Global Change and the Function and Distribution of Wetlands

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Beth A. Middleton
Editor

Global Change and the Function and Distribution of Wetlands

SWS

Editor
Beth A. Middleton
National Wetlands Research Center
US Geological Survey
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Contents

Response of Salt Marsh and Mangrove Wetlands to Changes in Atmospheric CO$_2$, Climate, and Sea Level

Karen McKee, Kerrylee Rogers, and Neil Saintilan

Abstract Coastal salt marsh and mangrove ecosystems are particularly vulnerable to changes in atmospheric CO$_2$ concentrations and associated climate and climate-induced changes. We provide a review of the literature detailing theoretical predictions and observed responses of coastal wetlands to a range of climate change stressors, including CO$_2$, temperature, rainfall, and sea-level rise. This review incorporates a discussion of key processes controlling responses in different settings and thresholds of resilience derived from experimental and observational studies. We specifically consider the potential and observed effects on salt marsh and mangrove vegetation of changes in (1) elevated [CO$_2$] on physiology, growth, and distribution; (2) temperature on distribution and diversity; (3) rainfall and salinity regimes on growth and competitive interactions; and (4) sea level on geomorphological, hydrological, and biological processes.

1 Introduction

Mangroves are the characteristic intertidal vegetation of sheltered tropical coastlines, and salt marshes dominate temperate coastal margins. Mangroves include a taxonomically diverse group of mostly trees and shrubs adapted to flooded,

K. McKee (✉)
U. S. Geological Survey, National Wetlands Research Center, Lafayette, LA, USA
e-mail: mckeek@usgs.gov

K. Rogers
School of Earth and Environmental Science, The University of Wollongong,
Wollongong, Australia
e-mail: kerrylee_rogers@uow.edu.au

N. Saintilan
Rivers and Wetlands Unit, Office of Environment and Heritage, Sydney, Australia
e-mail: neil.saintilan@environment@nsw.gov.au

saline conditions. Their sensitivity to cold temperatures limits their expansion into temperate latitudes (Fig. 1d). Salt marshes contain low-growing plants such as herbs, shrubs, and rushes, which are also adapted to tidal inundation, but are capable of surviving colder conditions, including periodic freezing. Salt marshes reach their greatest development on shorelines where mangrove establishment is precluded or development is limited (Kangas and Lugo 1990) in temperate, sub-arctic, and arctic zones (Mitsch and Gosselink 2000; Mendelssohn and McKee 2000). The distributions of these vegetation types often overlap at subtropical latitudes, forming an important ecotonal community in which global change effects may be studied (Fig. 1a–c).

Mangrove and salt marsh ecosystems provide a broad range of ecosystem services. In tropical locations, mangrove forests are an important forestry resource, and sustain the livelihoods and well-being of many human communities in developing countries (Saenger 2002). They can dampen wave energy protecting coastlines from recession (Alongi 2008). Both mangrove and salt marsh ecosystems are highly productive where tidal inundation is frequent, and provide

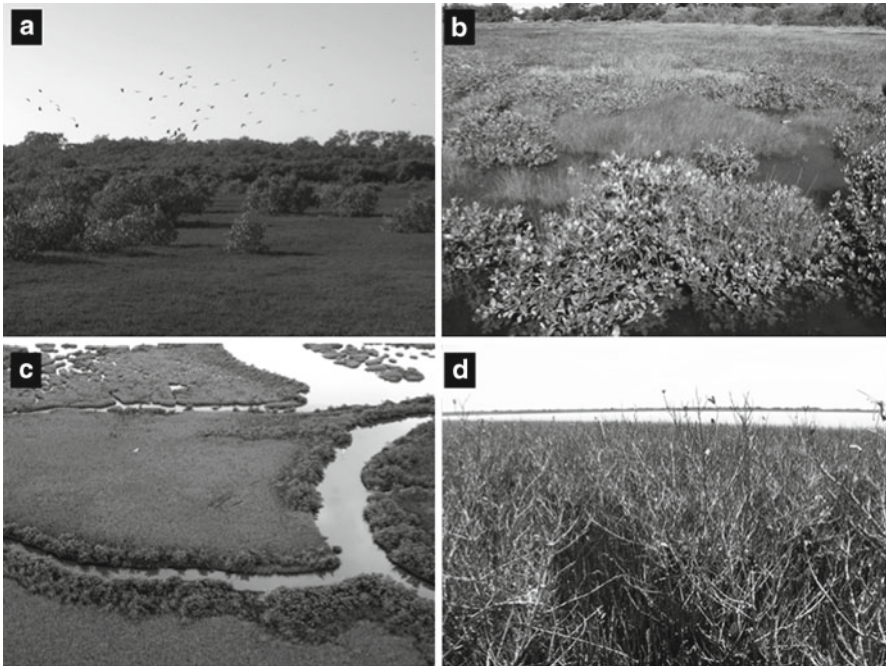**Fig. 1** Views of mangrove-salt marsh communities at subtropical latitudes. (**a**) *Avicennia marina* (grey mangrove) and *Sarcocornia* sp., southern Queensland, Australia, (**b**) *A. marina*, *Leptocarpus similis*, and *Juncus krausii*, Tauranga Harbour, New Zealand, (**c**) *A. germinans* (black mangrove) and *Spartina alterniflora* (smooth cordgrass), Louisiana, USA; (**d**) freeze-damaged *A. germinans* in Louisiana, USA

vital habitat to a range of crustaceans, molluscs, and fish, many of which are commercially important (Manson et al. 2005). There is also growing evidence that coastal wetlands are particularly effective at carbon sequestration, burying atmospheric carbon in belowground biomass where anaerobic conditions inhibit decay of organic matter (Chmura et al. 2003; Donato et al. 2011; McLeod et al. 2011).

There are several reasons why coastal wetlands are sentinels of climate change impacts in the coastal zone. Coastal mangrove and salt marsh communities are located within narrow elevation ranges, defined by the frequency of tidal inundation. There are sufficient paleo-environmental and historical observations to demonstrate widespread changes in the distribution of these communities with sea-level rise of the magnitude projected by climate change forecasts. Their location at the interface of land and sea also places them in the path of destructive winds and waves generated by extreme storm events, and hurricane impacts in mangrove forests can be extensive and long lasting.

Coastal mangrove and salt marsh species are also directly impacted by changes in atmospheric CO_2 concentrations, temperature, and rainfall. Inherent differences between mangrove and salt marsh species in sensitivity to cold and freezing temperatures will influence their relative responses to certain climate change events. Projected increases in temperature may alter the competitive interactions of mangrove and salt marsh in temperate regions where the two communities overlap, in some places profoundly changing the character of coastlines. Plant response to changes in rainfall and $[CO_2]$ will mediate these responses. Mangroves are predominately C3 species, which are most sensitive to changes in atmospheric $[CO_2]$, whereas salt marshes contain both C3 and C4 species, the latter being less responsive to changes in $[CO_2]$. Differential effects of higher $[CO_2]$ on mangroves and salt marshes will likely be mediated by other environmental conditions. The following sections consider how changes in these factors may influence mangrove and salt marsh vegetation.

2   Carbon Dioxide

Concentrations of atmospheric CO_2 have increased from 280 ppm in pre-industrial times to 390 ppm today and could double sometime during the twenty-first century (IPCC 2007). Independent, high-precision measurements conducted at several observation stations around the world all show that CO_2 and other greenhouse gases (methane, nitrous oxide) are increasing at rapid rates. Although the future concentrations of CO_2 are not certain and dependent on many factors, current models indicate that CO_2 will continue to rise even if all emissions cease today. As a "greenhouse gas", CO_2 contributes to global warming and associated changes in climate and sea level (Fig. 2). In addition to these impacts, CO_2 also has a direct fertilization effect on plants, which is the focus of this chapter

Fig. 2 Conceptual model of global change factors influencing coastal wetlands

section. A basic hypothesis is that higher $[CO_2]$ will promote higher abundance and/or spread of plant species that are responsive to CO_2 enrichment at the expense of less sensitive species. A change in the relative competitive ability of salt marsh or mangrove species may influence future range distributions at global, regional, and local scales. Consequently, information about species responses to elevated CO_2 (and interactions with other environmental factors) is essential to predicting future changes in marsh and mangrove distributions as well as changes in ecosystem function.

Many articles describing plant species responses to elevated CO_2 have been published (Long et al. 2004; Ghannoum et al. 2000; Urban 2003; Ainsworth and Long 2005, 2007; Bazzaz 1990). Much of the published work has been conducted (1) on isolated plants in greenhouse experiments, (2) in single-factor experiments without manipulation of other growth-limiting factors, and (3) with short-term exposures to elevated CO_2, all of which may overestimate potential growth responses and provide no information as to how CO_2 may alter competition with other species or response to other environmental changes. Most experiments have tested plant responses to CO_2 concentrations anticipated for the middle of this century (ca. 700–720 $\mu L\ L^{-1}$) in comparison with ambient conditions (ca. 350–390 $\mu L\ L^{-1}$) (1 $\mu L\ L^{-1}$ = 1 ppm). A number of studies have investigated plant responses under field conditions, in mixed plant assemblages, in multi-factorial experiments, or

to sub-ambient CO_2 concentrations. The reader is referred to synthesis or review articles such as those listed above for a broader overview of elevated CO_2 studies.

