

Chapter 2: Global Climate Change and Communities of Submersed Vegetation: Research Summary of Selected Environmental Impacts

by

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Abstract: Communities of submersed aquatic vegetation (SAV) are important components of many freshwater, brackish, and marine aquatic ecosystems. They provide erosion protection by baffling the impacts of waves, remove nutrients and other pollutants from river and runoff inputs to coastal areas, and provide nursery habitat for fish, shrimp, and other species, as well as forage for wintering waterfowl and endangered species such as sea turtles and manatees. Submersed aquatic plant communities, though, are susceptible to long-term environmental changes that are predicted to accompany global climate change. Our research was aimed at determining the responses of SAV to increased dissolved inorganic carbon, higher sea levels, and increased frequency and intensity of tropical storms. We found that photosynthesis of macrophytes changed little or not at all in response to bicarbonate additions, but photosynthesis did increase in response to additions of dissolved carbon dioxide for most species tested. The photosynthesis of benthic microalgae and of phytoplankton at saline sites was not affected by additions of either dissolved carbon dioxide or bicarbonate, but at freshwater sites, the addition of carbon dioxide did enhance phytoplankton photosynthesis. Increased dissolved inorganic carbon may also alter species allocation of biomass by increasing the proportion of belowground biomass relative to aboveground biomass. Experiments on the effects of sea-level rise indicate that at freshwater to oligohaline sites, species that are strong competitors will likely dominate, while salt-tolerant species will dominate areas with higher salinity. Our research on the effects of storm disturbance on SAV suggests that increased storm activity may favor seagrasses that dominate in sandy, nitrogen-poor sediments because of the increased likelihood of storm overwashes.

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Introduction

Communities of submersed aquatic vegetation (SAV) occur in all types of aquatic ecosystems within the northern Gulf of Mexico coastal zone. One of the most widely recognized values of SAV is as fish and wildlife habitat (Stevenson and Confer 1978; Zieman 1982; Zieman and Zieman 1989). Submersed aquatic vegetation serves as a critical food resource for waterfowl and as important feeding and nursery grounds for many commercially and recreationally important finfish and shellfish. In fact, changes in distribution of waterfowl populations (Kemp et al. 1984; Wicker and Endres 1995) and commercial landings of blue crabs (Orth and van Montfrans 1990) have been correlated with abundance of SAV. Submersed aquatic vegetation also provide critical habitat for threatened and endangered species such as sea turtles and manatees. The importance of SAV to aquatic ecosystems extends to physical and chemical functions as well. The leaves of submersed plants reduce waves and currents (Fonseca et al. 1982; Fonseca 1989) and root and rhizome systems bind sediments, both of which enhance shoreline stabilization. Finally, nutrient uptake and particulate sedimentation within SAV beds effectively ameliorate water quality (Ward et al. 1984; Short and Short 1984). Changes in SAV thus have profound implications for fish and wildlife, shoreline geomorphology, and biogeochemical cycles of aquatic ecosystems.

Primary production within beds of SAV is derived from many sources (Fig. 2-1). Phytoplankton, benthic

microalgae, and epiphytes, in addition to macrophytic vegetation, contribute to the production of organic matter. Any of the latter three groups may dominate primary production within the SAV community depending on location, type of SAV, and time of year (Morgan and Kitting 1984; Jensen and Gibson 1986; Mazella and Alberte 1986; Murray and Wetzel 1987; Moncreiff et al. 1992). The magnitude of production and the diversity of primary producer groups within SAV communities is a principal reason for their high biological diversity and value as feeding and nursery areas.

Submersed plant communities are distributed throughout the coastal zone of the northern Gulf of Mexico. Species of SAV restricted to fresh and brackish waters occur in the shallow areas of estuaries and river deltas along the gulf coast (Handley 1995); their greatest coverage occurs in large, shallow bays and in the shallow flats that form at river mouths. Marginal bands of SAV often line the shores of small tributaries and creeks, and small patches can be found in quiet zones along the edges of large rivers (Stout 1990). The composition of freshwater and brackish SAV communities is diverse; 24 species were identified in surveys of habitats in Mobile Bay, Alabama (Stout 1990). Many beds exist as mixed communities, although monodominant stands, particularly of invasive, nonnative species, are also common. Eurasian milfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*) are nonnative species found in this region. These species are often considered nuisance aquatic plants because of the dense, nearly impenetrable mats of vegetation they form.

