effects, including (1) limit physiological processes through enzyme denaturation or membrane damage, or (2) cause death of tissues or the whole plant, reducing its competitive vigor or eliminating it from a particular niche. Some symptoms of high-temperature injury are (1) chlorotic mottling of leaves, fruits, etc., (2) appearance of necrotic lesions, particularly on stems and hypocotyls (part of seedling below attachment of cotyledons), and (3) death. Plant organs usually suffer heat damage at temperatures between 40 and

55 °C. Heat sensitivity is also correlated with the stage of growth, i.e., actively growing tissues (meristems) or seedlings are more susceptible to heat than mature tissues.

In general, plants avoid heat damage by several mechanisms, which are observed in mangroves: heliotropism (reorientation of leaves to minimize interception of incident radiation) (Ball et al., 1988), increased reflectance properties of the leaf to decrease leaf temperature (e.g., hairs on abaxial leaf surfaces of *A. germinans* or the “silver” variety of *C. erectus*), dissipation of heat by evaporative cooling during transpiration, and establishment in cool habitats (shade, water). Plant tissues may experience high temperatures, but exhibit protoplasmic tolerance, which is genetically determined and varies among plant species (Larcher, 2001).

Rooting of *A. germinans* seedlings from coastal Texas was inhibited at 37 °C, whereas 10-min exposures to 43 °C were not lethal (McMillan, 1971). Forty-eight-hour exposures to 39–40 °C caused death and decay of rooted seedlings (prior to epicotyl expansion), but the same treatment did not damage seedlings with shoots and leaves (McMillan, 1971). One study found that root respiration rates of *R. mangle*, *A. germinans*, and *L. racemosa* seedlings increased linearly with temperature (20–45 °C), and their respective  $Q_{10}$  values differed significantly over the temperature range of 20–30 °C (1.5, 1.7, and 2.7), but were similar at 30–40 °C (1.3, 1.5, and 1.5) (McKee, 1996). Data indicated a major change in root metabolism or membrane integrity near 30 °C for all three species, and it was clear that small changes in soil temperature could have a potentially large effect on relative growth of mangrove seedlings.

### 3.4. Synthesis of temperature studies

Detailed information about temperature effects on early growth and physiology of mangroves is essentially lacking, and this information gap will greatly limit predictions of future effects of climate change on mangroves and interactions with subtropical and temperate vegetation. Temperature extremes are important in determining distributional limits of mangroves, but the physiological mechanisms responsible for reduced growth and mortality are not fully understood. Future work should endeavor to elucidate these mechanisms and to identify temperature thresholds for important species. Most work has emphasized low temperature stress, but high temperature extremes may be important, especially in arid habitats and in disturbed areas. Limited work suggests interspecific differences in temperature tolerance, but few mechanisms (e.g., biochemical components, xylem vessel anatomy, root respiration) have been examined experimentally. Similarly, population variation in low temperature sensitivity has been reported for a few mangrove species, but further work is needed to confirm ecotypic differentiation in these and other species. Finally, no work has examined interaction of temperature with other important growth-limiting factors such as flooding, salinity, nutrients, or CO<sub>2</sub>. Information about multi-stress interactions is necessary to make accurate predictions of mangrove seedling response to temperature.

## 4. Atmospheric CO<sub>2</sub> concentration

### 4.1. Photosynthesis and growth

Concentrations of atmospheric CO<sub>2</sub> have increased from 280 parts per million (ppm) in pre-industrial times to over 380 ppm today and are predicted to double over the next 50 years (IPCC, 2001). CO<sub>2</sub> enrichment may alter primary productivity of mangrove ecosystems due to enhanced net photosynthesis and photosynthetic water use efficiency (PWUE: carbon gain per unit of water lost) within certain ranges (Bazzaz, 1990; Urban, 2003). Studies have revealed increases in net photosynthetic rates with increases in CO<sub>2</sub> concentrations between 200 and 600 ppm with eventual saturation at concentrations of about 1000 ppm.

In addition to direct effects on assimilation rates, CO<sub>2</sub> concentrations also influence stomatal regulation of water loss. Under elevated CO<sub>2</sub>, many species reduce their stomatal aperture and increase their PWUE. Response to CO<sub>2</sub>, however, is further controlled by other growth-limiting factors such as nutrient availability and occurrence of stress factors such as salinity and flooding. The more nutrients are supplied to seedlings, the greater the absolute response to CO<sub>2</sub> enrichment. However, elevated CO<sub>2</sub> often reduces seedling demand for resources such as nutrients and water, so that relative growth responses to deficient conditions may be greater under elevated CO<sub>2</sub>.

Another consideration relevant to early growth of mangroves is that the potential response to CO<sub>2</sub> is very dependent upon the activity of carbon sinks (growing tissues) and presence of carbon reserves (e.g., in cotyledons). A final consideration is that CO<sub>2</sub> enrichment typically alters leaf tissue quality, i.e., increases the concentration of nonstructural carbohydrates while decreasing tissue nitrogen (Poorter et al., 1997). This effect may result from several possible mechanisms, but the potential consequences for mangrove seedlings is to alter susceptibility to (1) photoinhibition (e.g., changes in photo-protective compounds, but see Section 6, below), and (2) herbivores (e.g., changes in tissue palatability).

### 4.2. Specific studies on mangroves

Thousands of articles describing plant species responses to elevated CO<sub>2</sub> have been published over the last decade, but only a handful have targeted mangrove species (Ball and Munns, 1992; Farnsworth et al., 1996; Ball et al., 1997; Snedaker and Araujo, 1998). All of the published work on CO<sub>2</sub> effects on mangroves have been conducted on isolated plants in greenhouse experiments or were based on short-term exposures to CO<sub>2</sub> (e.g., Snedaker and Araujo, 1998), both of which may overestimate potential growth responses and provides no information on how CO<sub>2</sub> may alter competition with other species or susceptibility to herbivores (e.g., through changes in tissue chemistry).

One species, *R. mangle*, was grown in ambient (350 μl L<sup>-1</sup>, or ppm) and elevated (700 μl L<sup>-1</sup>) atmospheric CO<sub>2</sub> concentrations for over 1 year in replicate greenhouses (Farnsworth

et al., 1996). CO<sub>2</sub> enrichment significantly increased biomass, total stem length, branching, and total leaf area. Enhanced biomass under elevated CO<sub>2</sub> was attributed to higher relative growth rates and higher net assimilation rates. Photosynthesis rates were initially increased under elevated CO<sub>2</sub>, but later declined and were not different from controls. Elevated CO<sub>2</sub> treatment also accelerated development of aerial prop roots and reproductive buds and increased foliar C:N ratios.

In another study, two Australian mangroves, *Rhizophora apiculata* and *R. stylosa* (3-month-old seedlings) were grown individually for 14 weeks in a multi-factorial experiment of salinity (25 and 75‰ seawater), humidity (43 and 85% relative humidity), and atmospheric CO<sub>2</sub> concentration (340 and 700 μl L<sup>-1</sup>) (Ball et al., 1997). CO<sub>2</sub> had little effect on these species at higher salinity levels, but enhanced growth rates at low salinity, particularly in the less salt tolerant and faster-growing species (*R. apiculata*). Enhanced growth under elevated CO<sub>2</sub> was attributed to increased net assimilation rate as well as to increased leaf area ratio (under lower humidity) and improved PWUE. Farnsworth et al. (1996) also found that net photosynthesis of *R. mangle* grown at ambient CO<sub>2</sub> increased 22% when transferred to higher CO<sub>2</sub>, and measured values were significantly higher than rates in plants grown and measured at elevated CO<sub>2</sub> concentrations.

More recently, the CO<sub>2</sub> response of black mangrove (*A. germinans*) growing alone and in mixture with a C<sub>4</sub> grass (*Spartina alterniflora*) has been investigated in an 18-month greenhouse study (McKee, 2006). This experiment used native sods of marsh in mesocosms (19 L containers) maintained at two nitrogen levels, targeting streamside and inland porewater concentrations of NH<sub>4</sub>-N (0.5 and 10 mol m<sup>-3</sup>) and two atmospheric CO<sub>2</sub> concentrations (365 and 720 μl L<sup>-1</sup>) in replicate greenhouses. *A. germinans* responded to CO<sub>2</sub> enrichment with increased growth and biomass when grown alone, especially at higher nitrogen. However, seedling growth was severely suppressed when grown in mixture with *S. alterniflora*, and CO<sub>2</sub> and nitrogen enrichment could not reverse this effect.