Relatively few studies have investigated CO_2 effects on marsh species, and only a handful has targeted mangrove species. The majority of these studies have been conducted in greenhouses or growth chambers, which have the advantage of close control of experimental conditions, treatment replication, and manipulation of interacting factors difficult or impossible to modify in the field. Fewer studies have been carried out under more natural conditions with mesocosms containing native soil and plants (McKee and Rooth 2008) or in the field (Drake et al. 1989). With these limitations in mind, we consider potential impacts of higher CO_2 concentrations on salt marshes and mangroves.

Higher CO_2 concentrations may alter growth rates of plant species due to enhanced net photosynthesis and water use efficiency (Urban 2003; Bazzaz 1990). Photosynthesis is stimulated because of enhanced carboxylation efficiency of Rubisco (ribulose-1, 5-bisphosphate carboxylase/oxygenase), the enzyme catalyzing the initial fixation of CO_2. Carboxylation efficiency of Rubisco depends on the partial pressure of CO_2 at the site of synthesis (the stroma of chloroplasts); as CO_2 concentrations increase, CO_2 assimilation rates increase. Eventually, CO_2 saturation occurs at concentrations of about 1,000 ppm. Species belonging to the C4 photosynthetic pathway exhibit a CO_2 concentrating mechanism at the site of assimilation and are typically less responsive to elevated CO_2 (in the range from 200 to 600 μL L^{-1}). A number of salt marsh grasses (e.g., *Spartina* spp.) exhibit C4 metabolism and would not likely respond to CO_2 enrichment with higher net assimilation rates. In contrast, C3 species, which lack this CO_2-concentrating mechanism, increase net photosynthetic rates over the same CO_2 concentration range. Mangroves are C3 species and are potentially responsive to CO_2 (Farnsworth et al. 1996; Ball et al. 1997; McKee and Rooth 2008; Ball and Munns 1992). A number of marsh species also belong to the C3 group and respond to elevated CO_2 treatment: *Scirpus maritimus* (Rozema et al. 1991), *Schoenoplectus americanus* (Cherry et al. 2009; Rasse et al. 2005), *Puccinellia maritima* (Gray and Mogg 2001; Rozema et al. 1991), *Elymus athericus* (Lenssen et al. 1993), and *Aster tripolium* (Lenssen et al. 1995).

Initial stimulation of photosynthesis and/or growth may fade with time (often referred to as CO_2 acclimation) due to (1) a decrease in other growth-limiting factors such as nutrients, light (self-shading), and water as plants grow larger, (2) feedback inhibition of photosynthesis by starch accumulation in chloroplasts, or (3) a natural decline in growth as plants age (Johnson et al. 1993; Poorter 1993). A common neotropical mangrove, *Rhizophora mangle*, exhibited initial increases in photosynthetic rate in response to elevated CO_2 (700 μL L^{-1}), but rates later declined to those of controls (350 μL L^{-1}) (Farnsworth et al. 1996). CO_2 enrichment still significantly increased biomass, total stem length, branching, and total leaf area of *R. mangle* and also accelerated the development of aerial roots and reproductive buds. Growth increase by a European salt marsh species, *Elymus athericus*, under elevated CO_2 (380 vs. 720 μL L^{-1}) declined after 71 days and was associated with a decrease in specific leaf area (Lenssen et al. 1993). In a field study, stimulation of net CO_2

exchange by a brackish marsh sedge (*S. americanus*) exposed for 17 years to elevated CO_2 rapidly dropped from 80% at the onset of the experiment to a long-term stimulation average of about 35% (Rasse et al. 2005). The biochemical mechanisms underlying the latter response included changes in Rubisco concentrations (or activation state) and carboxylation efficiency of the enzyme under elevated CO_2 (Jacob et al. 1995).

In addition to increased assimilation rates, higher CO_2 concentrations also influence plant water loss through stomata. Under elevated CO_2, many species reduce their stomatal aperture, decreasing water loss and increasing water use efficiency (i.e., carbon gain per unit of water lost). Since leaf expansion is driven by turgor, an improvement in water use efficiency can by itself lead to higher plant growth rates. For C3 plants common to saline habitats, improvement of water use efficiency can be especially advantageous. In a study of two Australian mangroves, seedlings of *Rhizophora apiculata* and *R. stylosa* were grown hydroponically for 14 weeks in a multi-factorial experiment: salinity (25% and 75% seawater), humidity (43% and 85% relative humidity), and atmospheric CO_2 concentration (340 and 700 μL L^{-1}) (Ball et al. 1997). Growth of both species was enhanced under elevated CO_2 due to increased net assimilation rate and improved water use efficiency as well as to increased leaf area ratio under low humidity. A study of two C3 salt marsh species, *A. tripolium* and *P. maritima*, found that elevated CO_2 stimulated net photosynthesis and decreased stomatal conductance (Lenssen et al. 1995). In a long-term field study, evapotranspiration of a *S. americanus* (C3 sedge) community was lowered 19% over 12 years exposure to elevated CO_2 (Li et al. 2010). In the latter study, ecosystem water use efficiency was increased 83% in both the C3 sedge and C4 grass communities under elevated CO_2.

Some C4 species may show enhanced growth under elevated CO_2 as a result of decreased water loss (Ghannoum et al. 2000). In a study of C3 and C4 grasses of Northern European marshes, elevated CO_2 increased growth of both *P. maritima* (C3) and *S. anglica* (C4) with the latter response occurring mainly belowground (Gray and Mogg 2001). Other work also found that C4 grasses responded to high CO_2 with improved water relations: *S. patens*, *S. anglica* (Rozema et al. 1991), *S. maritima* (Mateos-Naranjo et al. 2010b), and *S. densiflora* (Mateos-Naranjo et al. 2010a). Nevertheless, not all C4 species respond to CO_2 enrichment with increased growth. Long-term exposure to elevated CO_2 did not significantly alter total biomass of the C4 species, *S. patens*, in a Chesapeake Bay marsh (Erickson et al. 2007). A study of the C4 grass, *S. anglica*, in Dutch salt marshes found a reduction in total dry weight of plants grown under elevated CO_2 (720 μL L^{-1}).

The capacity of plants to respond to CO_2 is influenced by growth-limiting factors such as nutrient and water availability and stress factors such as salinity and flooding (Langley et al. 2009; Langley and Megonigal 2010; Cherry et al. 2009). In a long-term study of elevated CO_2 effects on brackish marshes of the Chesapeake Bay, total biomass production in the C3 sedge-dominated community was increased 35% on average, and this stimulation was greatest during rainy, low salinity years (Erickson et al. 2007). In general, the greater the nutrient supply, the greater the absolute response to CO_2 enrichment (Poorter and Perez-Soba 2001). In some cases, plants

growing under elevated CO_2 may have less demand for nutrients and water, so that relative growth under stressful conditions may be greater under elevated CO_2 compared to control plants at ambient CO_2. Examination of CO_2 response under future scenarios relevant to coastal wetlands, such as increased temperature, flooding, and/or salinity, is important to fully understand and predict impacts of climate change. In a study of North European salt marshes, higher temperatures (+3°C) and CO_2 (+340 μL L^{-1}) produced the greatest biomass of the C3 species, *P. maritima*. Instead of a direct effect, CO_2 enrichment may ameliorate stresses that accompany climate change. For example, CO_2 enrichment enhanced productivity of a mixed brackish marsh community by modifying C3 (*S. americanus*) response to salinity (Cherry et al. 2009). Improvement of stress tolerance by CO_2 is not always the case. Higher [CO_2] enhanced growth rates of two mangrove species at low salinity, particularly the less salt tolerant and faster-growing species (*R. apiculata*), but had little effect at higher salinity (Ball et al. 1997).

Another consideration relevant to early plant growth is that the potential response to elevated CO_2 is very dependent upon the activity of carbon sinks (growing tissues) and presence of carbon reserves (e.g., in cotyledons). For example, the presence of large cotyledonary reserves in some mangrove species, such as *Rhizophora* spp. or *Avicennia* spp., could result in little or no response to higher CO_2 during initial growth stages. Significant effects of elevated CO_2 on *R. mangle* seedlings were not apparent until after 8 months of exposure, but a response eventually occurred after the seedlings were more reliant on leaf photosynthesis than on maternal reserves (Farnsworth et al. 1996). Similarly, *A. germinans* seedlings did not increase stem diameter in response to higher CO_2 concentrations until after the cotyledonary reserves were depleted (ca. 100 days) (McKee and Rooth 2008). A delayed response to elevated CO_2 means that higher concentrations may not aid such C3 species in competition with C4 species or to offset effects of stressors such as salinity and flooding until later growth stages.

A final constraint on plant response to elevated CO_2 is competition, both intraspecific and interspecific. Several studies have shown that CO_2 response by plants grown in isolation is not necessarily predictive of the response(s) in mixed communities (Poorter and Navas 2003). When grown alone in mesocosms, the black mangrove, *A. germinans*, responded to the combination of higher CO_2 (720 μL L^{-1}) and soil nitrogen with increased growth and aboveground biomass (McKee and Rooth 2008). In mixture with the C4 grass, *S. alterniflora*, however, mangrove growth was strongly suppressed, and the elevated CO_2 treatment had no effect. Mangrove seedlings from CO_2-treated plants were similarly suppressed when transplanted to a salt marsh dominated by *S. alterniflora* (McKee and Rooth 2008). This latter experiment further showed that mangrove mortality due to herbivory could potentially negate beneficial effects of CO_2 or nitrogen enrichment on seedling performance. In a study of brackish marsh species grown in mixture and monoculture, growth of the C3 sedge was negatively affected by the C4 grass (without a reciprocal competitive effect) (Cherry et al. 2009). Such findings suggest that the presence of a strong competitor for resources can limit or prevent the response of a C3 species to elevated CO_2.