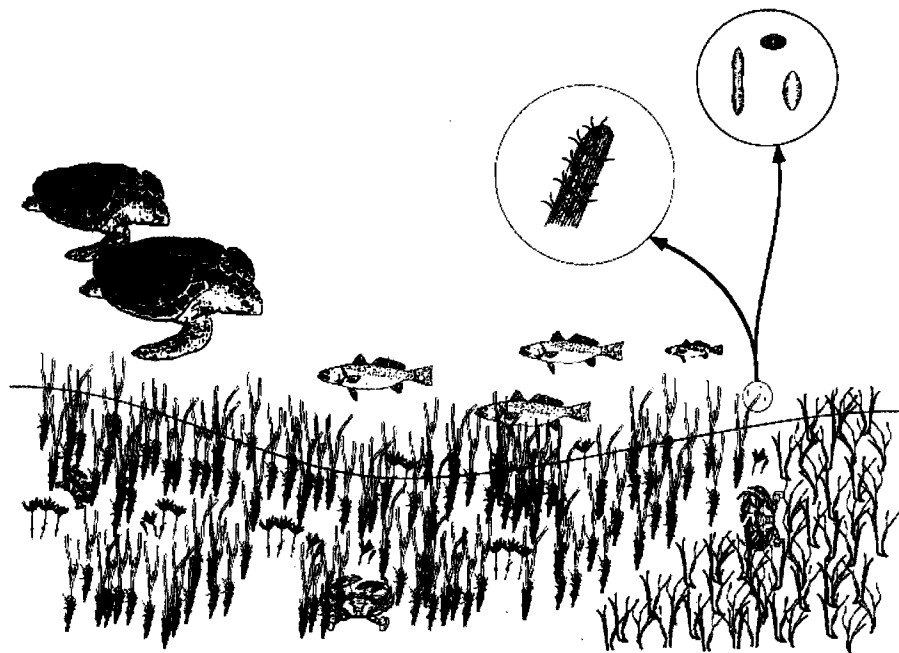


Figure 2-1. Important components of a typical submersed aquatic vegetation ecosystem, including marine animals, macrophytes, epiphytes, and phytoplankton.

Seagrasses, or marine SAV species, form the most extensive SAV systems along the northern gulf coast. Five seagrass species grow in this region: turtlegrass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), shoalgrass (*Halodule wrightii*), star grass (*Halophila engelmannii*), and paddle grass (*Halophila decipiens*). Widgeongrass (*Ruppia maritima*), a submersed plant with a broad salinity distribution, occurs with seagrasses in the lower salinity areas of the marine environment. Seagrass beds are often quite heterogeneous, with individual species exhibiting patchy distributions within expansive, continuous seagrass beds. As such it is difficult to assign overall dominance in the gulf to a particular species (Kenworthy 1994). The most recent estimate of total seagrass coverage in the shallow, nearshore waters of the Gulf of Mexico coastal states is 1.02 million ha (Duke and Kruczynski 1992). The largest seagrass beds in this region occur in Florida Bay (550,000 ha; Zieman and Zieman 1989), the Big Bend area of Florida between St. Marks and Tarpon Springs (300,000 ha; Iverson and Bittaker 1986) and the Laguna Madre of Texas (73,000 ha; Onuf 1995). Most of the remaining seagrass beds are within estuarine areas of Florida and Texas (Handley 1995). Isolated patches and narrow bands occur in sounds protected by the barrier islands of Louisiana, Mississippi, and Alabama. The largest continuous seagrass bed in this region is found in Chandeleur Sound of coastal Louisiana (5,657 ha; Handley 1995).

Effects of Global Climate Change

The distribution and abundance of SAV habitats in the northern Gulf of Mexico have declined precipitously during the past 50 years, most notably from widespread deterioration of water quality (Neckles 1994). The productivity, distribution, and composition of submersed plant communities are also susceptible to stresses associated with a changing global climate (Rizzo and Neckles 1993). Increases in concentration of dissolved inorganic carbon (including both carbon dioxide [CO₂] and bicarbonate [HCO₃⁻]) may affect SAV directly and may have indirect effects through influences on attached and unattached algae in SAV systems. A rise in sea level will increase the depth of water at any given position and will cause inland and upstream intrusion of salt water, both of which will affect existing SAV. The direct effect of temperature on plant physiological processes may ultimately influence SAV community composition and the latitudinal distribution of species. In addition, if changes in global climate result in a warmer tropical ocean, the frequency and intensity of tropical storms likely will increase (Emanuel 1987), which would further increase the inland extent of saltwater penetration. Any increase in the frequency or intensity of physical disturbance from storms may also have direct effects on SAV habitats. The environmental effects of a changing

global climate may exacerbate existing human-caused stresses on SAV and accelerate habitat alteration or loss. There is, however, little information from which to predict the direction and magnitude of potential changes in SAV associated with global change. Therefore, minimizing and adapting to the effects of a changing global environment require foremost a better understanding of potential SAV responses to these environmental variables.

The research results summarized here address the possible effects of elevated dissolved inorganic carbon, sea-level rise and salinity increases, and increased storm disturbance on various aspects of the ecology of SAV ecosystems. Each section includes a brief background statement followed by a research summary. Research on the effects of elevated dissolved inorganic carbon examined the growth response of two macrophyte species and the photosynthetic responses of the phytoplanktonic, benthic microalgal, and macrophytic components of these habitats. Studies on sea-level rise and salinity increase focused on the effects of these variables on macrophyte survival, competition, and community structure. The effects of disturbance on the community structure of seagrass communities was undertaken to evaluate the possible long-term effects of increased storm activity.

Effects of Increased Carbon Dioxide Concentration

There is overwhelming evidence that high concentrations of atmospheric carbon dioxide will directly impact global vegetation. Most studies to date have focused on terrestrial or emergent plants, where common responses to elevated levels of carbon dioxide include increased photosynthesis and biomass, enhanced root growth relative to shoot growth, and elevated tissue carbon-to-nitrogen ratios (e.g., Cure and Acock 1986; Mooney et al. 1991; Dahlman 1993). Although an increase in concentration of atmospheric carbon dioxide causes a linearly proportional increase in that of dissolved carbon in aquatic environments (Wetzel and Grace 1983), comparatively little information exists on responses of submersed plant communities to carbon dioxide enrichment and the potential ecosystem consequences.