### 4.3. Synthesis of CO<sub>2</sub> studies

Some important points can be made regarding potential effects of CO<sub>2</sub> on mangrove seedlings. First, the majority of experiments with other plant species indicate a huge range of potential growth enhancement for plants (Saxe et al., 1998). Given the taxonomic diversity of mangroves, there will likely be variable response to increases in atmospheric CO<sub>2</sub> due to inherent characteristics. The four species examined so far show a growth response to instantaneous and long-term exposure to elevated CO<sub>2</sub> ranging from -27 to 71% of ambient controls (Table 1). Second, elevated CO<sub>2</sub> can stimulate early growth of mangroves when grown in isolation under relatively optimal conditions. However, competition from other species may limit or prevent mangrove seedling response to CO<sub>2</sub> (McKee, 2006). This observation is consistent with other work showing that CO<sub>2</sub> response of plants grown in isolation is not predictive of future changes in vegetation (Poorter and Navas, 2003). Third,

Table 1  
Summary of mangrove growth responses to elevated CO<sub>2</sub>; responses (biomass, net primary productivity (NPP<sup>a</sup>) or relative growth rate (RGR)) given as a percent of controls grown under ambient CO<sub>2</sub>

Species <sup>b</sup>	CO <sub>2</sub> Treatment		Other factors	Response		Citation
	Level	Duration		Type	% Change from control	
RHMA	700	408 Days	–	Biomass	+40	Farnsworth et al. (1996)
RHMA	700	408 Days	–	RGR	+21	Farnsworth et al. (1996)
RHMA	361–485	Instantaneous <sup>c</sup>	–	NPP	–14	Snedaker and Araujo (1998)
RHAP	700	14 Weeks	High humidity	RGR	+36	Ball et al. (1997)
RHAP	700	14 Weeks	Low humidity	RGR	+71	Ball et al. (1997)
RHST	700	14 Weeks	High humidity	RGR	+40	Ball et al. (1997)
RHST	700	14 Weeks	Low humidity	RGR	+25	Ball et al. (1997)
AVGE	720	18 Months	Low nitrogen	Biomass	+18	McKee (2006)
AVGE	720	18 Months	High nitrogen	Biomass	+35	McKee (2006)
AVGE	361–485	Instantaneous <sup>c</sup>	–	NPP	–12	Snedaker and Araujo (1998)
LARA	361–485	Instantaneous <sup>c</sup>	–	NPP	–27	Snedaker and Araujo (1998)
COER	361–485	Instantaneous <sup>c</sup>	–	NPP	–8	Snedaker and Araujo (1998)

<sup>a</sup> NPP, g CO<sub>2</sub> m<sup>-2</sup> min<sup>-1</sup>.

<sup>b</sup> AVGE, *Avicennia germinans*; COER, *Conocarpus erectus*; LARA, *Laguncularia racemosa*; RHAP, *Rhizophora apiculata*; RHMA, *Rhizophora mangle*; RHST, *Rhizophora stylosa*.

<sup>c</sup> Plant leaves were exposed to higher CO<sub>2</sub> concentrations only during the measurement (10–30 s).

mangrove response to elevated CO<sub>2</sub> during early growth may be delayed due to the presence of maternal reserves or other phenological factors (Farnsworth et al., 1996). Experiments must be of a sufficient duration (e.g., >1 year) to assess the potential to respond to CO<sub>2</sub>. Fourth, the CO<sub>2</sub> response will generally depend on other growth-limiting factors such as salinity and nutrient availability. Thus far, it appears that mangroves growing under conditions of lower salinity and higher nutrient availability will show the greatest response to rising CO<sub>2</sub>. Such settings occur at the transition between mangrove and other lowland tropical vegetation (Clark and Guppy, 1988; Lovelock et al., 2005); areas influenced by groundwater (Semenuk, 1983; Mazda et al., 1990; Ovalle et al., 1990; Whelan et al., 2005) or high rainfall (Ewel et al., 1998b); and areas impacted by nutrient loading due to agricultural or urban activities (Valiela et al., 2001). Fifth, predictions that stress tolerance or competitive ability will be enhanced under elevated CO<sub>2</sub> are not supported by the work conducted thus far. Finally, CO<sub>2</sub>-induced changes in tissue chemistry have been observed and may have consequences for susceptibility to photoinhibition (protective secondary compounds) or to herbivory (tissue palatability).

## 5. Salinity

Salinity is one of the most important drivers in mangrove establishment and early development (e.g., Ball, 2002). Most mangroves are facultative halophytes (i.e., they grow better in some salt but do not necessarily require it for growth), and studies have demonstrated that optimal growth rates occur in 5–75% seawater concentrations (Burchett et al., 1984, 1989; Naidoo, 1987; Hutchings and Saenger, 1987; Ball, 1988a; Smith and Snedaker, 1995), depending on species and seedling growth stage. Mangroves can grow in a range of salinities, extending from primarily freshwater environments into

hypersaline areas (Chapman, 1976). All mangrove forests are exposed to some salinity, be it at daily, monthly, seasonal, or extreme tidal events (Watson, 1928). Accordingly, propagules have to be tolerant of a wide range of environmental conditions as most mangroves are passively dispersed via tides (Rabinowitz, 1978a,b; Hogarth, 1999). Inherent physiological and ecological tolerances influence not only plant physiognomy, but also interspecific and intraspecific competitive abilities.

### 5.1. Specific salinity effects and coping mechanisms

The ocean is approximately 35 parts per thousand (ppt) salt, depending on the degree of tidal exchange, freshwater input, and evaporation. This salt is 86% NaCl (483 mM Na<sup>+</sup>, 558 mM Cl<sup>-</sup>). Mangroves, therefore, have to maintain continuous water uptake, and regulate ion uptake and compartmentation against a strong external salt gradient (Ball, 1996). To maintain water uptake, mangroves not only have to restrict water loss by having conservative morphological and physiological adaptations, but also they need to maintain sufficiently low water potentials. Agricultural crops under well-saturated conditions generally have water potentials of approximately –1.0 MPa. However, as the osmotic potential of seawater is approximately –2.5 MPa (Sperry et al., 1988), mangrove leaf water potentials have to range between –2.5 and –6.0 MPa (e.g., Scholander et al., 1966; Medina et al., 1995; Aziz and Khan, 2001; Sobrado and Ewe, 2006).

Maintaining low water potentials is achieved by passively accumulating and synthesizing both organic and inorganic molecules for osmotic adjustment. Mangroves accumulate inorganic ions such as sodium (Na<sup>+</sup>) and potassium (K<sup>+</sup>) (e.g., Sobrado, 2005; Naidoo, 2006; Sobrado and Ewe, 2006) as well as organic compounds (proline, glycinebetaine, mannitols, cyclitols, quaternary ammonium compounds) for osmotic regulation (Popp et al., 1984; Popp and Polania, 1989; Popp,



1995). Ions are accumulated in the vacuole while in non-vacuolar regions (i.e., cytoplasm, intercellular spaces), organic compounds are used in regulating salinity because mangrove enzymes and metabolic processes are just as sensitive to salts as those in non-halophytes (e.g., Flowers et al., 1977; Ball and Anderson, 1986; Larcher, 2001; Lüttge, 1997). Various researchers (e.g., Medina and Francisco, 1997; Paliyavuth et al., 2004; Sobrado, 2005; Sobrado and Ewe, 2006) have demonstrated that leaf and xylem sap osmolality increase with higher soil salinity.

In addition to accumulating osmotica, mangroves also exclude and secrete salts, and increase succulence as a means of maintaining ionic balance within the plant (Popp, 1995). Mangroves exclude uptake of at least 90% of the external salt (Scholander et al., 1962, 1966) in a physical process (Scholander, 1968; Werner and Stelzer, 1990) that occurs via the symplastic pathway at the tips of 3–4th order roots (Moon et al., 1986); this can lead to the salinization of the soil around the roots (Passioura et al., 1992). Consequently, mangrove water uptake rates and concurrent salt exclusion at the roots have to be balanced by the flushing rates of the surrounding soil by tides and rainfall.