CO_2 enrichment may also alter leaf tissue quality, such as increasing the concentration of non-structural carbohydrates while decreasing tissue nitrogen (Poorter et al. 1997). This effect may result from several possible mechanisms, but the potential consequences for plants are to alter susceptibility to (1) photoinhibition (by increases in photoprotective compounds) and (2) herbivores (by decreases in tissue palatability). Another consequence is the potential effect of tissue chemistry on plant decomposition rates (Norby et al. 2001). Little information exists on the changes in tissue chemistry of wetland species or consequences for decay rates. In a long-term study of brackish marsh species, elevated CO_2 decreased tissue nitrogen in both C4 grass and C3 sedge species (Erickson et al. 2007). In contrast, a greenhouse study of a C3 mangrove and C4 salt marsh grass found no significant effect of elevated CO_2 on leaf tissue C:N ratios, whereas fertilization with N did alter tissue chemistry and led to higher seedling mortality in the field due to crab herbivory (McKee and Rooth 2008).

Recent work has found that elevated CO_2 increased belowground production and accumulation of organic matter in a brackish marsh community, leading to upward expansion of the soil surface (Langley et al. 2009; Cherry et al. 2009). Both greenhouse mesocosm and field experiments measured the effects of CO_2 enrichment on a brackish marsh community containing a mixture of C3 (*Schoenoplectus americanus*) and C4 (*Spartina patens*) species. Stimulation of belowground production resulted in an increase in soil volume, which increased rates of elevation gain. This response was due primarily to stimulation of the C3 species by elevated CO_2 (Cherry et al. 2009). In addition, the elevated CO_2 effect was modified by salinity and flooding. Such a response may aid some coastal wetlands in maintaining surface elevations relative to sea-level. These studies showed that the elevated CO_2 response was maintained for up to 2 years, but further work is required to determine if the effect persists.

Predictions of elevated CO_2 effects on coastal wetlands are problematic due to limited data. Most studies show that several marsh and mangrove species respond with increased growth and biomass, which can be sustained over long time periods (at least in some cases). Less clear is the potential effect of rising CO_2 on shifts in species composition of coastal wetlands; however, we can say that the simple prediction that C3 species will become more abundant in mixed communities will not be realized in all situations, as seen for the sub-tropical mangrove-marsh community (McKee and Rooth 2008). Even if species shifts do not occur, CO_2 may have an effect on plant community structure or function through stimulation of one or more component species. Although insufficient data exist to make specific predictions about interactions of CO_2 with other environmental factors, the data do suggest that several factors may be important modifiers of CO_2 response by marsh and mangroves species, including nutrients, salinity, flooding/anaerobiosis, humidity, and air temperature (Table 1). In most cases, the CO_2 response by marsh and mangrove species was greater under more stressful conditions. Because the study of CO_2 effects on coastal wetland plants (particularly under field conditions) is technically challenging and expensive, our understanding and prediction of future response to rising CO_2 will likely depend on modelling approaches.

Table 1 Summary of marsh and mangrove species responses to elevated CO_2 as percent change from control (ambient CO_2). Species identified by photosynthetic pathway (Type); CO_2 Treatment Level (concentration in ppm) and Duration (instantaneous (*inst.*), days (*d*), weeks (*wk*), months (*mo*) or years (*yr*)); additional factors examined (Other factors); observed response to elevated CO_2 expressed as percent change from control condition

Species	CO₂ treatment				CO₂ response		Citation
	Type	Level	Duration	Other factors	Type	% Change from control	
Rhizophora mangle	C3	700	408 d	–	Biomass	+40	Farnsworth et al. (1996)
R. mangle	C3	700	408 d	–	RGR[a]	+21	Farnsworth et al. (1996)
R. mangle	C3	361–485	inst.[b]	–	NPP[b]	–14	Snedaker and Araujo (1998)
Avicennia germinans	C3	361–485	inst.[b]	–	NPP[b]	–12	Snedaker and Araujo (1998)
Laguncularia racemosa	C3	361–485	inst.[b]	–	NPP[b]	–27	Snedaker and Araujo (1998)
Conocarpus erectus	C3	361–485	inst.[b]	–	NPP[b]	–8	Snedaker and Araujo (1998)
R. apiculata	C3	700	14 wk	High humidity	RGR	+36	Ball et al. (1997)
R. apiculata	C3	700	14 wk	Low humidity	RGR	+71	Ball et al. (1997)
R. stylosa	C3	700	14 wk	High humidity	RGR	+40	Ball et al. (1997)
R. stylosa	C3	700	14 wk	Low humidity	RGR	+25	Ball et al. (1997)
A. germinans	C3	720	18 mo	Low nitrogen	Biomass	+18	McKee and Rooth (2008)
A. germinans	C3	720	18 mo	High nitrogen	Biomass	+35	McKee and Rooth (2008)
Schoenoplectus americanus	C3	720	4 yr	–	Biomass	0	Langley and Megonigal (2010)
S. americanus	C3	720	4 yr	+ Nitrogen	Biomass	+120	Langley and Megonigal (2010)
Spartina patens	C3	720	4 yr	–	Biomass	0	Langley and Megonigal (2010)
S. patens	C3	720	4 yr	+ Nitrogen	Biomass	–66	Langley and Megonigal (2010)
Scirpus maritimus	C3	580	6 wk	10 mM NaCl/aerated	RGR	+34	Rozema et al. (1991)
S. maritimus	C3	580	6 wk	10 mM NaCl/anaerobic	RGR	+16	Rozema et al. (1991)
S. maritimus	C3	580	6 wk	250 mM NaCl/aerated	RGR	+44	Rozema et al. (1991)
S. maritimus	C3	580	6 wk	250 mM NaCl/anaerobic	RGR	+15	Rozema et al. (1991)
Puccinellia maritima	C3	580	6 wk	10 mM NaCl/aerated	RGR	+71	Rozema et al. (1991)
P. maritima	C3	580	6 wk	10 mM NaCl/anaerobic	RGR	–5	Rozema et al. (1991)
P. maritima	C3	580	6 wk	250 mM NaCl/aerated	RGR	+95	Rozema et al. (1991)

(continued)

Table 1 (continued)

Species	Type	CO$_2$ treatment		Other factors	CO$_2$ response		Citation
		Level	Duration		Type	% Change from control	
P. maritima	C3	580	6 wk	250 mM NaCl/anaerobic	RGR	+45	Rozema et al. (1991)
S. patens	C4	580	6 wk	10 mM NaCl/aerated	RGR	+57	Rozema et al. (1991)
S. patens	C4	580	6 wk	10 mM NaCl/anaerobic	RGR	−77	Rozema et al. (1991)
S. patens	C4	580	6 wk	250 mM NaCl/aerated	RGR	−48	Rozema et al. (1991)
S. patens	C4	580	6 wk	250 mM NaCl/anaerobic	RGR	−76	Rozema et al. (1991)
Spartina maritimus	C3	580	6 wk	10 mM NaCl/aerated	Net Ps[c]	+26	Rozema et al. (1991)
S. americanus	C3	+340	8 yr	–	Net Ps	+100	Jacob et al. (1995)
Elymus athericus	C3	720	71 d	0 mM NaCl	Biomass	+5	Lenssen et al. (1993)
E. athericus	C4	720	71 d	300 mM NaCl	Biomass	+33	Lenssen et al. (1993)
S. anglica	C4	720	71 d	–	Biomass	−20	Lenssen et al. (1993)
S. anglica	C4	720	71 d	50 mM NaCl	Biomass	−10	Lenssen et al. (1993)
S. anglica	C4	720	71 d	400 mM NaCl	Biomass	+7	Lenssen et al. (1993)
S. anglica	C4	720	71 d	50 mM NaCl/flood	Biomass	−10	Lenssen et al. (1993)
S. anglica	C4	720	71 d	400 mM NaCl/flood	Biomass	−10	Lenssen et al. (1993)
Aster tripolium	C3	720	62 d	200 mM NaCl	Biomass	+4	Lenssen et al. (1995)
A. tripolium	C3	720	62 d	500 mM NaCl	Biomass	+2	Lenssen et al. (1995)
A. tripolium	C3	720	62 d	200 mM NaCl/flooded	Biomass	+11	Lenssen et al. (1995)
A. tripolium	C3	720	62 d	500 mM NaCl/flooded	Biomass	+25	Lenssen et al. (1995)
Puccinellia maritima	C3	720	62 d	200 mM NaCl/flooded	Biomass	+65	Lenssen et al. (1995)
P. maritima	C3	720	62 d	500 mM NaCl/flooded	Biomass	+181	Lenssen et al. (1995)
P. maritima	C3	+340	11 mo	–	Biomass	−10	Gray and Mogg (2001)
P. maritima	C3	+340	11 mo	+3°C temp	Biomass	+101	Gray and Mogg (2001)
Spartina anglica	C4	+340	11 mo	–	Biomass	+90	Gray and Mogg (2001)
S. anglica	C4	+340	11 mo	+3°C temp	Biomass	−42	Gray and Mogg (2001)
S. americanus	C3	+340	17 yr	–	NECE[d]	+35	Rasse et al. (2005)