The size of the total pool of dissolved inorganic carbon is a result of complex interactions between biota, atmospheric carbon dioxide partial pressure, temperature, pH, alkalinity, and salinity. The dissolved inorganic carbon pool is partitioned into carbon dioxide, bicarbonate, and carbonate (CO₃²⁻; Fig. 2-2). The distribution of dissolved inorganic carbon among these three fractions depends strongly on pH, which is expected to decrease slightly as a result of carbonic acid formation from increased dissolution of carbon dioxide (Wetzel and Grace 1983). The variability in dissolved inorganic carbon concentrations and the distribution among the major constituents is much

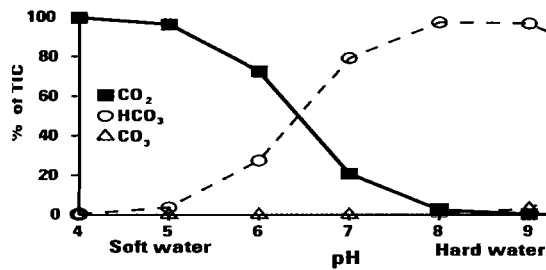


Figure 2-2. Relationships between dissolved inorganic carbon constituents (carbon dioxide bicarbonate), pH, and alkalinity (soft water to hard water) in aquatic ecosystems (after Wetzel 1975).

greater in fresh water than marine systems because of the constant ionic composition and buffering capacity of seawater.

The limited research available typically has found an increase in SAV photosynthesis with carbon dioxide enrichment (e.g., Beer and Wetzel 1981; Titus and Stone 1982; Nielsen and Sand-Jensen 1989; Rattray et al. 1991; Durako 1993; Madsen et al. 1993). Submersed plant species exhibit a wide range of responses, however. All SAV take up carbon dioxide preferentially during photosynthesis, but most can also use bicarbonate to some degree. In general, species that are inefficient bicarbonate users show the greatest photosynthetic response to carbon dioxide increases (Madsen et al. 1993). Thus, although total dissolved inorganic carbon can limit SAV photosynthesis and growth, an unfavorable partitioning of dissolved inorganic carbon among constituents can also limit some species (Vadstrup and Madsen 1995). Increased concentrations of carbon dioxide may not only increase primary production of organic matter but also, by altering the outcome of competition, lead to shifts in species composition.

Epiphytic algae can limit the supply of dissolved inorganic carbon to SAV leaf surfaces by increasing the thickness of the layer through which carbon must diffuse (Sand-Jensen et al. 1985) and by actual carbon uptake. These algae are also susceptible to carbon limitation of photosynthesis and would be expected to respond positively to increased availability of carbon dioxide. One potential consequence is enhanced algal growth and a shift in the balance between epiphytes and macrophytes.

Wetzel and Grace (1983) summarized the literature on the response of autotrophs to carbon dioxide enrichment by making generalized predictions on the magnitude of the response. They predicted a doubling of photosynthesis for both marine and freshwater macrophytes (single plant responses) with a doubling of carbon dioxide concentration, for optimal conditions of light and water mixing. They predicted no increase for marine phytoplankton and a response for freshwater phytoplankton ranging from no response to an increase of about 1.5 times ambient. While there was a limited data base on SAV responses, there were even fewer

studies on phytoplankton and no studies on the benthic microalgal components of SAV habitats.

Macrophyte Photosynthetic Responses to Elevated Dissolved Inorganic Carbon

Initial quarterly studies of the photosynthetic response of macrophytes to elevated carbon dioxide and bicarbonate were carried out for *Vallisneria americana*, *Halodule wrightii*, *Ceratophyllum demersum*, and *Ruppia maritima*. Additional, more intensive sampling was conducted for *Ceratophyllum demersum*, *Hydrilla verticillata*, and *Vallisneria americana*. Species collected from saline sites included *Halodule*, a true seagrass from Galveston Bay, and *Ruppia*, from a brackish environment at Rockefeller National Wildlife Refuge (NWR), Louisiana. The other species were collected from freshwater environments (a pond at the National Wetlands Research Center, Lafayette, Louisiana, and Vermilion Lake and Spreafico Lake, Louisiana), a wetland in Cameron Parish, Louisiana (*Vallisneria*), and Lake Martin, Louisiana (*Ceratophyllum* and *Hydrilla*).

Only *Ceratophyllum* showed significant responses to addition of bicarbonate: enhancement in one experiment and inhibition in another. The instance of enhancement probably resulted from an increase in inorganic carbon substrate at a time when this species may have been using bicarbonate as a primary carbon source. Conversely, the inhibition probably resulted from a decrease in free carbon dioxide, the preferred carbon source for plants, as a result of an increase in pH from the bicarbonate addition. The generalized lack of response to bicarbonate additions suggests either that plants are exclusively using free carbon dioxide as a primary carbon source or that ambient concentrations of bicarbonate are already sufficient to maximize photosynthesis in plants using this less desirable carbon source.

Typical curves of the response of macrophyte photosynthesis as a function of increasing concentration of dissolved inorganic carbon (as added carbon dioxide) are shown in Fig. 2-3. In a number of cases, photosynthesis was still increasing even at the maximum added concentration of 2-4 times ambient. *Vallisneria* photosynthesis increased with carbon dioxide additions in all nine experiments, while *Ruppia* photosynthesis increased in 0 of 3 experiments. *Halodule* responded in 2 of 4 experiments, *Ceratophyllum* in 20 of 26 experiments, and *Hydrilla* in 7 of 14 experiments. The results for *Halodule* are particularly significant because seagrass photosynthesis is often thought to be not limited by dissolved inorganic carbon because of the abundance of bicarbonate in marine environments. *Hydrilla* and *Halodule* responded to carbon dioxide additions principally during the most active phase of growth in spring and early summer. With the exception of January 1995, *Ceratophyllum* responded consistently to carbon dioxide addition until the summer of 1995.