All mangrove species have a range of salt-coping mechanisms. Some mangrove genera have salt excretion glands (e.g., *Avicennia* spp., *Sonneratia* spp., *L. racemosa*) while others accommodate salt in the shoots by increasing succulence (e.g., *Ceriops tagal*, *Xylocarpus* spp., *Osbornia* spp.) (e.g., Smith et al., 1989; Hogarth, 1999; Sobrado and Greaves, 2000; Suarez and Sobrado, 2000; Aziz and Khan, 2001). Salt excretion is an energy-dependent process that moves ions against large electrochemical potentials within the leaves (Lüttge, 1997). Consequently, salt-excreting mangroves have higher metabolic and nutritional demands than non-salt-excreting species, a tradeoff against higher growth rates at lower salinity conditions (Ball, 1996). In addition, salts are also translocated among the leaves to allow excess ion removal with leaf senescence (Cram et al., 2002). For example,  $K^+$  is retranslocated from older leaves to younger leaves, resulting in increasing  $Na^+/K^+$  ratios in senescing leaves (Werner and Stelzer, 1990; Cram et al., 2002; Wang et al., 2003).

### 5.2. Influence of salinity on propagule establishment

Ungar (1982) observed that the early seedling stage was likely the most sensitive life stage in halophytes. In a laboratory study, McMillan (1971) observed that *A. germinans* propagules were able to produce roots in salt contents ranging from 0 to 57 ppt but only 10% of propagules in 75 ppt were able to root. Leaf emergence rates for two subspecies of *Ceriop tagal* decreased with increasing salinity and mortality was greatest at 60 ppt (Smith, 1988). At salinity >25 ppt, seeds of *Acanthus ilicifolius* failed to germinate (Ye et al., 2005).

Propagules prematurely abscised from the parent plant and newly emergent seedlings are prone to desiccation if they fail to strand or root properly (Ewe, unpublished data). Although most mangrove propagules can tolerate a wide range of salinities, the persistence and exposure to physical and

physiological desiccation increases with temperature and increased salinity.

### 5.3. Influence of salinity on propagule/seedling development

The optimal range of physiological function and growth of seedlings is approximately from 3 to 27 ppt (e.g., Field, 1984; Hutchings and Saenger, 1987; Ball and Pidsley, 1995; Aziz and Khan, 2001) although salinity optima have been shown to vary with seedling age (Hutchings and Saenger, 1987). Above or below the optimal salinity, gas exchange and growth are reduced (e.g., Ball and Farquhar, 1984; Ball, 1988a; Ball et al., 1997; Tuffers et al., 2001; Munns, 2002; Krauss and Allen, 2003a; Biber, 2006).

Photosynthesis of mangroves, like that of many vascular woody plants, on average ranges between 5 and 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (e.g., von Caemmerer and Farquhar, 1981; Andrews et al., 1984; Clough and Sim, 1989; Naidoo et al., 2002). Under favorable conditions of low salinity, the rate of photosynthesis can exceed 25  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Clough and Sim, 1989). At higher salinities, gas exchange becomes restricted by both stomatal and non-stomatal (i.e., biochemical) limitations in many halophytes (e.g., Flowers and Yeo, 1986; Kozlowski, 1997; Munns, 2002).

When freshwater is limiting (i.e., physiological drought) mangroves have to be more restrictive with water loss. Stomatal restrictions reduce photosynthesis and transpiration rates and increase PWUE (Ball and Farquhar, 1984; Clough and Sim, 1989; Lin and Sternberg, 1992; Sobrado and Ball, 1999; Sobrado, 2005). Mangroves exhibit conservative water use patterns relative to other woody vascular plants as increased water use efficiency is an effective mechanism at maintaining metabolic function in highly saline environments (Clough, 1992; Sobrado, 2000, 2001). Transpiration is decoupled from salt exclusion at the roots, since salt flux to the leaves does not increase with higher transpiration (Ball, 1988a). Instead, stomatal constraints restrict water loss under conditions of limited water availability. In what is known as the desiccation–starvation dilemma (Lüttge, 1997), plant  $\text{CO}_2$  uptake for growth occurs simultaneously with transpirational water loss via the stomates. Consequently, to grow, mangroves have to allow for some degree of water loss. The observed patterns of growth in mangroves may have developed as strategies to avoid vascular embolisms and excess salt accumulation around the roots (Ball and Passioura, 1994).

At high salinities, the non-stomatal limitations to gas exchange are purportedly the result of biochemical damage to a leaf's Photosystem II: chronic exposure to salinity can lead to the collapse of plant biochemical function, cell damage, and ultimately plant death (Flowers and Yeo, 1986). However, studies of *Avicennia marina* and *A. germinans* have not demonstrated these biochemical impairments. Instead, reduced net carbon assimilation at 60 ppt was a function of higher PWUE coupled with greater photorespiration (Sobrado and Ball, 1999); similar observation was also found in *R. mangle* by López-Hoffman et al. (2006).

Growth responses of congeneric (e.g., Ball and Pidsley, 1995) and sympatric (e.g., Cardona-Olarte et al., 2006) mangrove seedlings have been shown to differ across a range of salinities and with salinity fluxes. Increasing salt tolerance, however, is at the expense of higher nutritional demands and lower maximal growth rates at low salinities (Ball, 1988a, 1996). Exposure to a constant salinity level might even be less physiologically demanding on a seedling than fluctuating salinity levels. For example, Lin and Sternberg (1992) showed that growth and leaf gas exchange rates of *R. mangle* were lower under fluctuating salinities compared to constant salinities. Prolonged high salinity exposure may result in restricted growth due to water uptake limitations: leaves become small and thick (e.g., Camilleri and Ribí, 1983; Medina and Francisco, 1997; Sobrado, 2001) and plants have less leaf area than those growing at lower salinity (Naidoo, 2006).

## 6. Light

Salinity limits water uptake in mangroves (Scholander, 1968; Clough, 1984) and causes decreased photosynthetic rates (Ball and Farquhar, 1984; Ball et al., 1987; Clough and Sim, 1989; Sobrado, 1999), but it is also important to note that conservative water use and low photosynthetic rates have consequences for mangrove light relations. First, the mangrove environment predisposes mangroves to the potential for photoinhibition (Björkman et al., 1988). Second, there are interactive effects between salinity and light; the mangrove light response depends on the salinity level of the growth environment (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a).

### 6.1. Photoinhibition

The saline environment and the potential for high radiation levels in tropical latitudes make avoiding photoinhibition a particular challenge for mangroves (Björkman et al., 1988). Accordingly, mangroves almost universally experience low stomatal conductances, high PWUE, and low light-saturated rates of photosynthesis (Farquhar et al., 1982; Ball and Farquhar, 1984; Krauss et al., 2006a). These strategies necessitate that mangroves protect proteins associated with photochemistry (especially Photosystem II, Osmond, 1994), as energy associated with the narrowest wavelengths of light are absorbed in excess by chlorophyll. Photoinhibition occurs when low photosynthetic rates combined with high radiation loads lead to an excess of excitation energy – more light is absorbed than can be used in photosynthesis. Typically, mangrove photosynthetic rates saturate at 40% irradiance or less (Ball and Critchley, 1982; Cheeseman, 1991), suggesting that irradiance may often be excessive.