Species	Type	CO_2	Duration	Treatment	Measurement	Response	Reference
S. americanus	C3	+340	18 yr	Low salinity	Biomass	+32	Erickson et al. (2007)
"	C3	+340	18 yr	High salinity	Biomass	+46	Erickson et al. (2007)
S. patens	C4	+340	18 yr	Low salinity	Biomass	0.5	Erickson et al. (2007)
"	C4	+340	18 yr	High salinity	Biomass	−15	Erickson et al. (2007)
S. patens	C4	+340	1 yr	Flooded, low salinity	AG production[e]	−54	Cherry et al. (2009); McKee unpublished data
"	C4	+340	1 yr	Unflooded, low salinity	AG productio	+5	
"	C4	+340	1 yr	Flooded high salinity	AG production	+73	Cherry et al. (2009)
"	C4	+340	1 yr	Unflooded, high salinity	AG production	−12	Cherry et al. (2009)
S. americanus	C3	+340	1 yr	Flooded, low salinity	AG production	−1	Cherry et al. (2009)
"	C3	+340	1 yr	Unflooded, low salinity	AG production	+68	Cherry et al. (2009)
"	C3	+340	1 yr	Flooded high salinity	AG production	+101	Cherry et al. (2009)
"	C3	+340	1 yr	Unflooded, high salinity	AG production	+130	Cherry et al. (2009)
S. patens	C4	+340	12 yr		NECE[d]	+13	Li et al. (2010)
S. americanus	C3	+340	12 yr		"	+36	Li et al. (2010)
Spartina densiflora	C4	700	90 d	0 mM NaCl	Biomass	+35	Mateos-Naranjo et al. (2010a)
S. densiflora	C4	700	90 d	171 mM NaCl	Biomass	+20	Mateos-Naranjo et al. (2010a)
S. densiflora	C4	700	90 d	571 mM NaCl	Biomass	0	Mateos-Naranjo et al. (2010a)
Spartina maritima	C4	700	30 d	0 mM NaCl	RGR	+40	Mateos-Naranjo et al. (2010b)
S. maritima	C4	700	30 d	171 mM NaCl	RGR	+40	Mateos-Naranjo et al. (2010b)
S. maritima	C4	700	30 d	571 mM NaCl	RGR	+40	Mateos-Naranjo et al. (2010b)

[a] *RGR* relative growth rate

[b] *NPP* g CO_2 m^{-2} min^{-1} (Plant leaves were exposed to higher CO_2 concentrations only during the measurement (10–30 s))

[c] Net photosynthesis

[d] Net ecosystem CO_2 exchange

[e] Aboveground production

3 Temperature

The increase in global temperature of 0.74°C in this century has been attributed predominantly to anthropogenic emissions of greenhouse gasses (Solomon et al. 2007). Average global temperatures are projected to increase at an accelerated rate in the twenty-first century, in a range from 1.1°C to 6.4°C (Solomon et al. 2007). A warmer planet will pose many threats and opportunities for mangrove and salt marsh species. While some mangrove species extend in range to temperate latitudes, all are found in the tropics and reach their greatest diversity and biomass along humid tropical coastlines (Duke et al. 1998). The decline in mangrove species diversity with increasing latitude is a feature common to Australia (Fig. 3), the Americas and Africa (Duke et al. 1998; Chapman 1977; Duke 2006), as well as island groupings (Duke et al. 1998). The differing latitudinal ranges of species have been attributed to their varying physiological tolerance of cold (Saenger and Moverley 1985; Duke 2006), although variation in aridity, habitat, and dispersal opportunities may explain differences in the latitudinal extent of many species (Duke et al. 1998).

The poleward limit of mangroves corresponds to coastlines where mean air temperatures of the coldest month are higher than 20°C and the seasonal range is not greater than 10°C (Walsh 1974; Duke et al. 1998; Chapman 1977), correlating with the 20°C isotherm for seawater (Duke et al. 1998). Regional deviations from this trend are explained by geographic barriers to dispersal (*Avicennia marina* var. *australasica*) in New Zealand (de Lange and de Lange 1994) or ecotypic variation in mangrove tolerance to cold in relict populations (as with *Avicennia marina* var. *australasica* in SE Australia (Macnae 1966; Duke et al. 1998)).

Mangroves in some locations appear to be expanding their latitudinal range. Recent reports indicate northernmost individuals of *R. mangle* on the Atlantic US coast at 29°40′N (Fort Matanzas, FL, USA) (Zomlefer et al. 2006) and of *A. germinans*
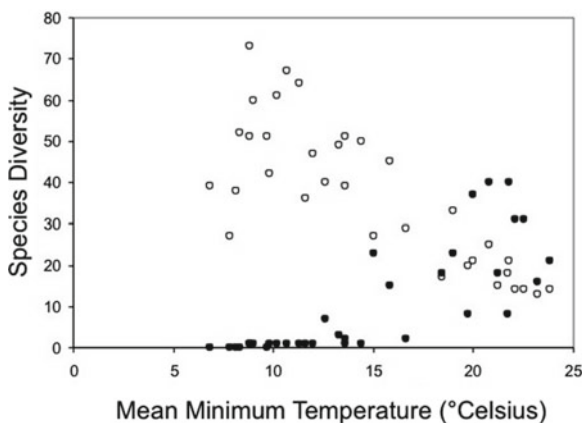

Fig. 3 Variation in numbers of mangrove (*closed circles*) or saltmarsh (*open circles*) species in Australia in relation to Mean Minimum Temperature for 34 coastal bioregions (Data from Duke (2006) and Saintilan (2009))

at 30°01.012′N (Indian River Lagoon, FL, USA) (I.C. Feller, personal communication) where historically both extended to Ponce de Leon Inlet (29°04′N). The range of *R. stylosa* has extended south on the east coast of Australia (Wilson 2009), with small populations of juveniles now found at South West Rocks Creek (30.52′S), 100 km south of the southern-most stand of adult trees (on the Corindi Creek). This expansion of range corresponds to a 100–200 km poleward extension in regional air temperature zones over the past few decades (Hennessey et al. 2004). Furthermore, the age structure in all estuaries south of the New South Wales (NSW)/Queensland border suggests rapid recent expansion within estuaries (Wilson 2009).

Sensitivity to frost has in the past prevented the northern expansion of mangrove in the southern United States (McMillan and Sherrod 1986; Sherrod and McMillan 1985). While some mangrove communities are capable of recovering after severe freezing (Lugo and Patterson-Zucca 1977), a sequence of severe freezes will lead to widespread mortality and a depletion of propagule reserves (Stevens et al. 2006). Such an event occurred in the 1980s in Florida (1983, 1985), and a catastrophic series of winters may have a recurrence interval of once in a century in Florida (Winsberg 1990). Climate scientists have predicted a lessening in the frequency of such events in the Northern Hemisphere (Meehl et al. 2004; Vavrus et al. 2006), a factor that might provide an opportunity for more widespread colonization of mangroves along the US Gulf coast.

Poleward expansion in other locations might be inhibited by barriers to dispersal. For example, the southern limits of *A. marina* in Australia and New Zealand are unlikely to be due to climatic conditions. Bass Strait forms an effective barrier to mangrove colonization in northern Tasmania, and weak tidal currents and tidal asymmetry in New Zealand may preclude colonization beyond their current southern limit (de Lange and de Lange 1994). Predicted desertification in some regions under global warming may inhibit the expansion of mangroves in some sub-tropical locations, such as the African West Coast (Dodd and Rafii 2002).

Higher temperatures will also influence the photosynthetic efficiency of mangroves. In colder climates, increases in temperature will increase photosynthetic efficiency up to a temperature optimum, which will vary among species and with location for individual species. For example, optimal temperature for photosynthetic assimilation in *R. stylosa* has been estimated at 29°C at Hinchinbrook Island, Australia (Andrews and Muller 1985) and 25°C in Japan (Okimoto et al. 2007). Temperature responses may therefore also adjust with the onset of warming, although assimilation declines between 30°C and 33°C for some species (Cheeseman 2004) and will cease if leaf temperatures climb to 38–40°C (Clough et al. 1982; Andrews et al. 1984). Globally, climate change might be expected to enhance assimilation, given the high relative increase in temperature in temperate compared to tropical regions (Solomon et al. 2007). At regional scales, changes in mangrove productivity are more likely to be driven by climate change impacts on precipitation, river flow, and sedimentation, with possible declines in productivity in arid regions (Red Sea, sections of northern Australia) and increases in SE Asia (Alongi 2008).

Temperature increases associated with global warming may also influence the timing of leaf emergence as well as the timing and success of reproduction (Gilman et al. 2008). This contention is supported by the existence of latitudinal clines, such as phenological shifts with latitude identified for *A. marina* between New Guinea and South Australia (Duke 1990). In contrast, Wilson (2009) found little difference in vegetative and reproductive phenology between *R. stylosa* at its southern limit in NSW, Australia, and elsewhere on the continent. Increases in temperature alone are thus unlikely to improve the growth rate and reproductive success of *R. stylosa* in sub-tropical locations.

At a global scale, salt marsh is the dominant intertidal vegetation on shorelines where mangrove establishment is precluded or development is limited by climatic factors (Kangas and Lugo 1990). Thus, while salt marsh vegetation can be classed into six biogeographical types: Arctic, Boreal, Temperate, West Atlantic, Dry Coast, and Tropical Types (Adam 1990), they are most common in temperate, subarctic, and arctic zones (Long and Mason 1983; Mitsch and Gosselink 2000; Mendelssohn and McKee 2000).