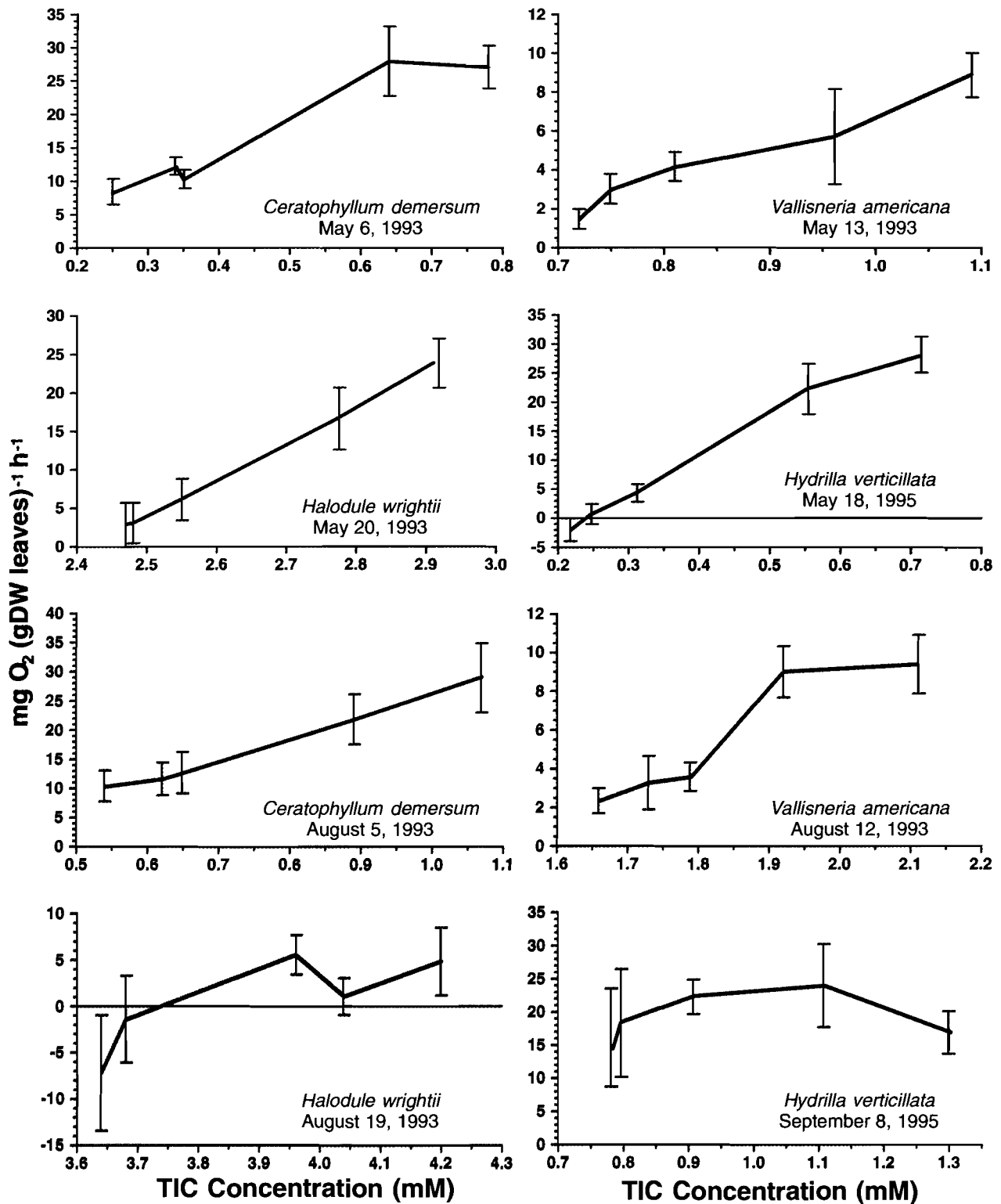


Figure 2-3. Growing season photosynthetic responses of four macrophyte species to increasing concentrations of dissolved inorganic carbon, added as carbon dioxide. The lowest concentration represents ambient concentrations at the collection site.

In fall of 1992, *Hydrilla* was discovered in Lake Martin. It covered about 50% of the lake surface by the end of summer 1994 and reached virtually complete surface coverage by the end of July 1995 (Fig. 2-4). Weekly monitoring samples at our littoral collection site showed a significant decrease in pH and increase in free carbon dioxide from 1994 to 1995. These conditions may have alleviated carbon dioxide limitation in this species during most of the latter half of 1996. The lack of response by *Ruppia* probably also resulted from the high concentrations of dissolved inorganic carbon and free carbon dioxide.

There was a more than threefold difference among species in the mean response to carbon dioxide addition in our experiments (Fig. 2-5). Photosynthesis by *Ceratophyllum* and *Hydrilla* doubled with addition of carbon dioxide, while *Vallisneria* and *Halodule* photosynthesis increased nearly threefold. The maximum response of *Ceratophyllum*, *Vallisneria*, and *Halodule* exceeded



Figure 2-4. Lake Martin, Louisiana, showing complete surface coverage by *Hydrilla verticillata* in late summer 1995. Boating became impossible on the lake, and fish kills ensued. Invasions by such exotic species may be abetted in an environment enriched in dissolved carbon dioxide.

