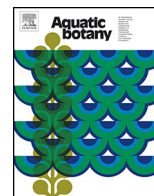




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Impacts of climate change on submerged and emergent wetland plants

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ABSTRACT

Submerged and emergent wetland plant communities are evaluated for their response to global climate change (GCC), focusing on seagrasses, submerged freshwater plants, tidal marsh plants, freshwater marsh plants and mangroves. Similarities and differences are assessed in plant community responses to temperature increase, CO₂ increase, greater UV-B exposure, sea level rise and other expected environmental alterations associated with GCC. Responses to most climate change variables are more similar within submerged plant communities, marine or freshwater, than between submerged vs. emergent plant communities. The submerged plants are most affected by temperature increases and indirect impacts on water clarity. Emergent plant communities (marshes and mangroves) respond most directly to climate change related hydrological alterations. Wetland plant communities overall appear to be adversely impacted by all climate change variables, with the exception of increased CO₂ in the atmosphere and the oceans, which in most cases increases photosynthesis. Effects of GCC on all these communities have already been seen with many others predicted, including: shifts in species composition, shifts in range and distribution, and declines in plant species richness. Other effects are associated with specific community types, e.g., salt marsh habitat lost to mangrove incursion, and decreases in submerged macrophyte coverage in lakes and estuaries, exacerbated by eutrophication. Sea level rise poses threats to all aquatic plant community types in the vicinity of the oceans, and changes in weather patterns and salinity will affect many. Overall, losses are likely in all these wetland plant communities yet their species can adapt to GCC to some degree if well managed and protected.

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1. Introduction

The wetlands evaluated here for their response to global climate change include submerged and emergent plant communities, ranging from marine to freshwater environments and including seagrasses, submerged freshwater plants, tidal marshes, freshwater marshes and mangroves. Most of these macrophyte communities are distributed in both tropical and temperate regions around the world, the exception being mangrove forests, which are restricted to the tropics (Tomlinson, 1986). Characterized by regu-

lar, seasonal, or occasional inundation, their health and survival is influenced by changes on adjacent land as well as adjacent and surrounding waters. Global climate change is likely to have greater and more immediate effects on wetland ecosystems than many habitats that are restricted to either terrestrial or oceanic environments. In developed areas, these plant communities are already stressed, sometimes to a great degree, by direct human activity; the indirect impacts of climate change will exacerbate existing stressors (Keddy, 2000).

The International Panel on Climate Change (IPCC, 2013; Pachauri et al., 2014) provides strong evidence that for the last three decades, globally averaged combined land and ocean surface temperatures have been successively higher than any prior decade since the first records in 1850 (Fig. 1). Ocean temperatures by 2100 are predicted

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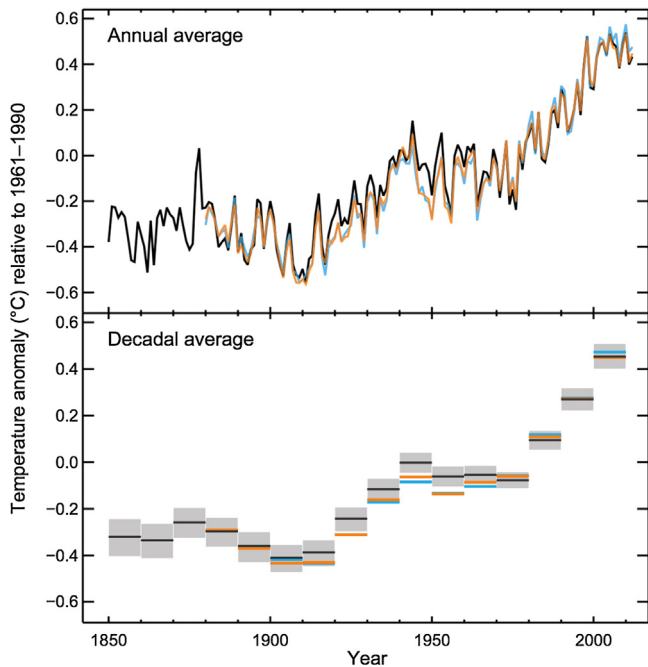


Fig. 1. Observed global mean combined land and ocean surface temperature anomalies, from 1850 to 2012 from three data sets. Top panel: annual mean values. Bottom panel: decadal mean values including the estimate of uncertainty for one dataset (black). Anomalies are relative to the mean of 1961–1990 (with permission, figure and legend taken from figure SPM.1 (a) from IPCC, 2013: Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK and New York, USA.

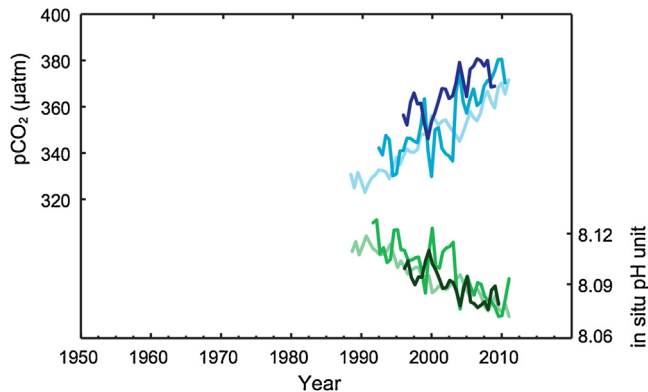


Fig. 2. Multiple observed indicators of a changing global carbon cycle: partial pressure of dissolved CO₂ at the ocean surface (blue curves) and in situ pH (green curves), a measure of the acidity of ocean water. Measurements are from three stations from the Atlantic (29°10'N, 15°30'W—dark blue/dark green; 31°40'N, 64°10'W—blue/green) and the Pacific Oceans (22°45'N, 158°00'W—light blue/light green). (with permission, figure and legend taken from Figure SPM.4 (b) from IPCC, 2013: Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK and New York, USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to increase 2 to 4°C due to greenhouse gas effects (Pachauri et al., 2014). Atmospheric carbon dioxide concentrations (Fig. 2) have increased by over 40% since the Industrial Revolution (Pachauri et al., 2014). Assessments show a sea level rise of 17–32 cm over the past 100 years; now, worst-case projections predict sea level

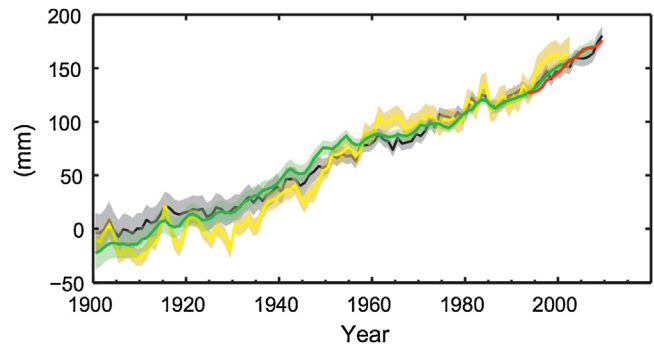


Fig. 3. Multiple observed indicators of a changing global climate: global mean sea level relative to the 1900–1905 mean of the longest running dataset, and with all datasets aligned to have the same value in 1993, the first year of satellite altimetry data. All time-series (coloured lines indicating different data sets) show annual values, and where assessed, uncertainties are indicated by coloured shading (with permission, figure and legend taken from figure SPM.3 (d) from IPCC, 2013: Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK and New York, USA (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rise (SLR) rates of 1.6 cm yr⁻¹ by 2100 (Pachauri et al., 2014) equivalent to a 1.9 m sea level increase over the next 100 years (Fig. 3). Other factors including changes in precipitation, salinity, and UV-B are also connected to climate change and will differentially affect various wetland plant communities.

The objectives of our paper are to review the pertinent recent literature and, from it, summarize the impacts to date of global climate change on wetland plants as well as projecting possible future impacts. Our approach is to assess the major submerged and emergent plant communities, considering the effects of rising temperature, increased CO₂, increased UV-B radiation, salinity changes, and sea level rise on their typical species.

The plant communities are ordered on an immersion gradient, from fully submerged salt and freshwater species to emergent salt and freshwater marsh species and finally, mangrove forests.