On the Australian coastline, floristic diversity in salt marshes increases with increasing latitude, a trend opposite to that of mangrove diversity (Saintilan 2009; Adam 1996). This trend is not due entirely to the presence of mangroves at higher latitudes, as salt marsh diversity is very high in Victoria and South Australia where the mangrove *A. marina* is common. In these environments, the upper intertidal environment is the preserve of salt marsh, while in tropical environments salt marsh development in the upper intertidal may be impeded by hypersalinity (in arid environments) and by competition with mangroves in humid environments.

Higher temperatures inhibit germination of some salt marsh species. For example, germination of *Phragmites australis* was inhibited by higher temperatures in experimental studies (Greenwood and MacFarlane 2006), and higher day-time temperatures limited germination of the halophyte *Atriplex triangularis* (Khan and Ungar 1984). There may be physiological reasons behind the close correlation between salt marsh species diversity and minimum monthly temperature in Australia (Figure 1, Saintilan 2009), but more experimental research is required to establish this relationship.

Significant increases in temperature pose a threat to the high diversity and endemism of salt marsh at higher latitudes. As mentioned above, decreases in the frequency of freezing temperatures, and in particular the succession of very cold winters required to substantially reduce mangrove extent in the southern USA, is likely to promote the development of mangroves within the Mississippi River Delta and elsewhere, at the expense of salt marsh. Further north, salt marsh diversity may decline as higher temperatures promote the dominance of *Spartina patens*, as suggested by experimental studies (Gedan and Bertness 2010). Salt marsh has declined significantly in southeast Australia due to the proliferation of the mangrove *A. marina* in upper intertidal environments close to the southern limit of its range (Saintilan and Williams 1999). The centers of highest diversity in the Australian salt marsh flora occur immediately adjacent to seaward barriers, both on the mainland and in Tasmania, limiting the adaptation options for many species.

4 Rainfall

Climate models indicate that mean precipitation will generally increase globally with climate warming, but the direction and magnitude of change will vary spatially and seasonally (Solomon et al. 2007). Models consistently predict increases in precipitation at high latitudes over all seasons in response to increasing global temperature. Precipitation also is predicted to increase at equatorial latitudes over both land and ocean (e.g., the South Asian and Australian monsoons). At sub-tropical and mid-latitudes, precipitation may decrease, and the occurrence of summer droughts will likely increase with global warming. Precipitation in Mexico and Central America, for example, is expected to decrease due to increased precipitation over the eastern equatorial Pacific region (Neelin et al. 2006). Summer drying and drought may lead to vegetation die-offs (Breshears et al. 2005), providing opportunities for vegetation shifts or possibly loss of wetland area. Another, somewhat paradoxical change associated with drought risk is the probability of more intense precipitation events and flooding (Solomon et al. 2007). This pattern results from the concentration of rainfall into fewer, intense events with longer intervening periods of drying.

In addition, a warmer climate is predicted to generate stronger tropical cyclones with greater wind speeds and more intense precipitation (Solomon et al. 2007). Models also predict more intense (but fewer) extra-tropical storms as well as a poleward shift of storm tracks by a few degrees latitude in both hemispheres (Yin 2005; Geng and Sugi 2003; Bengtsson et al. 2006). Changes in frequency of extreme events are likely to have a greater impact on vegetation than are changes in average precipitation. For coastal wetlands, extremes in precipitation and particularly runoff of freshwater may alter salinity regimes with consequent effects on vegetation.

The question is how might changes in rainfall affect coastal wetlands and what are the main mechanisms that underlie changes in wetland vegetation? A number of studies have documented that changes in rates and patterns of precipitation influence wetland community structure (Table 2). Early work in salt marshes of southern California (USA) documented impacts of heavy rainfall and flooding on temporary reduction in salinity of normally hypersaline soils and subsequent increases in biomass of plants (40% increase in *Spartina foliosa*, Tijuana Estuary; 160% increase in *Salicornia virginica*, Los Penasquitos Lagoon) (Zedler 1983). Temporal variation in plant species composition of a salt marsh at Bolinas Lagoon, California (USA) was associated with changes in annual rainfall (Allison 1992). In years with average or below-average rainfall during winter and spring, cover of *Salicornia virginica* increased, whereas cover of this species decreased with higher than average spring rainfall, as did abundance of rare species. Thus, under more stressful conditions, the salt-tolerant *S. virginica* became more dominant, whereas the community became more diverse during periods of abundant rainfall.

Another study of rainfall patterns and vegetation distribution and productivity was conducted in the Carpinteria Salt Marsh in central California (Callaway and Sabraw 1994). During dry years, *Hutchinsia procumbens* was more abundant, but was rare or absent in wetter years. The opposite pattern relative to rainfall was found

Table 2 Summary of wetland responses (+ increase, – decrease, 0 no change) to changes in rainfall frequency or amount (+ increase, –decrease; *obs* observation, *exp.* experimental)

Location	Method	Rainfall		Other factors	Species	Response		Citation
		Frequency	Amount			Variable	Change	
N. California, USA	obs.		– (Winter-spring)		SV	Cover	+	1
N. California, USA	obs.		+ (Spring)		SV	Cover	–	1
N. California, USA	obs.		+ (Spring)		"Rare species"	Cover	+	1
Mar Menor, Spain	obs.		+ (Runoff)	– Salinity	SF	Cover	+	2
Mar Menor, Spain	obs.		+ (Runoff)	– Salinity	PA	Cover	+	2
Mar Menor, Spain	obs.		+ (Runoff)	– Salinity	JM	Cover	+	2
Mar Menor, Spain	obs.		+ (Runoff)	– Salinity	LD	Cover	–	2
Central California, USA	obs.		–		HP	Abundance	+	3
Central California, USA	obs.		–		JB	Abundance	–	3
Central California, USA	exp.	+		Low elevation	HP	Density	+	3
Central California, USA	exp.	+		Low elevation	SM	Density	+	3
Central California, USA	exp.	+		Mid elevation	SM	Density	+	3
Central California, USA	exp.	+		Mid elevation	HP	Density	+	3
Central California, USA	exp.	+		Mid elevation	PI	Density	+	3
Central California, USA	exp.	+		Upper elevation	JB	Density	+	3
Massachusetts, USA	exp.		–	+ Waterlogging	SA	Biomass	+	4
Massachusetts, USA	exp.		–	+ Waterlogging	SP	Biomass	+	4
The Netherlands	obs.		–	+ Salinity	Salt marsh angiosperms	Salt marsh angiosperms	–	5
Nueces, Texas, USA	obs.			+ Flooding	SB	Abundance	+	6
Nueces, Texas, USA	obs.	+			BF	Cover & biomass	+	6
Nueces, Texas, USA	obs.	+			BF	Root:shoot	+	6
Nueces, Texas, USA	obs.	+			BM	Root:shoot	+	6
Nueces, Texas, USA	obs.	+			SL	Root:shoot	+	6

Location		Rainfall	Other treatments	Species	Response variable	Response	Citation
Nueces, Texas, USA	obs.			SV	Root:shoot	–	6
Moreton Bay, Australia	obs.	+		Mangroves	Landward extent	+	7
Nueces, Texas, USA	obs.		+ Flooding	Clonal vegetation	Abundance	+	8
Mississippi River Delta	obs.		– Sea level & river outflow	Spartina spp.	Cover	–	9
Mississippi River Delta	obs.		"	Juncus spp.	Cover	0	9
Mississippi River Delta	obs.		"	AG	Cover	+	9
New England, USA	obs.		+ (El Niño)	PA	Shoot production, height, repr.	+	10
S. California, USA	obs.		– Salinity		Seed germination	+	11
Tijuana Estuary	obs.		– (River flow) + Salinity	SFO	Height	–	12
Tijuana Estuary	obs.				Stem density	–	12
Tijuana Estuary	obs.		– Salinity	SFO	Biomass	+	13
Los Penasquitos Lagoon	obs.		– Salinity	SV	Biomass	+	13

Other treatments, in addition to rainfall are listed (+ increase, – decrease). Species: *Salicornia virginica* (SV), *Sarcocornia fruticosa* (SF), *Phragmites australis* (PA), *Juncus maritimus* (JM), *Limonium delicatulum* (LD), *Hutchinsia procumbens* (HP), *Juncus bufonius* (JB), *Spergularia marina* (SM), *Parapholis incurva* (PI), *Spartina alterniflora* (SA), *Spartina patens* (SP), *Spartina foliosa* (SFO), *Salicornia bigelovii* (SB), *Borrichia frutescens* (BF), *Batis maritima*, (BM), *Suaeda linearis* (SL), *Avicennia germinans* (AG)

Citations: 1. Allison (1992), 2. Alvarez-Rogel et al. (2007), 3. Callaway and Sabraw (1994), 4. Charles and Dukes (2009), 5. Deleeuw et al. (1990), 6. Dunton et al. (2001), 7. Eslami-Andargoli et al. (2009), 8. Forbes and Dunton (2006), 9. McKee et al. (2004), 10. Minchinton (2002), 11. Noe and Zedler (2001), 12. Zedler et al. (1986), 13. Zedler (1983)

for *Juncus bufonius*. Thus, when soil salinity was decreased during wetter seasons, aboveground productivity of annuals increased, and spatial patterns and density of species plants changed. A study of a semi-arid Mediterranean salt marsh adjacent to the Mar Menor saline lagoon found that increases in the water table (due to inflows from intensive agriculture) was accompanied by changes in soil salinity and expansion of *Sarcocornia fruticosa*, *Phragmites australis*, and *Juncus maritimus* at wettest sites and decreased cover of *Limonium delicatulum* (Alvarez-Rogel et al. 2007). These species shifts eliminated the original zonation pattern and reduced diversity.