However, mangroves have an uncanny capacity for avoiding photoinhibition (Cheeseman, 1991; Fig. 4). Yet, mangroves fluoresce light commensurate with higher rates of O<sub>2</sub> evolution from photosynthesis. Mechanistically, aside from some pre-filtering of ultraviolet radiation with phenolic compounds (Lovell et al., 1992), photosystem quenching of absorbed

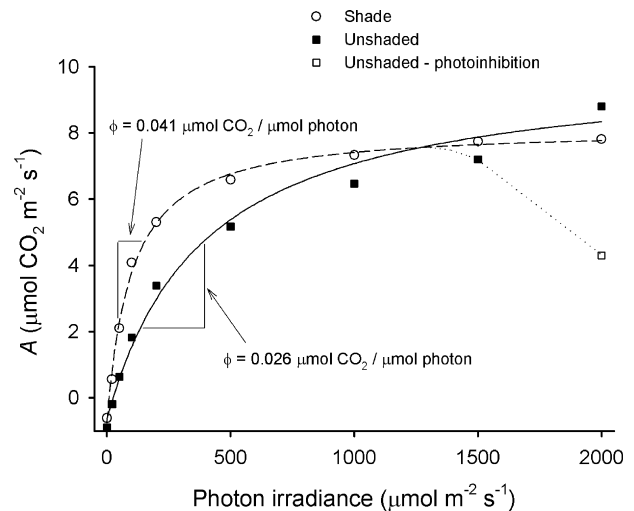


Fig. 4. Photosynthetic assimilation ( $A$ ) of *Rhizophora mangle* leaves grown while shaded ( $\circ$ ) versus unshaded ( $\blacksquare$ ) in a greenhouse in Hawaii. Quantum yield ( $\phi$ ) was higher in shade-grown leaves indicating a greater efficiency of energy conversion relative to unshaded leaves (as per Björkman et al., 1988). Shaded seedlings did not differ from unshaded seedlings in overall photosynthetic potential (Krauss and Allen, 2003a). Mangroves are unique in that they do not readily exhibit photoinhibition, as might occur according to the hypothetical curve drawn here ( $\square$ ).

light might be attained at least in part by absorbing photochemically derived electrons with excessive oxygen production from the physical processes of light capture (Cheeseman et al., 1997). Mangroves can also alter rate constants affecting the capacity for heat dissipation between photosystems through antenna complexes (Björkman et al., 1988). Important recent studies suggest that the combination of mechanisms used to avoid photoinhibition differs between species (Christian, 2005). For example, Lovell and Clough (1992) determined that *Rhizophora* spp. rely more on vertical leaf-angles, while *Bruguiera* spp., which have horizontally displayed leaves, are protected by larger xanthophyll pigment pools.

Because stomatal conductance and photosynthetic rates decrease with an increase in salinity, it might be expected that photoprotective responses should increase with salinity. Indeed, in an early laboratory study, Björkman et al. (1988) observed an increase in photoprotection in *R. stylosa* and *A. marina* with an increase in salinity from 10 to 100% seawater. However, a more recent field study with *A. marina* revealed no differences in photoprotection between 100 and 200% seawater treatments, possibly due to photorespiratory electron consumption (Sobrado and Ball, 1999). Further research is needed to understand photoinhibition and photoprotection in response to increased salinity (see also Christian, 2005), and changes in atmospheric CO<sub>2</sub> (see Section 4, above).

### 6.2. Interactive effects of light and salinity

In mangroves, conservative leaf-level water use and low photosynthetic rates result in reduced carbon gain at high salinity (Ball, 1988b). This pattern suggests that the negative effects of salinity on leaf-level carbon gain should be greater at

higher light levels, because at high light, photosynthesis is limited by conductance (Lambers et al., 1998). Several recent studies have shown that the combination of high light and high salinity may be most limiting to mangrove carbon gain and growth (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a).

In greenhouse experiments, seedling carbon gain increased more with an increase in light at low salinity than at high salinity, 20 and 167% seawater, respectively (López-Hoffman et al., 2006, 2007a). At high salinity relative to low salinity, stomatal conductance, leaf transpiration, and internal CO<sub>2</sub> concentrations were lower, and the ratio of leaf respiration to assimilation was much greater. Thus, stomatal limitations and increased respiratory costs may explain why at high salinity, seedlings are unable to respond to increased light levels with increased carbon gain (López-Hoffman et al., 2007a).

Consistent with the leaf-level, at the whole plant level, mangrove seedling mass and growth rate increase more with an increase in irradiance at low than high salinity (Ball, 2002). In addition, interactive effects of salinity and light have been observed in seedling biomass allocation patterns (López-Hoffman et al., 2007a). Mangrove seedlings at low salinity exhibit the typical plant response to increased irradiance: increased root mass and decreased leaf mass (Bouwer, 1962). However, at high salinity when seedlings already have a high root mass and root/leaf ratio, they did not further allocate to roots in response to increased light (López-Hoffman et al., 2007a).

Species differences in mangrove responses to the interactive effects of light and salinity may explain important differences in forest structure. In a study of Hawaiian mangroves, it was determined that the highly invasive, *R. mangle*, performs better under high light, high salinity conditions than the less invasive *Bruguiera sexangula*. This may explain why in moderate and high salinity zones, *R. mangle* is the canopy dominant and *B. sexangula* occurs only in the understory (Krauss and Allen, 2003a).

### 6.3. Interactive effects of light and nutrients

At lower nutrient and light levels, mangrove seedlings invest more in allocation to roots than to leaves. At higher nutrient levels, more biomass is allocated to leaves (McKee, 1995). As light increases, increased root mass at the expense of leaves is associated with greater requirements for water and nutrients (van den Boogaard et al., 1996). Furthermore, species differences to light and nutrients were more pronounced at high nutrient and light combinations (McKee, 1995).

### 6.4. The importance of light gap dynamics

The importance of canopy gaps for mangrove forest dynamics and regeneration have been investigated (Smith et al., 1994; Ewel et al., 1998c; Feller and McKee, 1999; Sherman et al., 2000; Duke, 2001; Clarke, 2004). Numerous studies have examined the effects of canopy gaps on mangrove seedling establishment and growth (Putz and Chan, 1986;

Smith, 1987c; Ellison and Farnsworth, 1993; McKee, 1995; McGuinness, 1997; Osunkoya and Creese, 1997; Sousa et al., 2003a). Some studies report higher seedling establishment and growth in gaps (e.g., Putz and Chan, 1986). Others report similar seedling establishment and survival rates in gaps and non-gaps, but higher seedling growth rates, and higher sapling densities in gaps (e.g., Clarke and Allaway, 1993; Clarke and Kerrigan, 2000). All of these studies discuss seedling light response and conclude that light gaps are important for mangrove forest dynamics. However, successful seedling colonization and initial growth may be followed by differential survivorship and progression to the juvenile stage within light gaps (López-Hoffman et al., 2007b).

Several studies have attempted to address the influence of canopy gaps by assessing juvenile densities as well as seedling growth (Clarke and Allaway, 1993; Clarke and Kerrigan, 2000; Whelan, 2005). One outcome of this work is a reconsideration of the gap dependence of *R. mangle*, historically considered a shade-tolerant species (Ball, 1980). The observation that *R. mangle* seedlings can establish at all light levels and that juvenile density is higher in gaps (Smith et al., 1994; Sousa et al., 2003b; Whelan, 2005), suggests that *R. mangle* may be dependent on gaps for regeneration (Whelan, 2005). This observation is supported by individual-based model simulations of mangrove population dynamics which indicate that *R. mangle* is dependent on light gap disturbances (Chen and Twilley, 1998; Berger and Hildenbrandt, 2000; Berger et al., 2006, 2008; López-Hoffman et al., 2007b).

More demographic studies are needed on the role of gaps in mangrove life histories and population dynamics. Furthermore, given the interactive effects of salinity and light on mangrove seedling performance (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a) and the influence that gaps have on soil characteristics (Ewel et al., 1998c), it will be important to compare the role of light gaps in low and high salinity mangrove forests.

## 7. Nutrients

In almost all plant communities nutrient availability is an important driving variable influencing community structure (Grime, 1979; Chapin, 1980; Tilman, 1987). This is also the case for mangrove forests (e.g., Onuf et al., 1977; Boto and Wellington, 1983; Lovelock and Feller, 2003). Mangroves occupy soils with a wide range of nutrient availability. Many mangrove environments have extremely low nutrient availability due to infertility of upland soils in tropical regions and limited terrigenous input (e.g., Lovelock et al., 2005). For example, on oceanic islands in the Caribbean where the peat soil substrate is comprised of mangrove roots, newly initiated roots colonize earlier root channels, mining for extremely low levels of nutrients (McKee, 2001).