2. Seagrasses

Seagrasses are rooted marine submerged flowering plants that inhabit the world's coastal oceans and provide numerous ecosystem services to these waters and beyond, including filtration, primary production, and habitat and food for fish and wildlife. They are found on the tropical, temperate, and sub-arctic shallow coastal margins of all continents except Antarctica. Seagrasses support food webs of importance to humans and are critical food for endangered sea turtles and sirenians. These plants are declining worldwide by about 7% per year and "... global climate change is predicted to have deleterious effects on seagrasses and is emerging as a pressing challenge for coastal management" (Waycott et al., 2009).

2.1. Temperature

Seagrasses are strongly influenced by water temperature, which affects plant physiological processes, growth rates, and reproduction patterns, and determines the geographic distribution of species based on their temperature tolerances (Short and Neckles, 1999). While seagrass shoot mortality rates have been shown to increase with rising water temperatures (Díaz-Almela et al., 2009; Oviatt, 2004; Reusch et al., 2005), higher temperatures generally result in an increase in production of reproductive shoots (Thom et al.,



Fig. 4. Seagrass, *Enhalus acoroides*, with bleached leaves after experiencing low-tide July seawater temperatures of 43 °C in Kavieng, Papua New Guinea (SeagrassNet 2001).

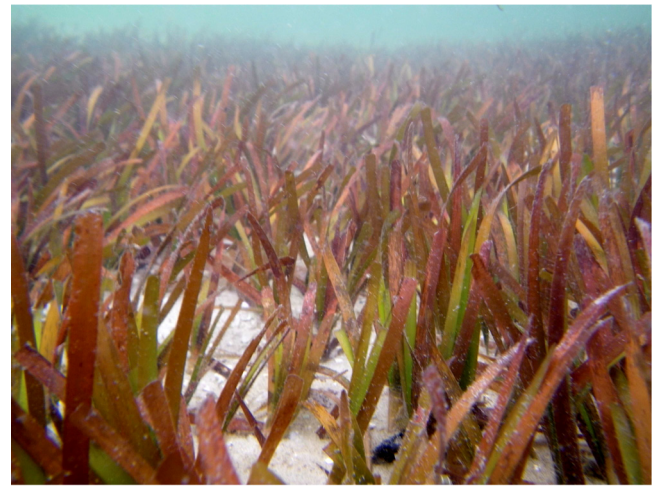


Fig. 5. Seagrass (*Cymodocea rotundata*) with red leaves resulting from UV-B exposure inducing anthocyanin production in Trang, Thailand (SeagrassNet 2008).

2014; Kaldy, 2014; Short and Coles, 2001; Short and Neckles, 1999). The relationship between increasing temperatures and seagrass reproduction can be seen in Díaz-Almela et al. (2007) where a mass flowering event in *Posidonia oceanica* occurred during a warm period in 2005.

Temperature stresses are most obvious at the edges of species ranges, particularly in the extreme tropics, at temperate-tropical interfaces, and at temperate-polar interfaces. The optimal growth temperature for temperate seagrass species ranges between 11.5 °C and 26 °C, whereas the optimal growth temperature for tropical/subtropical species is between 23 °C and 32 °C (Lee et al., 2007). There is a limited understanding of actual temperature tolerance by individual species although for the most studied temperate seagrass species, *Zostera marina* L., research has shown that temperatures above 25 °C result in responses that include growth reduction (Short, 1980; Kaldy, 2014; Thom et al., 2014) and declines in net primary production have been reported above 23 °C (Moore et al., 2014b).

Tropical seagrass species in the Gulf of Mexico (e.g., *Syringodium filiforme* and *Thalassia testudinum*) showed reduced productivity at high summer temperatures (Barber and Behrens, 1985). In Australia, at water temperatures above 40 °C, leaf growth rates of *Cymodocea rotundata*, *Halodule uninervis* and *Thalassia hemprichii* were reduced, with *C. rotundata* the most resilient to high water temperatures (Collier and Waycott, 2014). Shoot density declined in *Halophila ovalis* as well as *H. uninervis* and *C. rotundata* (Collier and Waycott, 2014) indicating change in plant resource allocation. Seagrass physiological stress was revealed in increased plant respiration rates at higher temperatures (Collier et al., 2011); reductions in PSII at 40 °C indicated photoinhibition or damage of PSII reaction centers (Campbell et al., 2006; Ralph, 1998).

In field monitoring near the equator in Papua New Guinea, damage to *Enhalus acoroides* was documented at water temperatures reaching 43 °C on a shallow subtidal reef flat during low spring tides, producing leaf death, although the below-ground roots and rhizomes survived (Fig. 4). Similar seagrass “leaf bleaching” has been reported in several locations after elevated temperature events (F. Short, pers. obs.). Large scale seagrass declines from high water temperature have only been reported from the Mediterranean, where seawater warming is triggering *P. oceanica* shoot mortality and thinning of meadows in relatively pristine areas (Pergent et al., 2015). Increased *P. oceanica* shoot mortality rates were reported at temperatures of 26–29 °C (Marba and Duarte, 2010).

Higher seawater temperatures increase the frequency and intensity of extreme weather events, which can include more rain, more runoff and turbidity, and reduced salinity as well as direct physical damage. Instances of storm damage, from denudation by a cyclone in Queensland, Australia (Birch and Birch 1984) to seagrass burial from a severe hurricane in Yucatan, Mexico (Marba et al., 1994), were documented and provided opportunities to assess seagrass recovery. More recent storms in Queensland caused extensive seagrass loss (Rasheed et al., 2014); after a major cyclone, seagrass and macroalgae cover declined greatly but then recovered in four years. A major *Z. marina* decline occurred after a typhoon in South Korea (Kim et al., 2015). In contrast, storms do not always harm seagrass plants: e.g., little damage was found in Florida after several hurricanes (Pu et al., 2014).

2.2. Carbon dioxide

Increasing atmospheric carbon dioxide is now known to be elevating the amount of CO₂ in coastal waters (Fig. 2), a process termed “ocean acidification,” with a 26% increase in acidity (0.1 pH unit in ~200 years) since the Industrial Revolution (Pachauri et al., 2014). Ocean acidification increases seagrass production (Garrard and Beaumont, 2014) and seagrass carbon storage (Russell et al., 2013). Locations with naturally high CO₂ (near volcanic vents) showed increased *Cymodocea nodosa* productivity (Apostolaki et al., 2014). Experimental work in *Z. marina* mesocosms showed that enrichment with CO₂ led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in full light, but did not alter biomass-specific growth rates, leaf size, or leaf sugar content of above-ground shoots (Palacios and Zimmerman, 2007). The uptake of CO₂ by seagrasses and other aquatic plants reduces the CO₂ concentration in seawater and buffers ocean acidification in shallow coastal waters.

2.3. UV-B radiation

With climate change comes increased solar UV (ultraviolet radiation; Heggelin and Shepherd, 2009), which has been shown to affect seagrasses via plant production of UV-B blocking compounds. Several species of seagrass from locations with high UV-B are documented having red-to-purple leaves or red spots, and the reddening (Fig. 5) has been linked to a build-up of anthocyanin molecules in the leaf tissue (Novak and Short, 2010, 2011). All observed leaf reddening is documented to occur in the tropics and the temperate

southern oceans (Novak and Short, 2010). Production of secondary compounds like anthocyanins requires plant resources that would otherwise contribute to growth and production (Novak and Short, 2012). These secondary UV-B blocking compounds likely protect the plants' photosystems; seagrass damage or death from increased UV-B has not been documented.

2.4. Salinity

Changes in freshwater run-off from land with global climate change may increase or decrease the salinity of coastal waters where most seagrasses grow. Predicted increases in rainfall as a result of increased and more intense storms will result in reduced salinities for possibly prolonged periods in many areas that support seagrass while drought or desertification in other areas may reduce run-off and raise coastal salinities.