In addition to observations of temporal change, experimental manipulation of rainfall caused shifts in species abundances leading to higher diversity (Callaway and Sabraw 1994). In watered plots at Carpinteria Salt Marsh, density increases occurred for *H. procumbens* and *Spergularia marina* (low elevation); *S. marina*, *H. procumbens*, and *Parapholis incurva* (intermediate elevation); and *J. bufonis* (upper elevations). A 13-year study of six salt marsh communities (Schiermonnikoog, Dutch Frisian Islands) showed that peak aboveground biomass varied in synchrony with rainfall deficits during the growing season, which influenced soil salinity and moisture; inundation frequency by tides, in contrast, did not explain temporal variation in vegetation (Deleeuw et al. 1990).

Floods and droughts resulting from fluctuations in local weather extremes can have dramatically different effects on vegetation. A study of a semi-arid, sub-tropical salt marsh in the Nueces Estuary, Texas (USA) found that periods of low to moderate flooding promoted stress-tolerant clonal vegetation, but catastrophic flooding caused plant mortality followed by colonization by the annual *Salicornia bigelovii* (Forbes and Dunton 2006). Depending on freshwater inflow, rainfall, and potential evapotranspiration, porewater salinities ranged from 30 to 59 ppt. In another study of Nueces Estuary marshes, higher than normal rainfall increased percent cover and biomass of less salt tolerant species (*Borrichia frutescens*) and shifts in root:shoot ratios of several species (*B. frutescens*, *Batis maritima*, *Suaeda linearis*, *Salicornia virginica*) (Dunton et al. 2001). Extensive dieback (~40,000 ha) of salt marsh in the Mississippi River Delta, USA coincided with a historic drought, low sea levels, and low river outflow (McKee et al. 2004). Although *Spartina* spp. experienced mortality, more drought-tolerant species, *Avicennia germinans* and *Juncus roemerianus*, were essentially unaffected. In some marshes, a shift from *Spartina* to *A. germinans* dominance was observed.

In contrast to wetlands of arid regions, those occurring in high rainfall environments may respond differently to climate extremes that reduce freshwater inputs and increase salinities. In a study of Micronesian mangrove forests, diameter tree growth varied from 7 to 80 cm^2 year^{-1} for *Sonneratia alba* and from 5 to 27 cm^2 year^{-1} for *Bruguiera gymnorrhiza* on high islands (Krauss et al. 2007). At all but one site, annual diameter growth for trees in riverine and interior sites was seven times greater than in the fringe zone adjacent to the ocean. Although salinity was not measured, the riverine and interior zones would likely experience greater fluctuation in salinity due to surface and groundwater inputs. In another study of Micronesian wetlands, mangrove sites were found to have salinities lower than seawater, indicating receipt of freshwater inflows (Drexler and Ewel 2001). In contrast, mean salinity was higher

than normal (15 vs. 6 ppt) during an ENSO-related drought, suggesting that climate extremes can modify coastal processes with potential impacts to vegetation.

Decreases in rainfall, leading to higher soil salinities, may limit seed germination or reduce plant growth. An experimental study of seedling emergence in three oligohaline marsh communities showed that higher salinity and flooding limited germination of most species (Baldwin et al. 1996). These three marsh types, which were dominated by different species, had seed banks with overlapping species composition and similar species richness and diversity – suggesting the potential for shifts in vegetation composition with future climate change. Rainfall variation can especially influence seed germination in high salinity marshes. A study in southern California found that high rainfall events, which were rare in the long-term record, created germination opportunities in upper intertidal marshes by lowering salinity and increasing soil moisture (Noe and Zedler 2001). Medium and small rainfall events also were followed by germination in these marshes. Germination and relative growth of annuals common in Mediterranean-climate marshes corresponded to the winter and spring salinities measured at field sites at Carpenteria, California (USA) (Callaway et al. 1990). In a study of tidal salt marshes in Massachusetts, USA, experimental manipulation of precipitation and warming generated changes in biomass and structure of the plant community (Charles and Dukes 2009). Lower rainfall increased total biomass of *S. alterniflora* (53%) and *S. patens* (69%), presumably by alleviating waterlogging stress. Decomposition was accelerated when precipitation was increased and slowed in a drought treatment, particularly in the *S. patens-D. spicata* community. At Tijuana Estuary, variation in amount and timing of stream flows affected soil salinity and plant stress (Zedler et al. 1986). When river and tidal flows were absent, soil salinity reached 104 ppt and was accompanied by reduced height (19%) and stem density (62%) of *Spartina foliosa*.

Changes in rainfall patterns may promote vegetation shifts at distributional boundaries. For example, a study of rainfall patterns and spatial distribution of mangrove forests in Moreton Bay, Southeast Queensland, Australia, over a 32-year period found a positive relationship between rainfall variables and landward expansion of mangroves (Eslami-Andargoli et al. 2009). Other factors such as geomorphology, disturbance, and local hydrology may modify rates and patterns of expansion. Additional explanations for landward transgression of mangroves into salt marsh habitats include altered tidal regimes or estuarine water levels, increases in nutrient levels and sedimentation, and human disturbance (Saintilan and Williams 1999).

Changes in precipitation patterns may lead to invasion and/or improved performance of nuisance species in coastal wetlands. A study conducted in southern New England found that increased precipitation during an El Niño year increased shoot production, shoot height, and number of inflorescences of *Phragmites australis*, an aggressive species in brackish and salt marshes (Minchinton 2002).

Impacts of changes in freshwater inputs from rainfall may be influenced by human activities, such as dam construction. A study of arid salt marshes in an estuary downstream of the Olifants River system in Western Cape, South Africa, found that plants (*Sarcocornia pillansii*) used saline groundwater during dry months to

survive, but depended upon winter rainfall to lower salinity and allow growth and reproduction (Bornman et al. 2002). Partial restoration of freshwater inflow in the Nueces Estuary, Texas (USA) led to vegetation changes in species occupying a hypersaline marsh (Alexander and Dunton 2002). Freshwater inundation during the fall promoted seed germination and rapid expansion of *Salicornia bigelovii*. Percent cover of *Batis maritima* also increased temporarily in response to periods of rainfall. In contrast, prolonged inundation leading to soil saturation had a negative impact on these species, which are adapted to hypersaline conditions. Flooding and salt leaching caused by heavy rains were augmented by reservoir discharge into the San Diego River and resulted in a long-term salinity change and shift from saline to freshwater marsh species (Zedler 1983). Not all flooding or rainfall events alter salinity regimes sufficiently to allow revegetation of hypersaline areas. The Orange Estuary in southern Africa lost 27% of its wetland area due to poor management in the 1980s (Bornman et al. 2002). Persistent high soil and groundwater salinity prevented the recovery of salt marsh. Flooding and above average rainfall in 2006 were found to have little impact on soil and groundwater salinity (although surface pools of lower salinity occurred); thus, revegetation of the salt marsh would likely require human intervention.

5 Sea-Level Rise

Mangrove and salt marsh communities generally occur between narrow elevation ranges and are dependent upon some degree of tidal inundation. The elevation range of these wetlands varies globally in response to the localized tidal range and is generally classified into two groups: macrotidal wetlands with a tidal range greater than 2 m and microtidal wetlands with a tidal range less than 2 m. Intertidal coastal wetlands are commonly distributed between mean sea level and the highest astronomical tide. The distribution of concomitant mangrove and salt marsh within this intertidal range is somewhat difficult to differentiate, with mangroves generally occurring at lower elevations and salt marsh growing at higher elevations (although the opposite pattern may occur in some settings). The essential factor determining their persistence is the maintenance of soil elevations with respect to water levels.

The maintenance of wetland elevations relative to water levels, henceforth termed relative elevation, is somewhat complex. Wetlands may range between those that are formed largely through the accumulation of allochthonous mineral matter to autochthonous wetlands that maintain their elevations entirely through the accumulation of organic material. Cahoon (2006) describes eight processes occurring at the surface or below the wetland surface that control wetland soil elevations: sediment (organic and mineral matter) deposition, sediment erosion, sediment compaction, soil shrinkage, root/organic matter decomposition, root growth, soil swelling, and lateral folding of the marsh root mat. These processes influencing wetland elevations may be categorised as geomorphological processes, biological processes, and hydrological processes (Cahoon et al. 1999) and operate in response to a range of

drivers including tides, sea-level change, nutrient availability, and climate. While these drivers and processes may result in the maintenance of relative elevation, the resilience of coastal wetlands to increasing sea level is limited, and breaching of thresholds may cause ecosystem collapse.

Over long time periods, many mangrove and salt marsh settings have reportedly maintained their elevations relative to water levels through the accumulation of mineralogenic sediments through tidal redistribution. In tide-dominated settings, coastal wetlands have reportedly kept pace with sea-level changes. Woodroffe (1990) found the mangrove forests on the Alligator River, Australia, kept pace with sea-level rise by accreting 12 m during the period 8,000–6,000 years before present (BP = 1950) through sedimentation rates averaging 6 mm year^{-1}. This phase of rapid sedimentation, known as the 'big swamp' phase, is evident on many rivers in northern Australia for this period until sea-level stabilised at approximately 6,000 years BP. Gehrels (1999) constructed a sea-level history for Maine salt marshes using 3–4 m-long peat cores, with rates of sea-level rise estimated at 0.75 mm year^{-1} for the period 6,000 to 1,500 BP.