Most mangrove species that have been studied have been found to be highly sensitive to variation in nutrient availability both in the laboratory (e.g., Boto et al., 1985; Naidoo, 1987; McKee, 1996; Yates et al., 2002) and in the field (e.g., Boto and Wellington, 1983; Feller, 1995; Koch, 1997; Feller et al., 2003,



2007; Lovelock et al., 2005, 2007; Naidoo, 2006). In the Atlantic East Pacific biogeographic province the response of the three dominant species, *R. mangle*, *A. germinans* and *L. racemosa*, to nutrient availability has been considered in multiple studies, but in the Indo-West Pacific region few studies documenting the effects of nutrient availability on mangrove species performances have been published. This is a large knowledge gap, given most of the mangrove forests of the world are within this latter region, and that they are under intense pressure from development but are extremely important for the sustainability of coastlines and coastal populations (Valiela et al., 2001; Alongi, 2002; Dahdouh-Guebas et al., 2005; Walters et al., 2008).

Enhancements in nutrient availability have mostly led to faster growth rates which are associated with an increase in allocation to leaf area relative to roots, along with a suite of physiological changes that include increased hydraulic conductivity and photosynthetic rates, and decreased efficiencies in nutrient resorption and use (McKee, 1996; Lovelock et al., 2004, 2006a). The responses to enhancements in the level of limiting nutrients are similar in mangroves as those observed in other species (Chapin, 1980). However, in some settings where high salinity, extreme aridity, or shade limits growth, nutrient additions have not enhanced growth (McKee, 1995; Lovelock and Ewe, unpublished data). Responses to nutrient additions are thus dependent on environmental conditions and on the identity of the species. Below we outline the traits that favor persistence of seedlings at low and high nutrient availability, and we consider the tradeoffs among traits that become important as other environmental parameters vary.

Species differences in both tolerance of low nutrient environments, and competitive ability under high levels of nutrient availability are often reflected in field distribution. For example, *R. mangle* often dominates in low nutrient environments, while *A. germinans* is often dominant in areas with higher nutrient availability (Sherman et al., 1998; McKee, 1993). What are the key physiological traits for seedlings of species that lead to tolerance of low nutrient environments and conversely foster a competitive nature under high nutrient availability?

## 7.1. Seedling traits beneficial in low nutrient environments

### 7.1.1. High biomass allocation to roots relative to shoots

Enhanced allocation to root biomass relative to shoot biomass is a common adaptation to low nutrient availability. In particular, allocation to fine versus coarse root biomass can greatly increase the surface area for nutrient absorption, especially in microsites of higher nutrient availability (Blair and Perfecto, 2001; Hodge, 2004). Fine root biomass, as a proportion of total biomass is usually higher in *R. mangle* compared to *A. germinans* (McKee, 1995). Additionally fine roots of *R. mangle* decompose slowly compared to those of *A. germinans* thereby slowing nutrient release and loss (Middleton and McKee, 2001). In more diverse forests of Asia, Komiyama et al. (2000) found that variation in shoot/root ratios was large and varied among species (Table 2). A general pattern of higher

Table 2

Variation in shoot to root ratio in forests dominated by different mangrove genera

Mangrove genera	Shoot/root ratio
<i>Sonneratia</i>	5.25
<i>Bruguiera</i>	3.01–4.58
<i>Rhizophora</i>	1.71–2.66
<i>Cerriops</i>	1.05
Temperate forest	2.7–3.7
Tropical forest	5.1–10.7

Ratios for terrestrial, temperate, and tropical forests are given for comparison (from Komiyama et al., 2000)

allocation to roots compared to shoots in representatives of the Rhizophoraceae, indicate that species of this family are more tolerant of low nutrient conditions than those of other families.

### 7.1.2. High levels of maternal reserves

Many mangrove species have large propagules (Tomlinson, 1986). The reserves contained within them support growth for an extended period of time. Ball (2002) observed that for seven species of the Rhizophoraceae, those with the largest propagule mass were larger after 1 year of growth compared to those species with smaller mass, although propagule mass did not influence survival. Similar importance of propagule size on intraspecific seedling vigor was reported for *R. mangle* (Lin and Sternberg, 1995). The nutrient status of the maternal tree and the provisioning of propagules may thus have a large influence on early seedling growth.

### 7.1.3. High levels of nutrient resorption

Prior to tissue senescence a proportion of the nutrient capital invested in the tissue is resorbed in the phloem to be allocated to new tissue. Nutrient resorption can be highly efficient in *R. mangle*, reaching maximum values recorded for angiosperms of 85% of phosphorus resorbed prior to senescence of leaves (Feller, 1995). In tidal environments where surface litter may be washed away, the evolution of high resorption efficiency may be particularly important to tolerating low nutrient concentrations, particularly in seedlings. Resorption efficiency declines with increases in the level of available nutrients (Feller, 1995; Feller et al., 2002; McKee et al., 2002). Resorption efficiency varies among mangrove species and is generally lower in *A. germinans* than in *R. mangle* under the same conditions (Feller et al., 2007). This trend is consistent with other traits of these two species, where *A. germinans* has higher maximum growth rates and higher nutrient concentrations in leaf tissue compared to the more conservative *R. mangle*.

### 7.1.4. High nutrient use efficiency of photosynthesis and other processes

In mangroves, photosynthetic nutrient use efficiency (i.e., maximum photosynthetic rate per foliar nutrient content: Field and Mooney, 1986) is high under limiting nutrients and declines with increasing nutrient availability (e.g., Feller et al., 2003). At low nutrient availability, species differ in their nutrient use efficiency. The limited data suggest *Rhizophora* has higher



nutrient use efficiency than *Avicennia*, although this order can be altered under differing salinity regimes (Lin and Sternberg, 1992). Root respiration, per unit biomass, and thus possibly per unit nutrient absorbed, is also very low in mangroves (McKee, 1996) and particularly so in *R. mangle* (McKee, 1996; Lovelock et al., 2006b). The capacity of mangroves to tolerate and to utilize high levels of ammonium may also be an important process that reduces the cost of nitrogen uptake by reducing the activity of nitrate reductase (Turnbull et al., 1996; Britto et al., 2001).

#### 7.1.5. Schlerophylly and tissue quality

Schlerophylly, which varies in leaves among species (e.g., Ball, 1988b), has been suggested to be an important trait for nutrient conservation. Tough, thick, carbon-rich leaves, and presumably tough roots reduce herbivory and slow decomposition, leading to retention of nutrients within plants and soils (e.g., Feller, 1995; Middleton and McKee, 2001). Typically leaves and roots of species within the Rhizophoraceae have higher levels of schlerophylly and higher C:N ratios than those of the Avicenniaceae, Combretaceae, and other families (Table 3; Rao et al., 1994; McKee, 1995).

#### 7.1.6. Mutualisms and other strategies for increasing nutrient availability

Mangroves have been observed to have vesicular arbuscular mycorrhizal (VAM) associations at low salinity (<25 ppt: Sengupta and Chaudhuri, 2002), but growth benefits of these associations have yet to be determined. Highly anaerobic soils may also prevent exploration of the soil by symbiotic VAM fungi (Kothamasi et al., 2006). Mangrove roots are also associated with N-fixing microorganisms, which may enhance soil nutrient availability (Bashan and Holguin, 2002; Kothamasi et al., 2006). The exudation of extracellular enzymes by either plants or soil bacteria may also increase nutrient availability (Rojas et al., 2001) and facilitate nutrient acquisition in low nutrient environments. Other work using stable isotopic analyses suggests a facultative mutualism between *R. mangle* and encrusting epibionts growing on prop roots (Ellison et al., 1996). Values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  indicate that *R. mangle* growing along tidal creeks obtains inorganic nitrogen from sponges encrusting the prop roots submerged in tidal creeks and sponges obtain carbon from root exudates (Ellison et al., 1996). It is not known to what degree seedlings use similar strategies.

Table 3  
C:N ratio of mangrove species from Gazi Bay (data from Rao et al., 1994)

Mangrove genera	C:N ratio
<i>Rhizophora</i>	78 ± 9
<i>Bruguiera</i>	70 ± 9
<i>Ceriops</i>	69 ± 4
<i>Xylocarpus</i>	39 ± 7
<i>Lumnitzera</i>	39 ± 1
<i>Sonneratia</i>	34 ± 1
<i>Avicennia</i>	27 ± 5
<i>Heritiera</i>	24 ± 1

## 7.2. Seedling traits beneficial in high nutrient environments

### 7.2.1. Large allocation to leaf area, high net assimilation rates, and rapid growth

Under high nutrient availability, traits that confer enhanced growth rates and facilitate occupation of space, shading of competitors, and monopolization of nutrient resources lead to canopy dominance (Poorter and Nagel, 2000). High growth rates are correlated with a suite of traits including reduced investment in carbon based defenses and structural tissues. Leaves are thinner, tannin concentrations are lower, and wood is less dense in fast growing compared to slow growing seedlings (Chapin, 1991; McKee, 1995).