Seagrasses in general do best at high salinities but there is considerable variation between species. Eelgrass (*Zostera marina*) germinates poorly at salinities <5 (Pan et al., 2011; Nejrup and Pedersen 2008; Salo et al., 2014). Survival and growth of adult eelgrass plants is maximal at a salinity of 30, with best growth generally between 12.5 and 30 (van Katwijk et al., 1999; Salo et al., 2014). The information in the literature indicates that seagrass salinity effects may differ with temperature, with plant adaptation to local exposure, or other conditions; e.g., the eelgrass wasting disease thrives in intermediate salinities of 12–25 and there is evidence that eelgrass survived the wasting disease epidemic of the 1930s in fresher parts of estuaries (Burdick et al., 1993). *Zostera muelleri*, like eelgrass a temperate species, germinates best at salinities <8 or with higher salinities intermixed with pulses of fresh water (Stafford-Bell et al., 2016). For *Amphibolis antarctica*, maximum growth and survival occur at high salinity (35–42) (Walker and McComb, 1988). In the Mediterranean Sea, *Posidonia oceanica* survives up to a salinity of 43 (Sandoval-Gil et al., 2012), while *Cymodocea nodosa* survives up to 47 (Terrados and Ros, 1991). Tropical species vary in their optimum salinity for growth: ~40 for *Thalassia testudinum* (Berns, 2003; Kahn and Durako, 2006; Lirman and Cropper, 2003); 25 for *Syringodium filiforme* (Lirman and Cropper, 2003); 30 for *Halophila johnsonii* (Torquemada et al., 2005); *Halodule wrightii* shows similar growth between 5 and 45 (Lirman and Cropper, 2003). In contrast, *Ruppia maritima* germinates and survives best between 0 and 10 and shows reduced growth at 20 (Berns, 2003; Kahn and Durako, 2006).

2.5. Sea level rise

The direct effects of sea level rise (Fig. 3) in the coastal oceans are only now beginning to be detected in seagrass ecosystems, but increasing rates of sea level rise intensify concern for these coastal habitats. Sea level rise has already caused regression of the deep edge of *Posidonia oceanica* in the Mediterranean, as seen by long-term monitoring programs (Pergent et al., 2015). Some losses at the deep edge of seagrass meadows may be compensated by migration shoreward, however this is often prevented by anthropogenic alteration of shorelines (Short and Neckles, 1999) leading to 'coastal squeeze' (Doody, 2004). In a model for Humboldt Bay, California, Stillman et al. (2015) predict that eelgrass could potentially support up to five times as many brant geese (*Branta bernicla*) because the habitat could redistribute shoreward onto intertidal mudflats, in response to higher sea level. Models have shown that a sea level rise of 1.1 m by 2100 would result in a 17% reduction in seagrass area in Moreton Bay, Australia due to insufficient light reaching the bed's deep edge but that a 30% gain in water clarity would compensate to sustain seagrass area (Saunders et al., 2013).

In conclusion, of the major aspects of global climate change, temperature increase probably poses the most immediate threat

to seagrasses, and is also the most broadly studied. There are many interactions between climate factors influencing both the magnitude of other stressors and the physiological responses of different seagrass species. Salinity impacts will depend on climate with increased storms reducing salinity and desertification creating hypersaline conditions. Sea level rise impacts will vary depending on coastal configurations; areas having extensive shallow mudflats will provide an opportunity for seagrass meadow expansion. Carbon dioxide increases will in large part enhance seagrass growth. Seagrass declines will have far reaching consequences for the many species of animals that rely on seagrass meadows for habitat and nutrition. Direct human impacts from coastal development and other activities continue to be the major factor affecting seagrasses worldwide but are exacerbated by climate change (Björk et al., 2008), and seagrasses continue to decline at alarming rates.

3. Submerged freshwater plants

Submerged plants play an important role in the ecological function of shallow lakes, reservoirs, and drainage systems (Jeppesen et al., 1998). These plants form important components of these freshwater ecosystems, creating refuges for zooplankton and young fish, habitat for organisms ranging from epiphytic algae and macroinvertebrates to amphibians, and a food source for, for instance, herbivorous birds. Furthermore, they prevent resuspension of sediment and are important competitors for nutrients and light with phytoplankton. A combination of these factors often results in macrophyte-dominated systems being clear and having good water quality. Eutrophication and herbivory are well-known stressors negatively affecting submerged macrophyte growth (e.g., Weisner et al., 1997). Climate change is a more recent threat to submerged macrophytes and often acts in synergy with eutrophication (Moss et al., 2011).

3.1. Temperature

Experimental work has shown that an increase in temperature may positively influence macrophyte growth (Barko and Smart, 1981; McKee et al., 2002). Depending on the species, it may either compress or extend the growing period (Barko and Smart, 1981; Jeppesen et al., 2010; Patrick et al., 2012). Comparisons of macrophyte cover in Dutch lakes between years with warm and cold springs confirm the positive influence of temperature (Scheffer et al., 1992). Earlier season warming has furthermore been related to deeper macrophyte growth and higher biomasses in freshwater lakes (Rooney and Kalff, 2000) as well as to higher biomasses in the Baltic Sea (Kotta et al., 2014).

Winter temperatures seem to play a crucial role as well. A cross-continental analysis suggests that in regions where climatic warming is projected to lead to fewer frost days, macrophyte cover will decrease unless the nutrient levels are lowered (Kosten et al., 2009). The effect of winter warming depends on local circumstances, however, with a resulting positive or negative effect on macrophyte biomass or coverage (Bayley et al., 2007). Severe winters delayed macrophyte growth in spring and lowered the maximum biomass yield in a Dutch lake (Best and Visser, 1987), whereas they triggered abundant macrophyte growth in a Swedish lake (Hargeby et al., 2004). Clearly, factors other than winter temperature play a role as well. A study on a large set of boreal lakes showed that 80% of the lakes switched from clear to turbid from one year to another. In these lakes, harsh winters lead to plant senescence and spring conditions – including temperature, water level and wind induced turbidity – determine whether phytoplankton or submerged macrophytes win the competition early in the year. In the Netherlands the decrease in macrophyte growth was

attributed to low spring temperatures slowing plant development, so that full maturity was attained only after diurnal insolation had already decreased (Best and Visser, 1987). In Sweden, on the other hand, severe winters with long ice cover cause fish kills resulting in low biomasses of benthivorous and planktivorous fish, which may set off a complex set of community interactions, including low bio-turbation and low internal nutrient recycling, favoring macrophyte growth (Hargeby et al., 2004).

As different macrophyte species respond differently to changes in average temperature (Barko and Smart, 1981; McKee et al., 2002; Netten et al., 2011; Scheffer et al., 1992; Zhang et al., 2015) as well as to heat waves (Cao et al., 2016) warming also directly influences macrophyte community composition. More importantly from the point of view of ecosystem functioning, warming may affect the competitive strength of submerged macrophytes relative to phytoplankton. In nutrient-rich lakes, warming tends to enhance eutrophication problems triggering a wide range of changes in community interactions and hampering macrophyte growth (Fig. 1 and Moss et al., 2011). In more nutrient-poor lakes, however, warming has more ambiguous effects on macrophyte coverage (Kosten et al., 2011). Climate change strongly impacts nutrient dynamics in freshwater systems, thereby indirectly influencing macrophyte growth. Temperature strongly influences internal nutrient loading, for instance, by enhancing sediment phosphorus release at higher temperatures (Boers, 1986; Smolders et al., 2006; Varjo et al., 2003) and by enhancing denitrification (Veraart et al., 2011).