The response of river-dominated systems is largely dependent upon how much sediment is supplied down river from the catchment and deposited within wetlands and deltas. Sediment budgets that translate to sedimentation rates equal to sea-level rise may enable intertidal coastal wetlands to remain relatively stable through geomorphological processes alone. Large-scale wetland loss in the interior regions of the Mississippi River Delta has been attributed to deficits between soil accretion and relative sea-level rise (Day et al. 2000, 2007). Since the early 1900s, overbank flooding of the Mississippi River Deltaic Plain and associated sedimentation in the interior of wetlands has been limited by the construction of levees. This period of wetland loss contrasts markedly with the period in which the Mississippi River Deltaic Plain formed during the previous 6,000–7,000 years. As the river switched course, wetland loss in abandoned delta lobes was counterbalanced by wetland creation in new areas. During this period of delta formation, sea levels were relatively stable; enabling riverine sediments to be deposited at the mouth and older distributaries, and by overbank flooding and crevasse formation (Day et al. 2007).

In contrast, intertidal wetlands in carbonate settings without substantial mineral sedimentation have kept pace with sea-level rise largely through biological processes of peat accumulation. Mangroves growing in sediment-deficient settings in the Caribbean, for example, build vertically via peat formation, in some cases reaching 10 m in thickness, with radiocarbon dating showing that biogenic accretion has kept pace with sea-level rise (e.g., Twin Cays and Tobacco Range, Belize) (McKee et al. 2007; Macintyre et al. 2004). In these settings, soils are a complex suite of water, organic matter (algae and microbial mats, living roots and rhizomes, and partially decayed plant material), and autochthonous sand (calcareous algae).

Until recently, the failure of coastal wetlands to maintain relative elevation has largely been attributed to lower rates of allochthonous sedimentation and ignores the autochthonous components of soil volume. This response may be an artefact of the decomposition of organic material and the apparent relationship between mineral sedimentation and maintenance of relative elevation within coastal wetlands
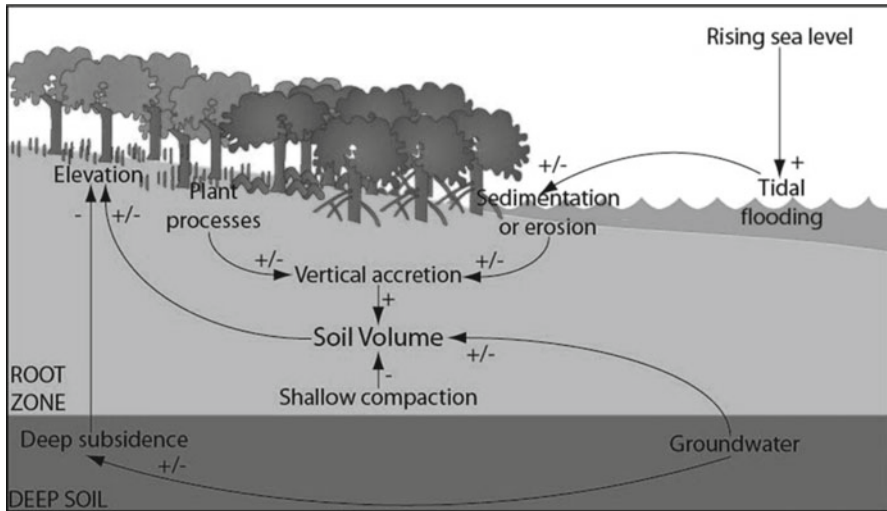
Fig. 4 Summary of processes influencing soil volume and surface elevation in coastal wetlands (Adapted from Cahoon et al. (1999))

over long-time scales (see for example Alligator River, Australia in Woodroffe 1990). This issue has largely been addressed through analyses of the soil bulk density and the contribution of organic and inorganic material to soil volume (see for example Bricker-Urso et al. 1989; Nyman et al. 1993; McKee et al. 2007; McKee 2011). The contribution of organic material and water to soil volume is reportedly as high as 96% in Narragansett Bay in Rhode Island; a tide dominated estuary (Bricker-Urso et al. 1989). The use of surface elevation tables in conjunction with estimates of sedimentation has also enabled the differentiation of surface and below-ground processes that build soil volume (Cahoon et al. 1999, 2003; Rogers et al. 2006; McKee 2011).

Biological processes that contribute to soil volume and the maintenance of mangrove and salt marsh elevations may occur at the surface or below the surface (Fig. 4). Surface plant litter accumulation (and slow decomposition) contributes to soil volume and relative elevation; however, little research has focussed on identifying the contribution of surface litter to wetland soil volume. Cahoon et al. (2006), for example, found positive relationships between litter standing stocks and vertical accretion in a basin forest in southwest Florida, while a similar relationship was not established within fringe forests. These differences were attributed to the saturation and slow decomposition of litter within basin forests compared to fringe forests that undergo frequent tidal flushing and faster leaf decomposition. The contribution of this variable accretion to elevation change requires further investigation. There is evidence to indicate that when organic matter accumulation is disrupted, wetland elevations may decline. In the Bay Islands, Honduras, mass mangrove mortality following Hurricane Mitch stopped organic matter accumulation, which was

followed by peat collapse, evident by a significant decrease in wetland elevation in the 1.5–3 year period following the hurricane (Cahoon et al. 2003).

Algal and microbial mats that form on wetland surfaces are reportedly highly productive (Zedler 1980; Weinstein et al. 2002) and may make a significant contribution to the elevation of the wetland surface and sedimentation (McKee 2011). Gunatilaka (1975) found that algal mats grew at rates of up to 11–15 mm per week on mud flats associated with mangroves in Ceylon. Rates of vertical accretion of up to 6 mm year^{-1} have been observed for microbial mats and 4 mm year^{-1} for filamentous algae and root mats in Belizean mangrove stands (Cahoon et al. 2006). The contribution of these algae and microbial mats to surface elevation remains largely unstudied and requires further consideration.

The role of belowground biomass contributions to wetland elevations has largely emerged through the use of surface elevation tables, in combination with measurements of plant growth (McKee 2011; Morris et al. 2002; Rogers et al. 2005a; McKee et al. 2007). At Homebush Bay, Australia, elevation increases in excess of vertical accretion coincided with a period of regrowth within a mangrove forest that had undergone extensive defoliation and was attributed to expansion of belowground mangrove biomass (Rogers et al. 2005a). Similarly, the application of nutrients and associated increases in plant productivity led to increases in wetland elevation (McKee et al. 2007; Cahoon et al. 2000; Morris et al. 2002). Recent research has also indicated that elevated CO_2 stimulated belowground production of a C3 salt marsh species, *Schoenoplectus americanus*, increasing soil volume and upward expansion of the wetland surface (Cherry et al. 2009).

Wetland hydrological processes influence wetland elevation through the delivery of sediments and organic matter to wetland surfaces and the regulation of plant growth and decomposition. Wetland hydrology conversely influences surface elevations directly though changes in water flux and storage. Soil expansion or contraction may occur through two mechanisms related to water movement. Firstly, large tides may compress the soil volume and cause lateral movement and uplift in adjacent areas (Nuttle et al. 1990; Cahoon 2006). Secondly, dilation may occur temporarily as water from tides (or rainfall) infiltrates sediments and causes temporary swelling of the soil volume, followed by shrinkage of the soil volume upon drying (Nuttle et al. 1990; Paquette et al. 2004; Rogers 2004; Cahoon et al. 2011). The temporal scale at which shrink-swell occurs may range from short periods, such as those associated with tide cycles or flood events (Rogers 2004), to extended periods of months to years when persistent drought conditions lead to depletion of groundwater resources and subsequent shrinkage of the soil volume (Rogers et al. 2005a, b).

While the effect of dilation over short periods, such as tidal cycles, is temporary, and elevations typically re-stabilize upon drying, shrinkage in response to longer perturbations may have a longer lasting effect on wetland elevations. Rogers and Saintilan (2009) reported shrinkage of the soil volume for a number of years in response to a severe El Niño-related drought in southeastern Australia with soil volumes swelling again once the prevailing climatic conditions had returned to normal. Shrinkage of soil volumes in response to longer-term perturbations, such as drought, may affect the capacity of wetlands to adapt to sea-level rise and maintain

their relative position within the tidal prism. This effect may become particularly apparent should climate change projections of increased frequency and intensity of drought events hold true for some regions of the world (Christensen et al. 2007; Kundzewicz et al. 2007).

Tides typically transport sediment for deposition within wetlands, and numerous studies have established relationships between inundation frequency or duration and vertical accretion within coastal wetlands (Bricker-Urso et al. 1989; Rogers et al. 2005a; Pethick 1981). In addition, short-term fluctuations in wetland elevations associated with dilation of sediments have been reported over tidal cycles (Rogers 2004; Paquette et al. 2004; Cahoon et al. 2006), while enhanced productivity and associated elevation increases from enhanced inorganic sediment trapping and in situ organic matter accumulation may also reflect inundation (Morris et al. 2002; Mudd et al. 2009). Alterations to the tidal regime associated with sea-level rise thus may alter relationships among tides, sedimentation, and wetland elevations. Engineering structures such as levee banks, flood gates, and culverts further complicate these relationships and may influence the capacity of wetlands to build elevation through accretion and plant productivity (see for example the Mississippi River Delta, USA in Day et al. 2000). Models of wetland surface evolution and field studies indicate that wetland surfaces will tend to attain equilibrium with sea-level rise through accretion processes (Allen 2000; Pethick 1981; Morris et al. 2002; Kirwan and Murray 2007; van Wijnen and Bakker 2001). Thus, increased inundation frequency and duration may promote self-adaptation of wetland elevations to sea-level rise, given sufficient time to equilibrate (Kirwan and Guntenspergen 2010). Nevertheless, the response rate of accretion to varying degrees of sea-level rise is poorly understood, leaving open the question of when a wetland surface may become unstable due to insufficient sediment supply and organic matter accumulation, commonly referred to as the threshold of resilience.