### 7.2.2. High PWUE

Under saline conditions, high growth rates are associated with high levels of water use during photosynthesis, which due to extraction of water for transpiration, salinizes the soil (Passioura et al., 1992). Salinization reduces the likelihood of the establishment of less salt tolerant competitors. Species of *Avicennia*, with their fast growth rates and capacity to withstand high salinity soils, may exclude other competitors in this way (Lovelock and Feller, 2003). Removal of the influence of adult roots enhanced growth of seedlings (Ball, 2002), which may reflect intense below ground competition or interference competition by salinization of soils. These are important traits for sustained dominance in the upper intertidal zone.

## 7.3. Tradeoffs and interactions with other factors

Many traits that lead to fast growth under high levels of nutrient availability are not favorable under conditions of environmental stress (Field et al., 1983; Chapin, 1991). Moreover, species differ in their capacity to withstand abiotic stress, and these differences lead to the complex situation where a species' capacity to acquire nutrients is moderated by the interaction between its inherent stress tolerance and the environmental setting in which it grows. For example, at a hypersaline site in Florida, growth of *A. germinans*, which is tolerant of high soil salinity, benefited from fertilizer additions, while *L. racemosa* showed lower growth enhancement with fertilization (Lovelock and Feller, 2003). At the leaf level, *L. racemosa* growth responses to fertilization were limited because this species had lower PWUE under saline field conditions than *A. germinans*. Low PWUE of *Laguncularia* gives rise to sensitivity to increasing salinity, where photosynthetic rates decline when salinity is high, resulting in reduced ability to utilize available nutrients. The differences in water and nutrient use efficiency among species may thus facilitate coexistence of *Laguncularia* and *Avicennia* under moderate salinity levels and low nutrient availability, while dominance of *Avicennia* would be predicted with hypersalinity and high nutrient levels, and dominance of *Laguncularia* predicted with low to moderate salinity and low nutrient availability.

Allocation of biomass to roots relative to shoots (Table 2) reduces growth rates and increases the potential for nutrient

acquisition. A significant proportion of fixed carbon in mangrove seedlings is lost through root respiration (PRR), and differences among *R. mangle* (20%), *A. germinans* (12%), and *L. racemosa* (8%) are inversely correlated with these species potential growth rates (McKee, 1995, 1996). Since the PRR partly reflects the proportion of biomass allocated to roots, an increase in root biomass to acquire limiting nutrients will also increase carbon loss to respiration and, consequently, overall growth. In addition to belowground roots, allocation of carbon to aboveground roots increases tolerance of anoxic soil conditions (McKee et al., 1988; McKee, 1996; Cardona-Olarte et al., 2006). Seedlings of species that can allocate high levels of carbon to aboveground roots (species within the family Rhizophoraceae) and also those that can modify their wood and bark anatomy (Yáñez-Espinosa et al., 2001), trade high growth rates for a strategy that ensures tolerance of, and dominance in, nutrient poor, low intertidal, and permanently flooded habitats (Cardona-Olarte et al., 2006).

## 8. Flooding and sea-level rise

### 8.1. Experimental studies on flooding

Flooding of mangrove communities can range naturally from seasonally tidal to near-permanent (Watson, 1928). Some mangroves respond to flooding by altering internal biochemical processes or by producing lenticels on basal stems or root structures to help offset the effects of lower soil oxygen levels (Tomlinson, 1986). During a flood event, oxygen concentrations in the soil can be reduced rapidly by as much as 28% after 6 h of flooding and as much as 72% after 20 h under experimental culture (Skelton and Allaway, 1996). Flooding alters soil condition so much that mangrove seedlings can respond as much to by-products imposed by flooding as to surface water alone (McKee, 1993; Youssef and Saenger, 1998). Lower oxygen partial pressures are reflected in root aerenchyma shortly after the onset of flooding (0.5–24 h) (McKee, 1996). Under flooding or experimental hypoxia, mangrove roots may metabolize anaerobically for short periods of time, allowing some energy production to continue (McKee and Mendelssohn, 1987; Chen et al., 2005). However, the most effective strategy is to avoid root hypoxia through internal aeration.

Differing soil oxygen states have been induced experimentally (Pezeshki et al., 1989). Anoxia alone can reduce photosynthesis by 39% for some mangrove seedlings relative to oxygen-rich controls (Pezeshki et al., 1997). However, stomatal conductance remained unaffected even though concentrations of root alcohol dehydrogenase (ADH) increased as soil oxygen concentrations decreased (Pezeshki et al., 1997). ADH, which is typically produced in roots as a catalyst to fermentation in response to flooding, can be stimulated in some species by lower root oxygen tensions (McKee and Mendelssohn, 1987), but the effects of ADH can be quite variable on leaf gas exchange in mangroves. For example, an increase in ADH activity in roots of *Kandelia candel* seedlings corresponded to reduced photosynthesis with prolonged flooding (Chen et al., 2005).

Leaf transpiration, photosynthesis, and growth of seedlings remained unaffected by experimentally induced hypoxia over 12 weeks; however, species differed in their abilities to maintain root aeration under these conditions (McKee, 1996). Current research suggests that mangrove seedlings can avoid flooding stress by maintaining high root oxygen concentrations (McKee, 1996) or by aerating the immediate rhizosphere (Thibodeau and Nickerson, 1986; McKee et al., 1988), which creates a buffer zone for oxidation of potentially toxic sulfide (McKee, 1993). The oxidized rhizosphere also may act as a boundary layer, minimizing the flux of oxygen from roots to the bulk soil, thereby conserving oxygen within the root system. The capacity for these two strategies may be juxtaposed in mangrove seedlings, since the ability to conserve oxygen promotes less oxygen diffusion to the soil adjacent to the roots (Youssef and Saenger, 1996).

There are a few studies that have established appropriate controls to address seedling responses to actual flood events (Table 4). In one of the earlier evaluations (Pezeshki et al., 1990), flooding of the soil surface with fresh water had no effect on leaf gas exchange or PWUE for three mangrove species over a 180-day period. Flooding did lead to a reduced leaf size in *L. racemosa* and *R. mangle*, and a reduced leaf dry weight in *A. germinans*. Flooding can create an overall reduced photosynthetic capacity and growth potential for seedlings by prompting a reallocation of leaf and whole-seedling biomass. This was evident for *R. mangle*, for example, where individual seedlings produced less total biomass while flooded (Pezeshki et al., 1990). Yet, evaluating flood effects alone in the absence of salinity is, in itself, problematic. Mangroves are facultative halophytes; maximum growth is realized under some optimal salinity concentration (see Section 5, above). In addition, flooding of seedlings by saltwater promotes a greater demand for osmotic adjustment than flooding by fresh water alone (Naidoo, 1985).