3.2. Storms and precipitation

Changes in precipitation patterns will strongly affect external nutrient loading with a likely increase in phosphorus and nitrogen loadings in regions where precipitation will increase (Bouraoui et al., 2004; Chang, 2004; Jeppesen et al., 2009; Jeppesen et al., 2011). The more eutrophic conditions resulting from increased loadings may favor the growth of floating plants and phytoplankton at the expense of submerged plants (Fig. 6). Drier periods in Mediterranean and semi-arid regions may lead to lower water tables or even complete (temporal) disappearance of water systems. Evapoconcentration of nutrients and an increase of fish per unit volume of water may have negative effects on submerged macrophytes, but reduced water levels may also improve light conditions and hence stimulate macrophyte growth (Beklioglu, 2006; Bucak et al., 2012; Coppens et al., 2015)

3.3. Carbon dioxide

The effect of increased atmospheric CO₂ concentrations on the production and species composition of submerged freshwater plants strongly depends on the type of water. In many regions a large portion of shallow lakes are naturally strongly supersaturated with CO₂ with respect to the atmosphere (e.g., Cole et al., 1994; Kosten et al., 2010). An increase in atmospheric CO₂ has relatively little influence on the CO₂ concentration in these often naturally strongly supersaturated waters. Certainly, CO₂ limitation can occur in eutrophic lakes in dense macrophyte stands during the day (Krausejensen and Sandjensen, 1998) and depending on the gas diffusion rate, increased atmospheric CO₂ may have a positive effect on growth in this case (Schippers et al., 2004). Still, recent work suggests that in a large share of shallow lakes most of the CO₂ originates from decomposition of organic matter in the sediment or through the input of groundwater (Weyhenmeyer et al., 2015).

In small eutrophic freshwater systems, an increase in atmospheric CO₂ may lead to the enhanced growth of floating plants or floating algal mats. Due to their position on the water surface they can profit most from the increased CO₂ availability (Speelman et al., 2009). Their increased growth may lead to low underwa-

ter light intensities due to which they can outcompete submerged macrophytes (Netten et al., 2010).

In oligotrophic softwater lakes that are naturally CO₂-poor, increased CO₂ (from the atmosphere and enhanced respiration within the lake and in its watershed) does pose a threat. These types of lakes occur in high numbers in high latitude regions and are characterized by isoetids (e.g., *Isoetes*, *Littorella* and *Lobelia*) (Murphy, 2002). Isoetids obtain most of their CO₂ via their extensive root systems. At higher CO₂ concentrations these communities can be replaced by species that better utilize CO₂ in the water column such as the elodeid *Myriophyllum* sp. Enhanced atmospheric CO₂ may therefore lead to a shift in species composition in these systems (Spiereburg et al., 2009; Spiereburg et al., 2010).

3.4. UV-B radiation

Similar to the effects of increased UV-B radiation on sea-grasses (see Section 2.3) the effect on freshwater macrophytes and charophytes varies among species and growing conditions. Several studies found negative effects (e.g., De Bakker et al., 2005; Farooq et al., 2000), some studies found no effect (e.g., Germ et al., 2002). Even positive effects of enhanced UV-B on species that are pre-adapted to a high UV-radiation environment are reported (Hanelt et al., 2006). Macrophytes have different mechanisms to protect themselves from UV-B damage which may vary with their position in the water column (Rae et al., 2001; see also Section 2.3); especially floating plants or plants subject to lowering water tables may be susceptible (De Bakker et al., 2005; Farooq et al., 2000). Although the increase in UV-B radiation is likely to be subtle, it may nevertheless lead to changes in macrophyte community composition (Vincent and Roy, 1993).

3.5. Sea level rise and salinity

Changes in salinity, either due to increased seawater intrusion or due to evapoconcentration, exert strong effects on freshwater ecosystems and submerged macrophytes are specifically vulnerable compared to other biota (see Fig. 4 in Herbert et al., 2015 for generalized salinity thresholds for different groups of biota). Laboratory experiments in which freshwater species were exposed to different levels of salinity reveal a wide range of salt sensitivities. Sublethal effects include depression of growth rate and plant size at higher salinities and halted or reduced sexual and asexual reproduction (e.g., James and Hart, 1993; Sim et al., 2006). Lethal effects of enhanced salinity have been described as well, with survival of adult plants decreasing at the same rate at which salinity increased (Sim et al., 2006). Abrupt changes in salinity, as occurring for instance during storms or due to seawater inlet to compensate for freshwater shortages, may be particularly detrimental for freshwater macrophytes. The negative effects of increased salinity on macrophytes in freshwater systems contrast with the apparent resilience of brackish species to variations in salinity as observed, for instance, in the Baltic Sea (Kotta et al., 2014).

Field observations also point to morphological changes induced by salinity. *Chara aspera*, for instance, tends to elongate its shoots when growing in freshwater conditions but not at higher salinities where the plants were short and often covered with filamentous algae or shaded by other rooted submerged macrophytes (Blindow and Schütte, 2007). Even when increased salinity is not lethal, the competitive unfavorable conditions may eventually lead to the disappearance of freshwater macrophytes from brackish systems. Paleo records from the Argentinean Pampa, that has undergone temporal shifts in salinity due to changes in the evaporation-to-precipitation ratios (Stutz et al., 2012), as well as field observations in Australia, where many freshwater systems are influenced by rising saline groundwater (Sim et al., 2006), confirm this: freshwa-

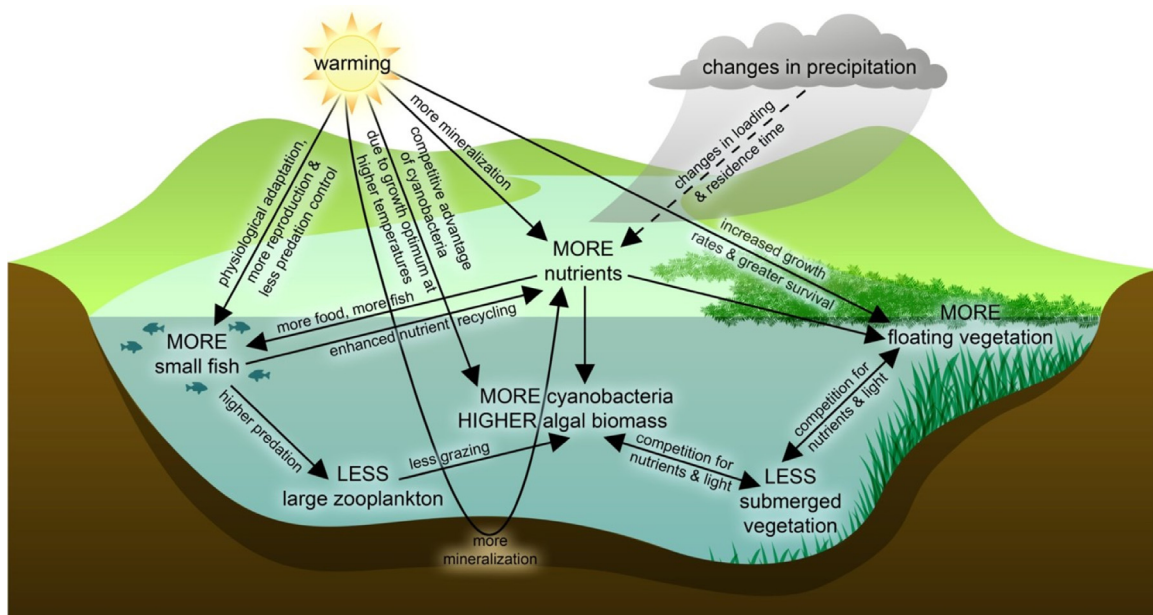


Fig. 6. Overview of complex community interactions that lead to less submerged macrophytes as a consequence of changes in temperature and precipitation (source: Moss et al., 2011). Reproduced by permission of the Freshwater Biological Association. Drawing by A.R. Joyner.

ter macrophyte communities may be fully or partially replaced by salt-tolerant species. Macrophytes may also disappear altogether with brackish systems switching to a microbial mat-dominated system (Davis et al., 2003; Strehlow et al., 2005). Even when macrophytes remain abundant in systems with rising salinity, their effect on water clarity is generally much lower than in freshwater systems due to co-occurring shifts in food web structures including a decrease in top-down control on phytoplankton (Jeppesen et al., 1994). This phenomenon has been described for multiple shallow Mediterranean lakes that are exposed to increasing droughts and coinciding increases in salinity (e.g., Beklioglu et al., 2007; Beklioglu and Tan, 2008).

In conclusion, climate change, particularly warming and changes in precipitation regimes, sets off a complex range of interacting processes that will likely lead to a decrease in submerged macrophyte coverage in mesotrophic and eutrophic lakes. In soft-water oligotrophic lakes, increased CO₂ concentrations will lead to a shift in community composition.