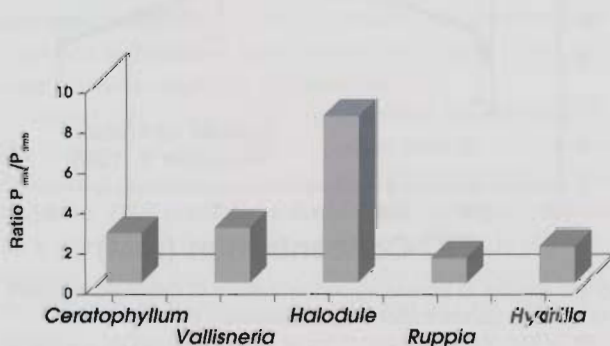


Figure 2-5. Photosynthetic enhancement as measured by the ratio of ambient photosynthesis (P_{amb}) and photosynthetic rates enhanced by carbon dioxide enrichment (P_{max}) for five species of submersed aquatic vegetation.

sixfold, while the maximum for *Hydrilla* was only threefold, underscoring the important differences among species.

Regression analyses indicated that factors such as temperature and the ambient rate of photosynthesis, an indicator of plant condition, were also important in controlling the responses of SAV to increased carbon dioxide concentrations. Consequently, both environmental and life history factors are important in determining when and how strongly a species will respond to an increase in carbon dioxide. The importance of temperature in controlling this response is particularly important since global temperatures are expected to increase along with concentrations of carbon dioxide.

Benthic Microalgal and Phytoplankton Photosynthetic Responses to Elevated Dissolved Inorganic Carbon

The benthic microalgal and phytoplankton studies also began as quarterly studies at all the macrophyte study sites (except Rockefeller NWR, where no benthic microalgal studies were conducted). Monthly phytoplankton sampling began in late 1993 and expanded to include lake sites that had no SAV but represented large differences in ambient dissolved inorganic carbon concentrations. Sites at Galveston Bay, Rockefeller NWR, and Cameron Parish all had high concentrations of dissolved inorganic carbon. Lake Martin and Vermilion Lake, Louisiana, had moderate dissolved inorganic carbon concentrations, the NWRC pond had high concentrations, and Spreafico Lake had low dissolved inorganic carbon concentrations.

Addition of either carbon dioxide or bicarbonate had no effects on the photosynthesis of benthic microalgae. At two freshwater sites, sediment regeneration of carbon dioxide greatly exceeded autotrophic demand, so it is unlikely that carbon dioxide would become limiting to photosynthesis in these environments. At a marine site, demand was much greater than regeneration, but concentrations of dissolved inorganic carbon, principally as bicarbonate, were high and probably supplied benthic microalgal requirements. Because of their microscopic size and high surface-to-volume ratio, benthic microalgae make much more efficient use of the less preferred bicarbonate carbon source than do macrophytes.

The number of experiments in which phytoplankton photosynthesis increased as a result of carbon dioxide addition is shown by site in Fig. 2-6. There was no increase in photosynthesis from additions of either carbon dioxide or bicarbonate at either site with measurable salinity. Photosynthesis was enhanced by carbon dioxide addition in most experiments at each of the freshwater sites except the NWRC pond, the site highest in dissolved inorganic carbon concentration. Even at that site, however, photosynthesis increased on two occasions. In contrast to the macrophyte experiments, phytoplankton photosynthesis was increased by bicarbonate additions on several occasions at three of

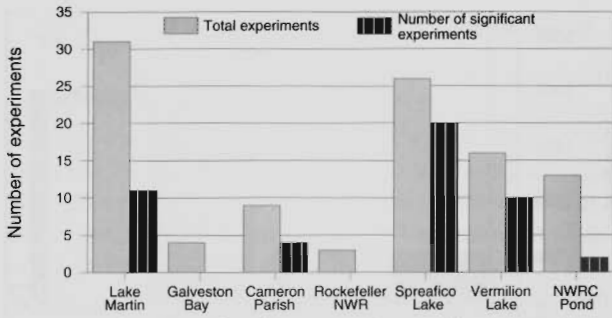


Figure 2-6. Total number of experiments per site and number of experiments in which phytoplankton photosynthesis increased because of carbon dioxide addition. The phytoplankton communities represent a salinity gradient from marine to freshwater and, for freshwater sites, a gradient of high to low dissolved carbon dioxide.

the four freshwater sites where bicarbonate additions were carried out. Also, additions of both carbon dioxide and bicarbonate caused inhibition of photosynthesis in a number of experiments. Inhibition by bicarbonate may result from the associated increase in pH, which can actually reduce concentrations of free carbon dioxide. Conversely, communities using only one dissolved inorganic carbon source may undergo brief metabolic shut down (i.e., inhibition) while shifting to an enzyme system capable of using the more abundant or energetically favorable dissolved inorganic carbon substrate when its availability is suddenly increased.

The increase in photosynthesis due to carbon dioxide addition is shown in Fig. 2-7. For experiments in which there was an increase with carbon dioxide addition, the level of increase was between 1.5 and 2.0 for three of the four freshwater sites. This level is slightly higher than that predicted by Wetzel and Grace (1983).