Episodic events, such as hurricanes, cyclones, storms, storm surges and associated flooding, hail, wind damage, lightning strikes, and freshwater flushing may also drive wetland elevation change (Cahoon 2006; Smith et al. 1994; Whelan et al. 2005; Cahoon et al. 2006). Since the intensity and frequency of these episodic events are projected to increase in association with climate change (Kundzewicz et al. 2007; Christensen et al. 2007), their influence on future wetland resilience may increase. Mechanisms by which episodic storm events affect soil elevations are summarised by Cahoon (2006) and may include substrate disruption and sediment redistribution (Cahoon and Reed 1995; Guntenspergen et al. 1995), loss of soil organic matter through tree mortality from high winds, lightning strikes, and hail damage (Whelan et al. 2005; Cahoon et al. 2003; Houston 1999), delivery of sediment from terrigenous sources (Cahoon et al. 1996), compaction of soil volume from large storm tides (Nuttle et al. 1990; Cahoon 2006), and changes in organic matter content of the soil volume due to salinity-induced growth reduction (Guntenspergen et al. 1995) or stimulation (Cahoon 2006).

Longer-term perturbations that drive wetland elevations, such as drought and associated depletion of groundwater reserves may also influence the resilience of wetlands to sea-level rise. Numerous studies have indicated decreases in wetland

elevation in response to extended periods of drought (Whelan et al. 2005; Rogers and Saintilan 2009), or over-use of groundwater resources (Dokka 2006; Belperio 1993; Walker et al. 1987). While wetland surfaces may rebound once prevailing climatic conditions return, or may even be enhanced when groundwater reserves are increased in response to greater rainfall (Cahoon et al. 2011), there is some concern that enhanced intensity and frequency of long-term climatic perturbations, as projected by the IPCC (Christensen et al. 2007; Meehl et al. 2007), may affect the relationship between wetland elevations and water levels and ultimately influence the resilience of wetlands to sea-level rise.

Mangrove and salt marsh resilience to sea-level rise is largely dependent upon the relationship between accretion (both allochthonous and autochthonous) and relative sea-level change. Analyses of the stratigraphy and chronology of Holocene deposits on coastal shorelines have been used to provide insight into the resilience of coastal wetlands to projected sea-level rise in the twenty-first century. Woodroffe (1990) found that mangrove shorelines have persisted under rates of sea-level rise as high as $10–15$ mm year^{-1}. As many coastal wetlands no longer occupy locations existing 18,000 years ago, prior to the post glacial marine transgression, saline coastal wetlands may exhibit a threshold of resilience, or a point at which rates of wetland elevations do not keep pace with rapid rates of sea-level rise. This threshold will vary between geomorphic settings due to varying capacities to build elevation at rates comparable to sea-level change (Woodroffe 1990). This hypothesis was supported by a subsequent analysis suggesting that low-elevation carbonate settings would collapse at rates of 12 cm per 100 years (Ellison and Stoddart 1991). However, several studies provide evidence that mangroves in carbonate settings have kept pace with Holocene sea-level rise (Maul and Martin 1993; Parkinson et al. 1994; Snedaker et al. 1994). In addition, there are many examples where mineral sedimentation allowed mangroves in other settings to maintain elevations during the Holocene (Hashimoto et al. 2006; Fujimoto et al. 1996; Miyagi et al. 1999; Lynch et al. 1989; Krauss et al. 2003; Alongi 2008; Woodroffe 1990).

Analyses of resilience are now largely focussed on incorporating non linear-feedbacks among inundation, plant productivity, sediment accumulation (allochthonous and autochthonous), and wetland elevations (Kirwan et al. 2010; Morris et al. 2002; Temmerman et al. 2003; D'Alpaos et al. 2007; Kirwan and Murray 2007; Mudd et al. 2009; French 2006). Results generally agree that the maximum rate of sea-level rise at which mineralogenic wetlands remain relatively stable is largely dependent upon tidal range and suspended sediment concentrations or sediment supply (Kirwan et al. 2010; French 2006) with small influences driven by carbon dioxide concentrations, freshwater inputs and pollutant inputs (Morris et al. 2002; Gilman et al. 2007; Rahmstorf et al. 2007; Cherry et al. 2009). Kirwan et al. (2010) propose that wetland resilience may be exhausted under rates of sea-level rise of only a few millimetres per year when suspended sediment concentrations are low ($\sim$1–10 mg L^{-1}), while wetlands may match sea-level rise of several centimetres per year when suspended sediment concentrations are high ($\sim$30–100 mg L^{-1}). Only those wetlands with tidal ranges exceeding 3 m and high suspended sediment concentrations (>30 mg L^{-1}) may survive rates exceeding 20 mm year^{-1}, while more

typical wetlands with suspended sediment concentrations of 30 mg L^{-1} and tidal ranges of 1 m are projected to undergo transition to subtidal settings by the end of the twenty-first century.

Rising sea levels will alter the structure of intertidal plant assemblages, favouring some species over others. Acceleration of sea-level rise in the New England coast of the USA coincided with the expansion of smooth cordgrass (*Spartina alterniflora*) into high-marsh spike grass (*Distichlis spicata*), and black needlerush (*Juncus gerardi*), a process that began in the late nineteenth century (Donnelly and Bertness 2001). Smith (2009) noted the decline of high marsh in the Cape Cod region since the earliest air photographs (1947), in some areas being replaced by *S. alterniflora* while in others by barren mudflat. Where mangrove and salt marsh co-exist, accelerated sea-level rise may promote replacement of salt marsh by mangroves. Saintilan and Williams (1999) observed the replacement of salt marsh by mangrove in many estuaries in SE Australia since the 1940s, a trend counter to the longer-term pattern of salt marsh replacing mangrove through the late Holocene as estuaries infilled (Saintilan and Hashimoto 1999). Studies of marsh sedimentation and accretion rates in the region using Surface Elevation Tables showed a correlation between the higher rate of mangrove encroachment and the rate of relative sea-level rise (Rogers et al 2006). In several estuaries, mangroves have gained elevation over periods of rapid sea-level rise, while salt marsh elevation gains have been modest (Rogers et al., unpublished). Modelling of these trajectories at a landscape scale using LiDAR-derived digital terrain models in the Hunter estuary, NSW suggest that mangrove extent in 2100 will increase under most IPCC sea-level rise scenarios, while the fate of salt marsh will be determined by decisions about the management of low-lying coastal land currently protected from saline intrusion (Rogers et al., unpublished).

6 Summary

Changes in atmospheric [CO_2], air and sea temperatures, precipitation, and sea level will give rise to complex interactions among variables influencing spatial distributions as well as structure and function of mangrove and salt marsh ecosystems. In addition to influencing climate and sea level, atmospheric [CO_2] will differentially affect plant growth through changes in photosynthetic rates and water use efficiency. The paucity of information about salt marsh and mangrove responses to CO_2, however, limits predictions of future shifts in species dominance and other responses. Until more field or greenhouse experiments can be undertaken, further insights may depend on modelling studies.

Similarly, few empirical data exist on responses of coastal plant communities to changes in temperature or precipitation; much of our understanding is based on observational studies, such as the response to episodic drought or freezing events. Limited predictions can be made based on observational data, in combination with general knowledge of species stress tolerances. Air and water temperatures determine

distributional limits of mangroves through low temperature stress and freezing events, and a warming climate can be expected to promote mangrove replacement of salt marsh in areas where dispersal is not limited. Aridity is also an important determinant of mangrove distribution at a global scale, and higher temperatures will drive regional changes in rainfall and the suitability of habitats for mangrove colonisation. Controls on distributional limits of salt marsh species have been less studied, but extreme events (droughts) have led to large-scale dieback, which allowed mangrove expansion; however, mangrove responses to aridity may be aided by improved water-use efficiency at higher levels of atmospheric CO_2.

Resilience of salt marsh and mangrove ecosystems to sea-level rise will depend on several factors and feedback relationships among processes controlling surface accretion and subsurface soil volume. Field studies involving Surface Elevation Tables in combination with measurements of physical and biological processes, as well as modelling efforts, have led to important insights into how salt marsh and mangrove wetlands may respond to increased rates of relative sea-level rise. Work during the past decade, in particular, has contributed to a more complete picture of geological, hydrological, and biological controls on soil elevations. Future work involving landscape-level approaches that incorporate geographic variation in sedimentary setting, tide range, climate and other global, regional, and local factors will facilitate predictions of salt marsh or mangrove persistence under anticipated sea-level rise scenarios.

This review has concentrated on the response of mangrove and salt marsh plants to climate change and associated drivers. Less is known of possible responses of fauna and ecosystem processes to future scenarios. Changes in temperature and humidity and the fragmentation and dislocation of habitats forced by global warming will have consequences for the resident and itinerant fauna and their interactions. Less obvious is how changes in atmospheric CO_2, climate, and sea-level will alter ecosystem-level processes, since these drivers in combination may have contrasting effects on primary production, decomposition, nutrient cycling, or food-web support. Future work will require multivariate approaches that allow simultaneous examination of several drivers of global change along with internal feedback pathways and linkages among physical and biological components.

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