4. Tidal marshes

Tidal marsh plant communities occur along salinity gradients in coastal estuaries, and include salt marshes, brackish marshes and tidal freshwater marshes. Unlike mangroves, tidal marsh vegetation can withstand periodic freezing events, so it is found in the colder climates of temperate, subarctic, and arctic zones along protected shorelines (McKee et al., 2012). As discussed below, the increasing temperatures and CO₂ levels, changes in rainfall patterns, and rising sea levels associated with climate change will directly affect plants in tidal marshes.

4.1. Temperature

Increases in temperature associated with climate change are predicted to result in greater marsh productivity, at least in northern latitude salt marshes. Kirwan et al. (2009) observed a latitudinal gradient in the aboveground productivity of tidal marshes dominated by *Spartina alterniflora* in North America, and predicted that a 2–4 °C temperature rise would result in a 10–40% increase in productivity. In experimental studies in New England, aboveground

growth of the dominant salt marsh species *Spartina patens* and *S. alterniflora* increased 15–45% with mild warming (Gedan et al., 2011), and maximum stem heights of the same species increased 8% (Charles and Dukes, 2009).

Higher temperatures are predicted to lead to reductions in salt marsh plant species richness and to changes in marsh species composition. Experimental studies in New England found that in warmed plots (0.33–3.28 °C temperature increase), *Spartina patens* outcompeted other plant species in highly diverse salt marsh forbs (Gedan and Bertness, 2009). And in Australian salt marshes, species richness was observed to be less at lower latitudes, where temperatures are higher (McKee et al., 2012).

Mangroves are predicted to displace salt marshes in many areas as the limits to mangrove growth imposed by freezing events decrease. When freeze frequencies are fewer than once every twelve years, mangroves expand into areas previously occupied by salt marshes (Henry and Twilley, 2013; see Section 6.1). Expansion of mangroves into former tidal marsh habitat has already occurred on at least five continents around the world (Saintilan et al., 2014). For example along the Texas coast, mangrove area increased by 74% from 1990 to 2010 (Armitage et al., 2015).

4.2. Rainfall

The response of tidal marshes to changes in rainfall patterns will depend on existing salinity levels in marsh soils, the degree of soil saturation, and the extent to which rainfall and discharge patterns change. Where soils are normally hypersaline, such as in southern California marshes, increased rainfall will reduce salinity levels, resulting in increased plant growth and greater seed germination (Zedler, 1983; Noe and Zedler, 2001). But in brackish and salt marshes where soil salinity levels are lower, more rainfall can contribute to greater productivity of nuisance or invasive species such as *Phragmites australis* (McKee et al., 2012).

Conversely, less rainfall can alleviate stress due to waterlogging in brackish and salt marshes, leading to increased productivity of marsh species such as *Spartina alterniflora* and *Spartina patens* (Charles and Dukes, 2009). But in marshes where soils are not waterlogged, less rain will increase soil salinity and will decrease moisture levels, resulting in reduced productivity. In northern

Netherlands, a thirteen-year study showed rainfall deficits to correlate with reduced peak aboveground biomass in four of six plant communities (*Elymus pycnanthus*, *Festuca rubra*/*Armeria maritima*, *Juncus gerardii* and *Artemisia maritima*) (De Leeuw et al., 1990). Changes in rainfall patterns may also result in shifts in marsh plant species composition (Zedler, 1983; McKee et al., 2012), and in the loss of salt marsh habitat to encroaching mangroves (Eslami-Andargoli et al., 2009).

4.3. Carbon dioxide

Elevated CO₂ levels can lead to increased carbon fixation and productivity of C3 tidal marsh plants such as *Bolboschoenus* (formerly *Scirpus*) *maritimus*, *Schoenoplectus americanus* and *Puccinellia maritima*, but this same effect has not been seen in C4 plants (including the *Spartina* species), which already have the ability to concentrate CO₂ at the site of carbon fixation (Erickson et al., 2007; McKee et al., 2012). Higher CO₂ levels may also contribute to the ability of C3-dominated plant communities to tolerate stressors associated with climate change such as increased flooding and salinity (Cherry et al., 2009).

With greater CO₂ levels, water use efficiency (amount of organic matter produced per amount water used) improves in both C3 and C4 plants, as stomata are not open as long when CO₂ concentrations are higher. For example, Li et al. (2010) observed an increase in ecosystem water use efficiency (EWUE) in both C3 sedge (*Scirpus olneyi*, 82% increase) and C4 grass (*Spartina patens*, 84% increase) communities over a 12 year field experiment in a Chesapeake Bay marsh where CO₂ levels were elevated +340 ppm above ambient levels in open top chambers. EWUE was determined as net CO₂ exchange divided by evapotranspiration.

Higher levels of CO₂ in the atmosphere should therefore lead to greater productivity and growth of C3 marsh plants and higher water use efficiency in both C3 and C4 marsh species. It follows that marsh species composition should change over time as a result of elevated CO₂, with C3 species outcompeting C4 species, but evidence for this is currently lacking. Interspecific competition has been observed to affect how C3 plants respond to higher CO₂ concentrations, and plants in mixed communities do not always respond in the same way as individual species (McKee et al., 2012). For example, in northern European salt marshes, where *Puccinellia maritima* (C3) and *Spartina anglica* (C4) are the dominant species at higher and lower elevations, respectively, *P. maritima* grew less in elevated CO₂ conditions (+340 ppm) when it had to compete with *S. anglica* than when it grew alone (Gray and Mogg, 2001).

More CO₂ can also have indirect effects on marsh elevation by stimulating plant growth belowground. In a mixed C3/C4 plant community brackish marsh, Langley et al. (2009) found that increasing atmospheric CO₂ levels 340 ppm above ambient levels resulted in greater belowground productivity, which contributed to gains in marsh surface elevation.

4.4. Sea level rise

In order to persist into the future, tidal marshes must balance surface elevation in relation to sea level (Fig. 7). Mineral sedimentation and organic matter accumulation rates must be able to keep pace with sea level rise, and marsh plants influence both processes (Morris et al., 2002). Aboveground vegetation slows down moving waters on the marsh surface, trapping suspended sediment, while above- and belowground vegetative growth add to soil organic matter accumulation, contributing to marsh accretion (Baustian et al., 2012; Hatton et al., 1983; Nyman et al., 2006; Langley et al., 2009). Belowground roots and rhizomes are also important in stabilizing soils and preventing erosion (Gedan et al., 2011). Because some marshes accrete primarily via organic matter

accumulation whereas others depend more on sediment deposition, models designed to predict marsh response to sea level rise can give contradictory results. Several predictive models have concluded that marshes dominated by inorganic sediment inputs respond better to rising sea levels than those with scant inorganic sediment supply. But if marsh plant productivity is high, even tidal marshes whose soils are built primarily by organic matter inputs may persist (Fitzgerald et al., 2008).

Sediment load in the water column and tidal range are reported to be the most important factors in determining whether a marsh will keep up with sea level rise (Kirwan and Megonigal, 2013). Because these conditions vary in estuaries around the world, Kirwan et al. (2010) modeled threshold rates for sea level rise under different tidal range and sediment load combinations. They predicted that where sediment concentrations or tidal ranges are low, marshes are likely to be replaced by subtidal habitat in the near future, given conservative projections of sea level rise (~0.5 cm yr⁻¹). The models also predicted that if SLR is >2.0 cm yr⁻¹, even marshes with a tidal range of 1 m and sediment concentrations of 30 mg l⁻¹ will drown by the end of the century.

If marshes gain in elevation, they can migrate shoreward into upland or freshwater wetland areas, unless natural or human-constructed barriers block their paths, resulting in “coastal squeeze” (Redfield, 1965; Doody, 2004; Chmura, 2011). Or, if accretion does not keep pace with sea level rise, marshes will become unstable, reaching their threshold of resilience, and drown (Fitzgerald et al., 2008; Kirwan et al., 2010; McKee et al., 2012).