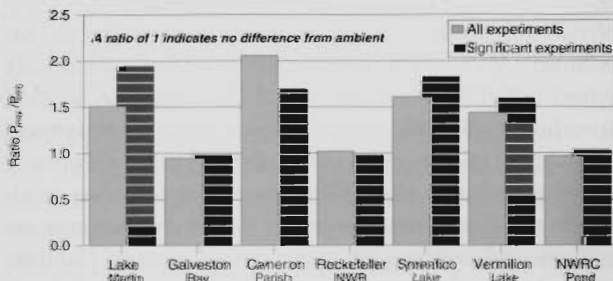


Figure 2-7. Photosynthetic enhancement as measured by the ratio of ambient photosynthesis (P_{amb}) and photosynthetic rates enhanced by carbon dioxide enrichment (P_{max}) for phytoplankton communities from the various seven study sites.

Macrophyte Growth Responses to Elevated Carbon Dioxide

Studies of various vegetation types have indicated that the initial metabolic impacts of increases in carbon dioxide diminish substantially as plants acclimate to higher ambient concentrations. Therefore, although our laboratory experiments showed significant effects of short-term increases in dissolved inorganic carbon concentrations on SAV photosynthesis, these effects might not necessarily translate into longer-term effects on growth and production. To assess the potential responses of a freshwater and a marine species of SAV to elevated dissolved inorganic carbon, we used mesocosms, or large experimental systems designed to simulate natural ecosystems. Because the photosynthesis of all species increased most consistently in response to carbon dioxide additions during our laboratory experiments, we focused on this dissolved inorganic carbon constituent for our longer term measurements (Fig. 2-8).

Our experimental mesocosms were planted with intact sods of either *Halodule wrightii* from coastal Texas or *Vallisneria americana* from coastal Louisiana. Conditions were maintained in the tanks to mimic the natural environment as closely as possible. The tanks were filled with water at the same salinity and depth as at the collection sites. The experimental treatment consisted of continuous aeration of the tanks with ambient or carbon-dioxide enriched air for six weeks. Dissolved inorganic carbon concentrations in the air and water were monitored daily.

Contrary to the results of other studies, carbon dioxide enrichment did not affect total macrophyte biomass (Fig. 2-9a) or final shoot density (Fig. 2-9b) for either species. However, consistent with a large body of research on other systems, the final ratio of aboveground to belowground biomass decreased with carbon dioxide enrichment (Fig.



Figure 2-8. Mesocosms set up in a greenhouse at the National Wetlands Research Center. Such mesocosms enable studies of macrophyte responses to discrete variables such as carbon dioxide concentration or salinity.

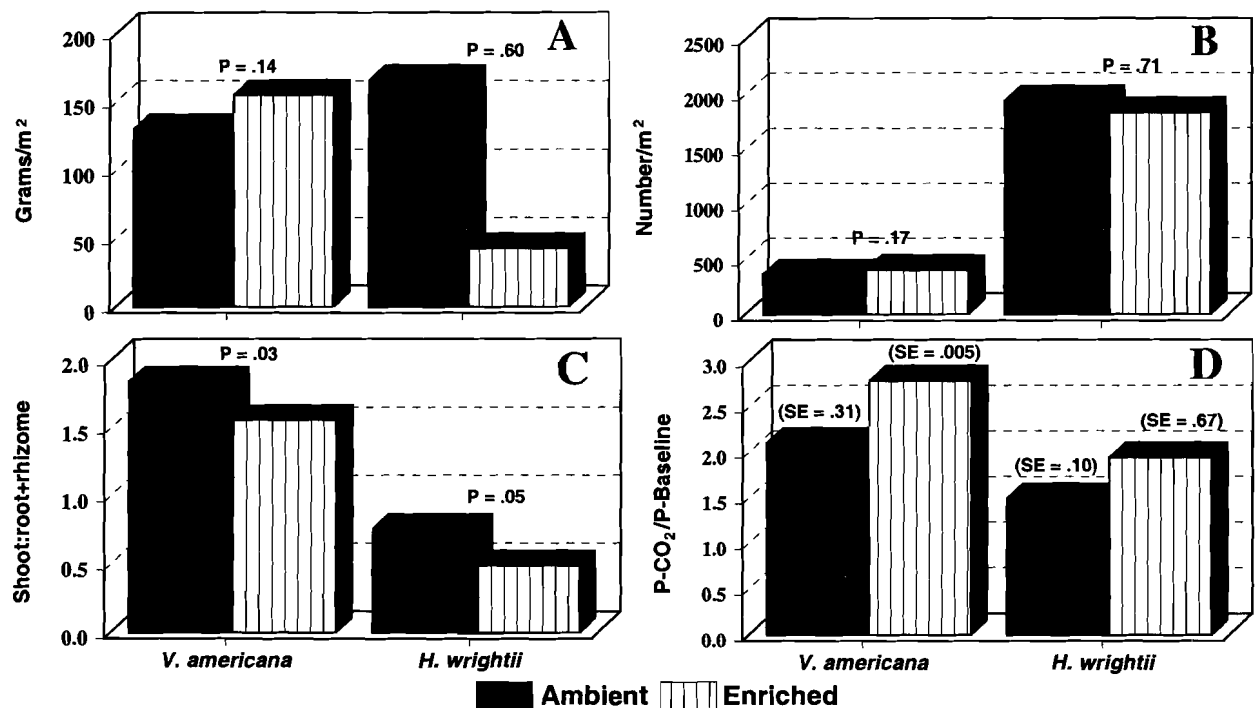


Figure 2-9. Growth responses to elevated carbon dioxide for two species of submersed macrophytes. Responses are shown after 6 weeks of growth under either ambient or enriched concentrations. A. Total macrophyte biomass. B. Macrophyte density. C. Ratio of shoot to root+rhizome biomass. D. Potential for altered photosynthetic capacity as determined by the enhancement of photosynthesis by carbon dioxide addition ($P\text{-CO}_2$) relative to rates with no carbon dioxide addition ($P\text{-Baseline}$).