Field observations and experimental studies have established that many mangroves also grow best around optimum flood levels and durations (Fig. 1). Ellison and Farnsworth (1993), for example, found that growth and survival of *A. germinans* seedlings were compromised at intertidal positions indicative of either greater or lesser flooding from that of mean water level. *R. mangle* fared better at the deeper water levels and longer hydroperiods indicative of lower intertidal positions (Ellison and Farnsworth, 1993). Similarly, among neotropical mangroves *R. mangle* generally survives within the broadest range of flood durations (Koch, 1996; Cardona-Olarte et al., 2006; Krauss et al., 2006b). Other mangrove seedlings partition responses similarly. For example, the relative growth rates of *Bruguiera gymnorrhiza* decreased with duration of flooding, while *K. candel* experienced no such reductions by allocating less carbon belowground in response to flooding (Ye et al., 2003). Flooding also affected both stomatal conductance and leaf water potential for *B. gymnorrhiza* seedlings (Naidoo, 1983), while tidal flooding reduced seedling height, diameter, leaf area, leaf biomass, stem biomass, and root biomass for *B. gymnorrhiza* relative to saturated controls (Krauss and Allen, 2003b). Seedlings of *K. candel* had reduced photosynthetic

Table 4

Summary of experimental studies conducted on the effects of environmental drivers on mangrove establishment and development associated with flooding and sea-level rise

Species <sup>a</sup>	Geographic location of study system	Stressor	Variable <sup>b</sup>	Study type <sup>c</sup>	Growth form <sup>d</sup>	Experiment duration (days)	Source
AVGE, LARA, RHMA	Belize	Anoxia	g, p	G	sdl	84	McKee (1996)
AVGE, RHMA	Florida, USA	Anoxia	g, p	G	sdl	60	Pezeshki et al. (1997)
AECO, AVMA, BRGY, RHST	Australia	Anoxia	p	G	sdl	28	Youssef and Saenger (1998)
AVGE, RHMA	Belize	Flood depth	g	F	sdl	365	Ellison and Farnsworth (1993)
AVMA	Qatar	Flood depth	p	G	sdl	14	Sayed (1995)
AVOF, BRCY, CETA, RHAP, RHMU, SOAL, XYGR	Thailand	Flood depth	g	F	sdl	365	Kitaya et al. (2002)
BRGY	South Africa	Flood duration	p	G	sdl	80	Naidoo (1983)
AVMA, BRGY, RHMU	South Africa	Flood duration	g, p	G	sdl	60	Naidoo (1985)
RHMA	Florida, USA	Flood duration	g	F	tre	530	Lahmann (1988)
AVGE, LARA, RHMA	Florida, USA	Flood duration	g, m, p	G	sdl	180	Pezeshki et al. (1990)
BRGY, KACA	Hong Kong	Flood duration	g, p	G	sdl	84	Ye et al. (2003)
AVGE, LARA, RHMA	Florida, USA	Flood duration	g, m, p	G	sdl, sap	424	Krauss et al. (2006a,b)
LARA, RHMA	Florida, USA	Flood duration	g, m	G	sdl	276–367	Cardona-Olarte et al. (2006)
AVMA	South Africa	Short-term flood pulse	p	F	tre	5–10	Naidoo et al. (1997)
AVGE, LARA, RHMA	Florida, USA	Short-term flood pulse	p	G	sdl, sap	6–22	Krauss et al. (2006a)
AVGE, LARA, RHMA	Florida, USA	Short-term flood pulse	p	F	tre	1–2	Krauss et al. (2007)
KACA	China	Tidal flood duration	g, p	G	sdl	70	Chen et al. (2004, 2005)
BRGY	China	Tidal flood duration	m	G	sdl	70	Wang et al. (2007)
AECO, AVMA, BRGY, RHST	China	Tidal flooding	g	F	sdl	365	He et al. (2007)
BRGY	Micronesia	Tidal flooding	g	G, F	sdl	178, 349	Krauss and Allen (2003b)
XYGR	Micronesia	Tidal flooding	g	G	sdl	178	Allen et al. (2003)
LARA, RHMA	Florida, USA	Tidal flooding	g, m	G	sdl	276–367	Cardona-Olarte et al. (2006)
RHMA	Belize	Tidal sea-level rise	g, m, p	G	sdl, sap	823	Ellison and Farnsworth (1997)
BRGY, KACA	Hong Kong	Tidal sea-level rise	g, m, p	G	sdl	120	Ye et al. (2004)

<sup>a</sup> AECO, *Aegiceras corniculatum*; AVGE, *Avicennia germinans*; AVMA, *Avicennia marina*; AVOF, *Avicennia officinalis*; CETA, *Ceriops tagal*; BRCY, *Bruguiera cylindrica*; BRGY, *Bruguiera gymnorhiza*; KACA, *Kandelia candel*; LARA, *Laguncularia racemosa*; RHAP, *Rhizophora apiculata*; RHMA, *Rhizophora mangle*; RHMU, *Rhizophora mucronata*; RHST, *Rhizophora stylosa*; SOAL, *Sonneratia alba*; XYGR, *Xylocarpus granatum*.

<sup>b</sup> Growth (g), morphological (m), physiological (p).

<sup>c</sup> Greenhouse (G), field (F).

<sup>d</sup> Seedling (sdl), sapling (sap), tree (tre).

light saturation levels and photosynthesis with longer immersion periods (Chen et al., 2005). Oddly, tidal flooding enhanced biomass attributes for *Xylocarpus granatum* seedlings, even though this species typically occurs naturally under low flood frequencies and durations (Allen et al., 2003). It is apparent that specific characteristics of flooding are important on a species-specific basis, but in general, seedling physiological efficiency and growth potential are reduced with increased flood durations and depths beyond some optimum.

Plant age might also be important for how mangroves respond to flooding. Leaves of young *A. marina* trees (1–2 m tall) had similar photosynthetic rates and greater stomatal conductance while flooded with dilute seawater than when unflooded on field sites (Naidoo et al., 1997), and saplings of *R. mangle* had higher photosynthesis and PWUE while flooded versus drained on some field sites in south Florida (Krauss et al., 2006a). This pattern suggests that mangroves may become less sensitive to flooding either with prolonged (and previous) exposure or with plant age. These hypotheses were tested

experimentally by partitioning flood responses among seedling, sapling, and mature trees. First, seedlings (<1 m tall) and saplings (>1 m tall) were exposed to a range of flood durations experimentally over two growing seasons (Krauss et al., 2006a). No differences were registered among three neotropical mangrove species in dark respiration ( $R_d$ ), quantum yield, photosynthesis, light compensation point, light level required to attain 1/2 of maximum photosynthesis ( $K$ ), or PWUE for flood durations of 0, 189, or 424 days. However, short-term flooding of 6–22 days stimulated a 20% reduction in maximum photosynthesis, 51% lower  $K$ , and a 38% higher demand from  $R_d$  in both seedlings and saplings (Krauss et al., 2006a). Second, growth was generally maximized at moderate to permanent flood durations (Krauss et al., 2006b). Field studies, on the other hand, indicate that the interrelatedness of site hydroperiod and soil P concentrations control growth of mangroves more than hydroperiod alone under many conditions (Chen and Twilley, 1999; McKee et al., 2002; Krauss et al., 2006b). Third, short-term flooding did reduce sap flow in mature *R. mangle*, *A.*

*germinans*, and *L. racemosa* trees (Krauss et al., 2007) similarly to reductions registered for seedlings and saplings, and suggested that seedlings might actually provide a surrogate for rating environmental effects on mature trees. Overall, flooding appears to stall physiological processes associated with photosynthetic light initiation in seedlings and saplings, but recovery after prolonged exposure under some conditions is probable.

## 8.2. Sea-level rise

The overall persistence of mangrove ecosystems as global sea levels rise is ultimately controlled by shoreline geomorphology, sedimentation, and the actual rate of sea-level rise for a particular coastline (Woodroffe, 1990, 1999; Semeniuk, 1994; Gilman et al., 2008). Individual plant responses are also important, and have been the focus of a few recent experimental studies. One year old seedlings of *A. marina*, for example, were subjected to a prolonged high tide (14 days) associated with projected sea-level rise (Sayed, 1995). As expected, stomatal conductance declined rapidly (within 1 day) and leaf xylem water potentials also decreased. More importantly, the recovery of these functions was rapid once simulated high tides were removed.

In a 2½-year study, responses of tidally maintained *R. mangle* seedlings were compared under three relative tidal flood regimes simulating high (+16 cm), static, and low (−16 cm) sea levels (Ellison and Farnsworth, 1997). Seedlings maintained 1–7% fewer stomata per unit area, 6–21% greater photosynthetic rates, and 3–23% greater absolute relative growth rates in control treatments than for plants grown at low or high relative sea levels (Ellison and Farnsworth, 1997). Growth was also eventually reduced with increased levels of inundation, leading to the conclusion that any projected seedling or sapling growth benefit that may occur in response to a greater atmospheric supply of CO<sub>2</sub> with climate change might be offset by reduced growth of mangroves in response to longer hydroperiods and deeper flooding. Mangrove species from other locations have registered similar response; *K. candel* and *B. gymnorhiza* grew rapidly over the first 2 months after sea-level rise simulations of 30 cm but were not able to maintain this rate beyond the initial period (Ye et al., 2004). Mangrove seedlings are fairly consistent in allocating more relative biomass to aboveground structures with prolonged flooding, but the degree to which this strategy serves to benefit mangrove seedling establishment and growth with rising sea-levels, altered nutrient regimes, and physico-chemical shifts remain uncertain. It is clear that continued seedling recruitment and adequate growth under persistent sea-level rise would warrant mangrove colonization of new intertidal areas (Sayed, 1995).