Increasing exposure to tidal waters creates stressful conditions for marsh plants, due to more reduced soil conditions, higher salinity levels and the accumulation of phytotoxins such as sulfide (Lamers et al., 2013). It is most likely that the species composition of tidal marshes will change with rising sea levels. In salt marshes along the northeastern U.S. coast, the high marsh species *Spartina patens* will decline and the low marsh *S. alterniflora* will increase (Langley et al., 2013; Donnelly and Bertness, 2001; Smith, 2009). In tidal freshwater and brackish marshes, exposure to higher salinity levels for an extended period of time will cause a decline in species richness as more salt-tolerant species invade (Sharpe and Baldwin, 2012). Species richness decline is already occurring in some tidal freshwater marshes, with the encroachment of *S. alterniflora* and the invasive *Phragmites australis* (Sutter et al., 2015). In the Netherlands, Van Dobben and Slim (2012) monitored plant species composition in a subsiding tidal marsh and then modeled future alterations due to climate change factors, including increased sea level, storm frequency, and precipitation. They predicted a strong change in species composition in the next century as a result of sea level rise, with a loss of common species and an increase in rare species of extreme habitats.

It is challenging to predict how tidal marshes will respond to sea level rise because the feedback mechanisms that have historically contributed to marsh stability are influenced by multiple factors. These include the increasing temperatures and CO₂ levels associated with climate change, but also greater nitrogen inputs and the introduction of new plant and animal species (Kirwan and Megonigal, 2013).

4.5. Interacting factors

Predicting the effects of climate change on tidal marshes requires considering the interactions of a variety of factors, which researchers are now investigating using modeling and experimentation. For example, Kirwan and Mudd (2012) modeled the effect of warming and sea level rise on a *Spartina* marsh and discovered that at low rates of SLR, warming led to reduced organic matter accumulation. But at higher SLR rates, warming resulted in greater organic matter accumulation, allowing marshes to accrete and per-

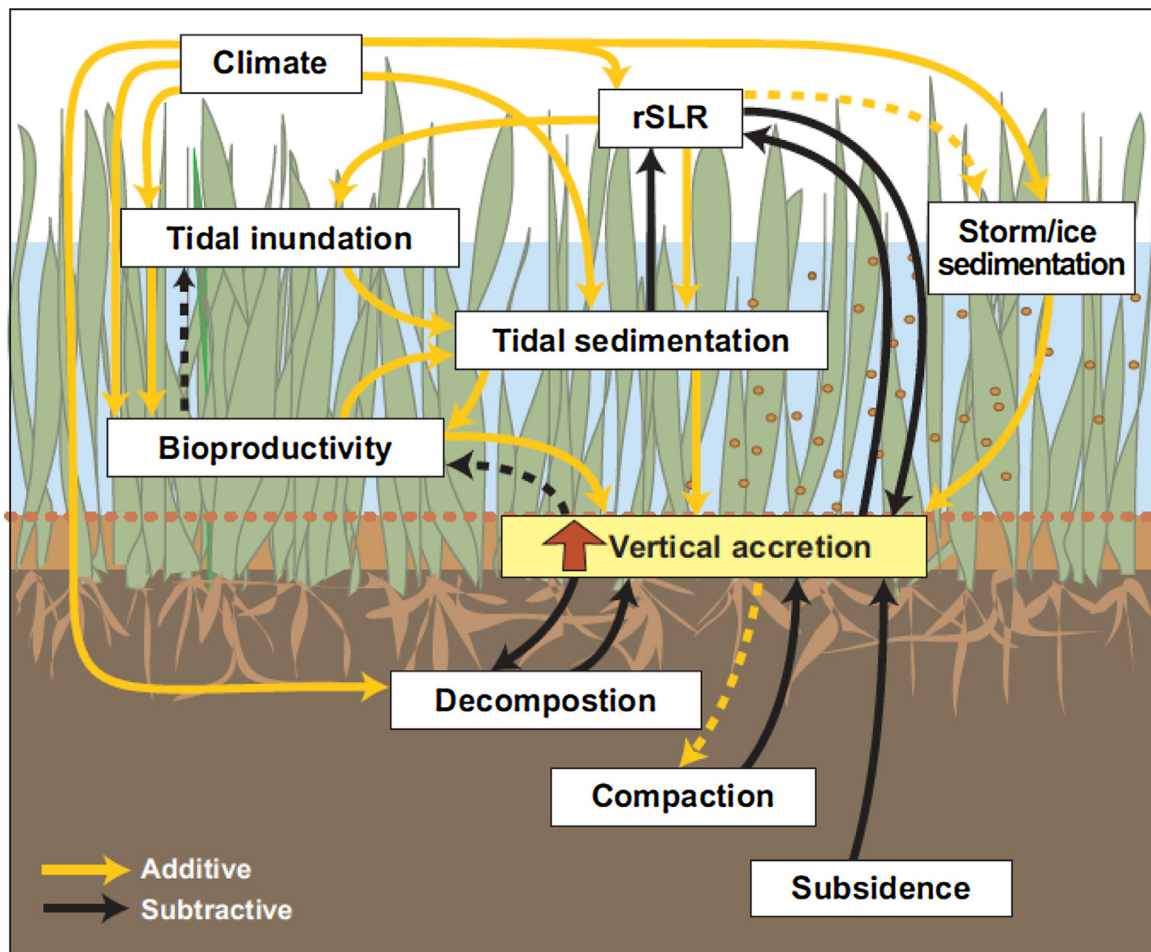


Fig. 7. Conceptual model of major factors affecting salt marsh elevation. “Additive” = increases marsh elevation; “subtractive” = lowers marsh elevation; rSLR = relative sea level rise (Fitzgerald et al., 2008).

sist. These accretion rates were maintained until 2075, followed by marsh drowning 10 years later.

The effects of elevated levels of nitrogen, combined with higher CO₂ concentrations and flooding stress on tidal marshes is an active area of research. In one study, additional CO₂ and nitrogen initially led to increased productivity of C3 plants in a brackish tidal marsh. But by year three, plant community composition had shifted due to added nitrogen, with expansion of C4 species limiting the ecosystem’s ability to respond to elevated CO₂ levels (Langley and McGonigal, 2010). In another study, where sea level was manipulated along with CO₂ and nitrogen over two growing seasons, researchers found that sea level was the dominant factor, with more flooding resulting in decreased above- and belowground marsh plant growth. Depending on the flooding regime, the effect of added nitrogen on plant growth and survivorship varied (Langley et al., 2013). To predict the interacting effects of climate change stressors plus other anthropogenic impacts on tidal marshes, additional research that includes multiple variables is needed.

In summary, the effects of climate change on tidal marshes are difficult to predict, given the variety and range of influencing factors. It is likely, however, that marshes will experience a decline in plant species richness and that their species composition will change. Plant productivity and water use efficiency will increase in many marshes, possibly mitigating some negative effects, but marsh habitat will be lost due to marsh drowning, coastal squeeze and displacement by mangroves.

5. Freshwater marshes

Freshwater marsh is a broad class of wetlands that contains emergent herbaceous vegetation adapted to inundated conditions (Mitsch and Gosselink, 2007). Productivity rates range from low to high, but the low potential for carbon loss through respiration make these ecosystems important in the global carbon cycle (Zedler and Kercher, 2005). Exchanges of energy and mass are tightly coupled, resulting in dynamic hydrological conditions that capture and store carbon for long time periods (Keddy, 2000; Reddy and DeLaune, 2008). Occurring most frequently in areas where precipitation is in excess of evapotranspiration and runoff, hydrology (water depth and inundation duration) is the major driver of freshwater marsh ecosystem function and vegetation composition (Davis and Ogden, 1994). As a result this hydrologic influence, freshwater marshes are among the most vulnerable ecosystems to climate change (Burkett and Kusler, 2000; Ferrati et al., 2005; Erwin, 2009). Changes in air temperature, precipitation, atmospheric CO₂ concentrations and sea level rise have the potential to affect the productivity, rate of wetland type conversions, geographic location, and the number of wetlands within most ecoregions (Erwin, 2009; Johnson et al., 2005).