2-9c), indicating increased biomass allocation to root and rhizome tissue. Thus carbon dioxide enrichment does have longer term consequences for these species. The lack of overall growth responses may have been due to the timing of the experiment (plants were already near peak biomass at the onset of treatment). Also, a longer experiment may have made a greater difference in total biomass. Alternatively, plant growth may have been subject to limiting effects of factors other than carbon dioxide, although tissue nutrient concentrations and carbon-to-nitrogen ratios suggest that growth was not nitrogen limited.

Both species did exhibit an increase in photosynthetic capacity following growth under elevated carbon dioxide concentrations (Fig. 2-9d). Higher primary production with increased concentrations of carbon dioxide may benefit consumer organisms. Similar responses by nuisance canopy forming species, however, would cause recreational and socioeconomic problems by killing fish and hindering boating (Fig. 2-4). The relatively low biomass of epiphytes on *Vallisneria* did not increase with carbon dioxide enrichment, but the epiphyte biomass on *Halodule* nearly doubled. This increase of epiphyte biomass on *Halodule* suggests the potential for a shift in balance between epiphytes and seagrasses with rising concentrations of atmospheric carbon dioxide. In eutrophic waters where nutrient limitations

to algal growth are alleviated, rising carbon dioxide concentrations could result in excessive epiphytic growth and ultimately in SAV declines.

The ratio of carbon to nitrogen in *Vallisneria* leaf tissue increased with carbon dioxide enrichment, whereas in *Halodule* leaf tissue it remained unchanged. We can only speculate on the cause of the difference between species. Differences in epiphyte response may have been partly responsible, that is, *Halodule* leaves under enriched conditions were more epiphytized and thus effectively exposed to lower carbon concentrations at the leaf surface than were *Vallisneria* leaves. This explanation suggests that the carbon-to-nitrogen ratio of *Halodule* leaves with a lower epiphyte load would also increase under carbon dioxide enrichment. Alternatively, responses of individual species may reflect differences in carbon metabolism between species; specifically, *Halodule* may be more effective at internal recycling of photorespired carbon dioxide and consequently less responsive to external increases. High carbon-to-nitrogen ratios may result in poorer forage for consumer organisms and decrease the decomposition rate of plant detritus, thereby slowing nutrient recycling. Integrated, long-term studies are sorely needed to predict such consequences of rising atmospheric concentrations of carbon dioxide for SAV ecosystems.

Effects of Accelerated Sea-level Rise

An increase in global temperatures would accelerate present rates of sea-level rise through thermal expansion of ocean water and melting of polar ice caps (Titus 1988). Predicted increases range from 15 to 95 cm by the year 2100 (Houghton et al. 1995). The most obvious effect of a rise in mean sea level on submersed vegetation is an increase in the depth of water overlying SAV beds. The dependence of SAV distribution, production, and long-term survival on light availability is well established (Dennison 1987; Goldsborough and Kemp 1988). Because light is attenuated exponentially through the water column, small changes in depth may greatly reduce the amount of light transmitted to rooted plants, resulting in decreased productivity and shoreward shift in plant distribution. In areas where coastal development limits the potential for shoreline migration, an increase in water depth will result in a decrease in subtidal vegetated habitat.

Another major consequence of a rise in sea level will be the inland and upstream intrusion of salt water in rivers, bays, and wetlands, subjecting coastal sites to increases in both average salinity and the peaks of salinity pulses (Titus et al. 1991). The distribution and abundance of SAV along salinity gradients has been described for many estuaries, and we can thus associate general groups of species with broad salinity zones (Stevenson and Confer 1978; Verhoeven and van Vierssen 1978; Howard-Williams and Liptrot 1980; Brock and Lane 1983). However, understanding of the mechanisms underlying these patterns is limited. Community structure at any location reflects the salinity tolerances of individual species and biotic interactions with other species. Although salinity tolerances have been determined experimentally for various North American species (Haller et al. 1974; Twilley and Barko 1990), estimates for single species vary widely, probably because of both true ecotypic variation and experimental technique. Information is lacking for many species. There is very little information on the relative importance of biotic interactions in structuring SAV communities, particularly under changing environmental constraints. Therefore, to improve our ability to predict how changes in salinity will affect SAV communities, we simultaneously evaluated the abiotic and biotic controls of submersed macrophyte responses to salinity intrusion within experimental mesocosms.

Macrophyte Responses to Salinity Intrusion

We assessed the effects of salinity on some of the most common species of SAV found in coastal waters of the southeastern United States. We selected six species representing a range of habitat types (from freshwater to brackish) and values (important wildlife food plants versus nuisance species). Our experiments were designed to determine the direct effects of salinity on community structure through physiological tolerances of individual species and

the indirect effects through the potential for changing competitive hierarchies along a salinity gradient.