## 9. Biotic influences on environmental drivers

While a mangrove's fundamental niche may be defined by the physiological responses of its seedlings to microclimatic and edaphic conditions, direct and indirect inter-

actions with other biota, especially crabs and insects, can play a large role in shaping a species' realized distribution, growth, and demography at early developmental stages. Other contributions to this special issue document the direct effects of consumers on mangrove recruitment and early growth, including the impacts of propagule predation by crabs and herbivory by leaf-feeding and stem-boring insects (Cannicci et al., 2008). Here, we examine: (1) how these plant-herbivore interactions may be mediated by local environmental conditions and (2) how modification of the soil physico-chemical environment by burrowing crabs can indirectly alter recruitment, establishment, and performance of mangrove seedlings.

### 9.1. Biota and local environmental conditions

The impact of arthropod consumers on the survival of mangrove propagules or seedlings has been demonstrated to vary with light/temperature conditions in several different systems. In an Australian forest on the northeast Queensland coast, Osborne and Smith (1990) found that rates of predation by crabs on tethered propagules of *A. marina* were higher in the understory than in adjacent canopy gaps, and declined with increasing light gap size. They attributed this pattern to a soil temperature-related shift in the distribution of crabs: herbivorous grapsid crabs, the most important propagule predators, were observed to be more abundant in the cooler microclimates of the understory and small gaps than in large gaps, where daytime soil temperatures are much higher. Working at another site in the same region of Australia, Clarke and Kerrigan (2002; see also Clarke, 2004) also measured lower rates of crab predation on tethered propagules in large light gaps than small ones or in the adjacent, shaded understory, and concluded that large gaps afford a refuge from crab predation for mangrove propagules. In contrast, a similar study on the Caribbean coast of Panama (Sousa and Mitchell, 1999) found no difference in crab predation rates between understory and gap environments and no relationship between canopy gap area and the rate of propagule predation by crabs. Daytime soil temperatures also increased with gap size at the latter site, but the crab species are different and may not respond in the same manner as Australian species to variation in conditions with gap size.

The effects of insect herbivores on seedling survival can also vary with light environment. Two independent studies, one on the Caribbean coast of Panama (Sousa et al., 2003b) and the other in the Florida Everglades (Devlin, 2004), have demonstrated that the stem-boring scolytid beetle, *Coccotrypes rhizophorae*, a specialist herbivore of *R. mangle*, causes much higher rates of seedling mortality in shaded understory environments than in light gaps. This predation prevents a layer of *R. mangle* saplings (i.e., advanced regeneration) from developing under a closed adult canopy; saplings of this species are largely restricted to light gaps and the areas immediately surrounding them. Why *R. mangle* seedlings are less vulnerable to beetle attack in gaps is not known. If female beetles disperse diurnally, they may avoid the high light intensity and



temperatures characteristic of light gap environments. Alternatively, seedlings that establish in or near light gaps may undergo morphological or chemical changes that defend them against beetle attack.

### 9.2. Biotic modifications to the physico-chemical environment

In addition to the direct effects of their predation on mangrove propagules, crabs have been shown to exert strong indirect effects on mangrove seedling establishment, growth and survival through their bioturbation of sediments during burrow construction and maintenance. This activity can produce mounds of excavated sediment, altering both the topography and particle size of the substrate surface. This mechanism of mound formation was confirmed by Warren and Underwood's (1986) experimental manipulation of the burrowing ocypodid crab, *Heloecius cordiformis*, in a mangrove forest near Sydney, New South Wales, Australia. When crabs were added to enclosed areas of flat substrate, their burrowing significantly increased the height of the substrate surface by as much as 55 mm over the 129-day trial, as compared to control areas from which crabs were excluded. The presence of crabs also reduced the proportion of fine sediments (silts and clays) and increased the proportion of coarse sediment particles in the top 5 mm of substratum.

Minchinton (2001) examined the consequences of this mounded topography for recruitment of the mangrove, *A. marina*, at another site near Sydney, Australia. His study forest was also inhabited by a dense population of *H. cordiformis*. Mounds of crab-excavated sediment covered up to 44% of the forest floor, and these mounds were larger and comprised a greater proportion of the substratum under a closed canopy than in disturbance-generated light gaps. Crabs appeared to be less abundant in light gaps, perhaps because the sunlit gap environment is more thermally stressful than that of the shaded understory; this difference in crab density may have accounted for the smaller number and size of mounds inside gaps. Propagules and recently established seedlings of *A. marina* were also more abundant under the canopy than in gaps, and on flat areas surrounding mounds than on the mounds themselves. The greater density of propagules and young-of-the-year seedlings under the forest canopy was probably due to highly localized dispersal of propagules from parent trees. Directional dispersal of propagules accounted for the topographic effect. When experimentally placed on mounds, most propagules dispersed off them, onto the surrounding flats. The disproportionate numbers of propagules that accumulated in flat areas resulted in a higher density of seedlings in these areas than on mounds, despite the fact that the few propagules that remained on mounds established as rooted seedlings more quickly and at a three-fold higher rate than those that dispersed to the flats. Nonetheless, the more rapid establishment of propagules on mounds and apparently better growth conditions resulted in the tallest seedlings and saplings being most abundant on mounds within gaps. Minchinton (2001) hypothesized that the coarser grained sediments and higher density of crab burrows on

mounds increase drainage, oxygenation and nutrient availability of these soils, creating better growth conditions for seedlings. Thus, the burrowing activity of crabs can have a marked indirect effect on spatial distribution of different age classes of juvenile mangroves across the forest floor.

An earlier study by Smith et al. (1991) in a *Rhizophora*-dominated mangrove forest in north Queensland, Australia provided strong evidence that changes in soil chemistry due to crab burrowing can benefit mangrove seedlings. When the density of burrowing grassid crabs was reduced by pitfall-trapping, concentrations of soil sulfide and ammonium increased significantly and stand productivity (estimated by stipule and propagule production) declined, compared to control plots. The changes in soil chemistry were attributed to a reduction in soil aeration as the density of crab burrows declined. While there is a critical need to replicate this study at other sites, it appears that crab burrowing and associated bioturbation of sediments can indirectly enhance mangrove forest productivity and seedling growth. Similarly, burrowing by fiddler crabs (*Uca* spp., Ocypodidae) has been shown to increase soil drainage and aeration, alter sediment chemistry, and increase aboveground plant productivity in temperate salt marshes where these crabs excavate extensive burrow systems (Montague, 1982; Bertness, 1985).

## 10. Conclusions

In this review, we took a comprehensive approach to describing the effects that multiple ecological factors may have on seedling ecophysiology and growth in mangroves. We discussed old ideas and new advances in our understanding of how salinity, light, nutrients, and flooding impact mangrove seedling establishment, and have indicated a principal research need for interactive studies. We have also explained how biota can affect the soil physico-chemical environment and influence seedling establishment indirectly. What is especially new to this review, however, is that we identified the importance of non-traditional factors – temperature, CO<sub>2</sub>, and sea-level rise – as important drivers not only to mangrove establishment on a global scale, but also to seedling growth and persistence on a local scale. Research should attempt to include these factors along with potentially more subservient site-specific factors of salinity, light, nutrients, and flooding in future evaluations.

The last two decades have witnessed the destruction of 35% of the earth's mangrove forests (Valiela et al., 2001). In order to ensure that specific mangrove locations will remain intact over the next two decades, seedling establishment in environments conducive to early development will need to be ensured. Our review underscores some of the critical global and local factors responsible for dictating seedling success in diverse intertidal locations.

## Acknowledgments

K.W.K. and K.L.M. were supported by the USGS Biological Resources Discipline Global Change Research Program, while the U.S. National Science Foundation (NSF) supported the

mangrove research of S.M.L.E. (DBI-0620409), L.L.H. (0409867), and W.P.S. (DEB-9221074, DEB-9615887, DEB-0108146, DEB-0613741).

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