5.1. Temperature

Air temperature affects hydrology, gas exchange, and metabolic rates in freshwater marsh ecosystems. Influencing the rate of water loss, changes in temperature could have important effects on water

depth and duration of inundation periods. In semi-permanent North American prairie wetlands, rising temperatures lead to lower water levels and a greater abundance of xeric species (Johnson et al., 2005). Higher temperatures are also likely to cause shifts in the location of semi-permanent wetlands to wetter regions (Johnson et al., 2005).

At higher latitudes, rising temperatures threaten freshwater marsh ecosystems by increasing permafrost melting which is changing large-scale surface and groundwater flow regimes (Burkett and Kusler, 2000). Shifts in the hydrology of subarctic wetlands could increase carbon loss from these systems, creating a positive feedback to global warming (Burkett and Kusler, 2000).

Although hydrology is a product of the climate (precipitation and temperature; Erwin, 2009) it also serves to dampen climate effects on ecosystem function. Water above the soil surface dampens extreme temperatures and reduces the temperature response of soil and macrophyte respiration by slowing gas exchange. Air temperature has been shown to drive ecosystem respiration rates (Jimenez et al., 2012), suggesting that changes in temperature could affect carbon dynamics in freshwater marshes through its impact on metabolic rates and gas exchange (Malone et al., 2014).

5.2. Rainfall

Patterns in precipitation have important influences on the hydrology of freshwater marshes (Malone et al., 2014), particularly in systems that depend on precipitation as the primary source of water (Burkett and Kusler, 2000). With declines in mean annual precipitation predicted with climate change for lower latitudes, in the future freshwater marshes are likely to have lower average water depths and shorter periods of inundation. These hydrological changes can lead to shifts in vegetation composition, with xeric species becoming more frequent and hydric species becoming scarcer. In coastal systems, a decline in freshwater resources could also lead to increased saltwater intrusion and conversions to brackish and saline marsh (McKee and Mendelssohn, 1989; Najjar et al., 2000; Neubauer, 2013). Where rainfall is likely to increase, higher water levels, greater freshwater flows, and enhancement of downstream accretionary processes are expected (DeLaune et al., 2003).

Strong climate teleconnections have also been shown to account for annual variation in rainfall patterns, hydrology, and net ecosystem exchange rates in freshwater marshes (Malone et al., 2015). Changes in hydrology have been linked to extreme El Niño Southern Oscillation phases (Piechota and Dracup, 1996; Allan and Soden, 2008; Malone et al., 2015) that are projected to increase in strength and frequency with climate change. In one of the largest wetland systems in the world, the Florida Everglades, El Niño phases increase dry season rainfall, causing higher dry season and annual water levels (Piechota and Dracup, 1996; Allan and Soden, 2008). In contrast, La Niña phases reduce dry season rainfall, leading to extreme drought and the water table dropping below the soil surface (Piechota and Dracup, 1996; Beckage et al., 2003; Allan and Soden, 2008). As La Niña phases are concurrent with extended dry seasons in the Everglades region, lower surface water levels, increased lightning strikes, and wildfires become more common (Beckage et al., 2003). Short-hydroperiod freshwater marsh ecosystems become a greater sink for CO₂ on an annual basis compared to El Niño and neutral years; long-hydroperiod freshwater marshes, which are generally a small source of CO₂ annually, become a sink for CO₂ in exceptionally wet years (El Niño phases) (Malone et al., 2014).

5.3. Carbon dioxide

Higher atmospheric concentrations of CO₂ are likely to enhance productivity rates in freshwater marsh (Burkett and Kusler, 2000); however, the extent and duration of this enrichment effect will vary with species and nutrient concentrations. Nutrient limitations have been shown to reduce the capacity of plants to respond to rising atmospheric CO₂ concentrations (Stitt and Krapp, 1999). Vegetation may initially respond to elevated atmospheric CO₂, but acclimation is reported to be more pronounced when plants are nitrogen limited (Wong, 1979; Bowes, 1993; Curtis, 1996; Stitt and Krapp 1999; Ward and Strain, 1999; Isopp et al., 2000). Differential enhancement of photosynthetic pathways of wetland plants may also lead to changes in species composition, where plants that use C3 photosynthetic pathways will be enhanced more by CO₂ enrichment than those with C4 systems (Burkett and Kusler, 2000; see also Section 4.3). Differences in photosynthetic response to elevated CO₂ could result in changes in plant community structure in freshwater marshes, a topic needing more research.

5.4. Sea level rise

In freshwater marshes near the coast, sea-level rise is of great concern and could increase saltwater intrusion and lead to wetland type conversions (McKee and Mendelssohn, 1989). The response of freshwater marsh to increased salinity has been shown to be variable and dependent upon a number of factors that include species composition, the abruptness and duration of saline water, and flooding depth and propagules of more-salt tolerant species (McKee and Mendelssohn, 1989). Although salt tolerance varies among freshwater marsh species, it is likely that increases in salinity will result in an expansion of saline marshes and a reduction in the health and resilience of freshwater marsh.

As the Mississippi River deltaic plain subsides and sea levels rise, intrusion of saline water into brackish and freshwater marshes has led to the conversion to saline marsh types (McKee and Mendelssohn, 1989). In a tidal freshwater marsh dominated by cutgrass (*Zizaniopsis miliacea*), elevated salinity levels reduced productivity rates (Neubauer, 2013). Net ecosystem production, the balance between gross ecosystem production and ecosystem respiration, decreased 55% when salinity levels were elevated and increased by 75% when freshwater inputs were increased (Neubauer, 2013).

In the Florida Everglades sea levels are projected to rise 25–35 cm between 2006 and 2080 (Rahmstorf, 2007; Walton, 2007). With over half of Everglades National Park less than 1 m above sea level, sea level rise will have a profound influence on the future structure and function of wetlands in this region (Jones and Price, 2007; Todd et al., 2012). Declines in productivity have been shown to occur with increases in salinity in Everglades sawgrass (*Cladium mariscus* subsp. *jamaicense* (Crantz) Kük.) dominated systems, suggesting that an increase in saltwater intrusion could impact freshwater marsh productivity and is likely to initiate shifts in species composition (Childers, 2006).

Overall, freshwater marshes are important globally for their disproportionate impact on biodiversity, biogeochemical cycling and ecosystem services. These systems exhibit dynamic hydrological conditions that capture and store carbon for long time periods. Sensitive to climate dynamics, hydrology is the major driver of freshwater marsh ecosystem function (Davis and Ogden, 1994), making the future of these ecosystems uncertain under the threat of global climate change. Climate change could be particularly severe in freshwater marsh (Poff and Hart, 2002; Erwin, 2009; Burkett and Kusler, 2000) and the destruction of these systems can enhance global warming by releasing carbon that is currently stored in the soil (Burkett and Kusler, 2000).

Vulnerability of freshwater marsh to climate change varies across marsh types and depends on how sensitive the vegetation and hydrology are to shifts in the climate regime. Climate change simulations for temperature, precipitation and atmospheric CO₂ concentrations in Everglades freshwater marsh show that although climate change projections might lead to slight shifts in the start and length of the wet season (~1 to 7 days), the existing hydrological regime and oligotrophic conditions lower ecosystem sensitivity (Malone et al., 2015). Although the Everglades is resilient to shifts in climate, sea level rise and changes in the disturbance regime may be the driving forces of change in the future.

6. Mangroves

Mangroves are the dominant coastal plant community of sheltered, accreting tropical coastlines, providing a wealth of ecological and economic functions and values (Lugo and Snedaker, 1974; Lugo et al., 1990). Mangroves have demonstrated a high degree of ecological stability over geological timescales that reflects concurrent shoreline evolution (Lessa and Masselink, 2006; Alongi 2008). Despite their importance, mangrove habitats are presently exhibiting global decline (Ellison and Farnsworth, 1996; FAO, 2007; Polidoro et al., 2010). Major impacts to mangroves include development, resource extraction, and coastal storms (Ellison and Farnsworth, 1996; Valiela et al., 2001), while estimates of sea level rise associated with climate change portend further loss of mangrove habitat and species (Farnsworth et al., 1996; Scavia et al., 2002; Solomon et al., 2007; Alongi, 2008; Hoegh-Guldberg and Bruno, 2010; McKee et al., 2012).

6.1. Temperature

While increases in air temperature will be less pronounced in tropical regions than predicted in higher latitudes, these increases will stress mangroves nonetheless. Mangroves are most productive within a temperature range of 15–25 °C (Hutchins and Saenger, 1987) while roots and seedlings experience thermal stress at 35 °C and higher (Clough et al., 1982). Less extreme increases in average temperature may increase productivity, alter phenology and lead to range expansion for some species (Ellison, 2000). At higher latitudes and range limits, mangroves have shown evidence of range expansion as the threat of limiting freezing conditions is reduced (McKee et al., 2004).

Increasing air temperatures are associated with concurrent increases in ocean surface temperatures which are estimated to increase by 0.1 °C per decade for the next century (Fig. 1), subsequently contributing to the strength and frequency of severe storms (Solomon et al., 2007). Such temperature-driven effects may impose cascading impacts on coastal fringing mangroves. Strong, destructive winds and extreme tides can cause physical damage to mangroves and exacerbate coastal erosion, and may also increase physiological stressors including salinity and anoxia associated with more frequent and prolonged periods of flooding, particularly in subtropical areas where these effects are predicted to be strongest.

6.2. Rainfall

Predicted changes in precipitation will likely alter local salinity regimes, affecting the influence of physiological stressors, and in turn altering species composition, diversity, and competitive interactions between mangroves and other coastal and inland wetland vegetation (Scavia et al., 2002; Hoegh-Guldberg and Bruno, 2010; McKee et al., 2012). These changes are expected to play out in two distinctly different ways. In higher latitudes, precipitation is predicted to increase, potentially influencing salinity regimes and

altering pore water chemistry in estuaries and near coastal waters that may result in increases in mangrove productivity, growth rates, and biodiversity. Evidence for this prediction comes from current global patterns where the tallest and most diverse mangrove assemblages are found along high rainfall shorelines (Duke et al., 1998). Formerly drier landward areas or salt barrens may become wetter and less saline (as noted in Section 4.2), allowing for landward migration for some species, particularly mangroves (Field, 1995; Henry and Twilley, 2013; Saintilan et al., 2014). Increased precipitation may also affect erosion and drainage patterns, potentially delivering more sediment to estuaries and allowing for some land building and accretion that may be exploited by pioneering mangrove species. However inadvertent, land building following coastal development has been suggested as a reason for local increases in mangrove area in some instances (Howari et al., 2009; Loughland et al., 2007; Moore et al., 2015).

In subtropical latitudes, the opposite effect is expected as predicted decreases in precipitation may suppress mangrove productivity and increase stress from salinity and anaerobic decomposition (Christensen et al., 2007 and examples therein). While productivity would decrease, reduced precipitation can lead to encroachment of mangrove into adjacent wetland habitats including saltmarsh and freshwater marsh, albeit by shorter and often physiologically stressed plants (Saintilan and Wilton, 2001; Henry and Twilley, 2013). Overall, decreased precipitation is expected to result in notable reduction of mangrove area caused by the conversion of upper tidal zones to drier, hypersaline flats (Field, 1995; Duke et al., 1998).

6.3. Carbon dioxide

It is expected that elevated CO₂ concentrations (Fig. 2) may increase mangrove growth rates by stimulating photosynthesis and water use efficiency (McKee et al., 2012), but this may not be true in all areas. Ellison et al. (1996) found that elevated CO₂ can result in measurable, beneficial effects on *Rhizophora mangle* in terms of growth and reproduction in typical conditions at a site in the Caribbean. However, doubling CO₂ in *Rhizophora apiculata* and *Rhizophora stylosa* growing in hypersaline environments in Australia had little effect on productivity (Ball et al., 1997). Increased growth rates, depending upon how biomass is allocated, may allow for mangrove to keep pace with sea level rise by building dense roots that lead to peat accumulation that in turn can elevate the soil surface.

When combined with other factors that reduce physiological stress to the plant, such as decreased salinity, elevated CO₂ would be expected to have its greatest potential benefit to mangroves. But this condition is expected to occur predominantly at the poleward limits of mangrove range, and thus affects a potentially small subset of the total area occupied by mangrove species. Ball et al. (1997) concluded that increased growth at mangrove range limits will not significantly alter ecological patterns for mangrove overall. However the effects of elevated CO₂ are complex and not well understood, suggesting considerable opportunity for more research to better predict responses on a global scale.

6.4. Sea level rise

Of all the climate change outcomes, relative sea level rise (Fig. 3) may be the greatest threat to mangroves (Field, 1995; McLeod and Salm, 2006; Lovelock and Ellison, 2007). Local sea level rise may vary considerably from the global average and be influenced by local factors, changes to the elevation of the wetland sediment surface, as well as tectonic processes, coastal subsidence, and sediment budgets. While elevated CO₂ may increase mangrove growth and productivity (Farnsworth et al., 1996), these benefits will be

tempered by the negative impacts to productivity resulting from increased tidal flooding associated with predicted sea level rise (Ellison and Farnsworth, 1997).

Direct anthropogenic impacts such as development, resource extraction and land conversion have contributed to the 1–2% decline of mangroves worldwide (FAO, 2007). Barriers to landward migration in retreat of sea level rise will likely increase the scale of mangrove loss as these threatened habitats try to keep pace with higher tides, prolonged flooding, and increased tidal energy. Direct anthropogenic impacts may have been more central to mangrove decline in recent history than currently documented sea level rise effects, but that trend appears to be shifting. Research in the Caribbean and Western Pacific suggests mangrove peat accretion is not keeping up with sea level rise (Cahoon and Hensel, 2006; McKee et al., 2007) and observations of flooded stands and lone trees awash off shore abound in published and unpublished literature and are confirmed by personal observations in the eastern and central Caribbean. Modeling of mangrove vulnerability to sea level rise in Grenada, for example, shows significant potential loss of mangrove from coastal squeeze due to existing infrastructure and topographic features that would effectively prohibit landward migration, and these findings are not unique (Moore et al., 2014a).

To summarize, while it seems clear that climate change effects will influence mangroves in complex ways, the effects are expected to be variable and often site-specific. Broadly, losses of suitable mangrove habitat are likely due to various barriers to landward migration and increased stressors such as flooding and tidal energy within primarily tropical latitudes. Yet mangrove gains may also be seen as higher temperatures and elevated CO₂ may allow for localized range expansion into uplands following associated disturbance to salinity regimes and the stability of adjacent plant communities including salt marshes and tidal freshwater wetlands.

7. Conclusions

Foreseen global climate change impacts on wetland plants are in many ways similar among the five aquatic plant communities evaluated in this overview, but there are also apparent differences between these habitats. These are most prominent between submerged and emergent plants, where climate changes expressed as water-borne and airborne alterations, respectively, influence plant structure, reproduction, distribution and physiology differently. Temperature range and increase is critical to all five plant communities, with the degree of effect varying with air vs. water exposure as well as location of plant populations within their tolerance range. For both the submerged and emergent plant communities in marine environments, added osmotic stress from salts and increased anoxia from seawater sulfate reduction impose challenges not typically seen in freshwater plants systems. The effects of increased CO₂ on all plants are positive at some level, however the greatest increase in plant photosynthetic response is within the seagrasses where restricted CO₂ diffusion and seawater carbonate chemistry often limit CO₂ availability. Increased UV-B radiation can impact plants through the necessity for secondary production of UV-blocking compounds. Under several climate change scenarios including increased tidal variation and greater exposure, seagrass, and to some extent freshwater aquatic plants, produce red/purple compounds for UV blocking. Salinity increases from seawater intrusion due to sea level rise, or salinity decreases caused by more storms and runoff, will affect coastal plant communities to a greater or lesser extent, depending on location, conditions and plant tolerances. The secondary impacts of climate change of more severe weather, increased storms, and watershed alterations, will be exacerbated by both air and water temperature increases. Inevitably, plant community survival will be affected and species distribu-

tions will shift. Predictions are difficult, but gains and losses are inevitable.

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