Abiotic Control

The first experimental series was designed to determine the tolerance of each species to salinity. We planted each species individually and, following a 3-week acclimation period, adjusted salinities to experimental levels of 0, 4, 8, or 16‰; the high end of this gradient is about half of full seawater strength. We determined the salinity tolerance of each species from measurements of growth, biomass allocation, and plant constituent concentrations after about six weeks at treatment salinities.

Species were classified as intolerant of high salinities, tolerant of high salinities, or intermediate in response. The maximum salinity at which the two intolerant species persisted was quite low (4‰ for *Hydrilla verticillata* and 8‰ for *Heteranthera dubia*). The total biomass and growth rate of these species declined steadily as salinity increased from 0‰ to the tolerance limit. The proportion of total biomass allocated to leaf material also began an early decline with increasing salinity, indicating that the decrease in growth associated with increasing salinity was indeed a stress response. In contrast, the two tolerant species (*Potamogeton pectinatus* and *Ruppia maritima*) maintained a high biomass and growth rate and a constant proportion of leaf material across the range of salinities tested, indicating physiological adaptation to high salinity. Finally, two species (*Myriophyllum spicatum* and *Vallisneria spiralis*) showed intermediate response. Although total biomass decreased with increasing salinity, plants persisted at the highest salinity tested. Patterns of biomass allocation suggested some degree of salinity adaptation, but growth rates at the highest salinities indicated that mortality would ultimately occur. Thus persistence at high salinity was a function of the short duration of the experiment; these species can probably withstand pulses of high salinity better than can the intolerant species, but they would be eliminated by long-term increases of 4-8‰. From these physiological tolerances we can predict the potential species composition along a gradient of mean salinities (Table 2-1).

Biotic Interactions

We designed a second experimental series to determine how these potential patterns might be altered by competitive interactions. For this series each species was grown in paired combinations at the same four test salinities. Rather than planting all pairwise combinations of species, we measured the performance of each one relative to a reference species. These relative performances we then ranked to generate a competitive hierarchy at each salinity. Using this approach we found that the relative performances of the species and the consequent order of species dominance generally remained constant from low to high salinities. Strong competitors such as *Hydrilla verticillata* and *Heteranthera*

Table 2-1. Potential changes in community composition of various species of submerged aquatic vegetation as a result of increased salinity. Given this assemblage of species, those species marked with an asterisk are expected to dominate the community.

A. Potential community composition determined from maximum salinity tolerances of individual species. An X indicates species presence at the given salinity.

	Salinity ‰			
	0	4	8	16
<i>Hydrilla verticillata</i>	X	X		
<i>Heteranthera dubia</i>	X	X	X	
<i>Myriophyllum spicatum</i>	X	X	X	X
<i>Vallisneria americana</i>	X	X	X	X
<i>Potamogeton pectinatus</i>	X	X	X	X
<i>Ruppia maritima</i>	X	X	X	X

B. Predicted community structure based on salinity tolerance and competitive performance. An X indicates species presence at a particular salinity.

	Salinity ‰			
	0	4	8	16
<i>Hydrilla verticillata</i>	*	X		
<i>Heteranthera dubia</i>	*	*	X	
<i>Myriophyllum spicatum</i>	*	*	X	X
<i>Vallisneria americana</i>	X	*	X	X
<i>Potamogeton pectinatus</i>	X	X	*	*
<i>Ruppia maritima</i>	X	X	*	*

dubia dominated at low salinities and were excluded from the high end of the salinity gradient by physiological intolerance to the abiotic conditions. Those species tolerant of high salinities, such as *Ruppia maritima* and *Potamogeton pectinatus*, were weak competitors; they were outcompeted at the low salinities and had a refuge at the stressful end of the salinity gradient. Salinity adaptation in this system thus appeared to result in a classic tradeoff between stress tolerance and competitive ability. At high salinities, information on salinity tolerance alone becomes sufficient to predict community structure.

Superimposing the effects of biotic interactions on the potential species composition as previously determined from salinity tolerances alone allows predictions for realized community structure along a salinity gradient (Table 2-1). Biotic interactions seem to play a large role in structuring the community at low salinities, and tolerance of abiotic conditions is more important at high salinities. These results are consistent with evidence from other systems in which species have shared preferences for habitat conditions, with competitive hierarchies excluding species at different distances along a stress gradient. Predictions for alterations in the salinity structure of any coastal area can be derived from physical information on local geomorphology,

watershed freshwater inputs, the volume of the tidal prism, and predicted sea-level rise. Given an existing SAV community composition and an expected change in salinity, information from this study can be used to predict changes in SAV community structure. It is important to note, however, that our experiments determined the potential for community changes following short-term salinity pulses based on competition for limiting nutrients by mature plants. More accurate predictions will require information on long-term salinity increases, the role of competition for other limiting resources such as light, and responses by other plant growth stages, particularly during propagule formation and recruitment.

Effects of Increased Storm Disturbance

An increase in the severity and frequency of tropical storms as a result of warmer tropical seas would have acute impacts on coastal SAV. Currents generated by strong winds cause erosional depressions (blowouts) that migrate through seagrass beds (Patriquin 1975). Blowouts are recolonized from seeds or vegetative branching, favoring species that can tolerate unstable mineral sediments. Thus recurrent blowouts may cause a species shift favoring colonizing species such as *Halodule wrightii* and *Syringodium filiforme* over "climax" species such as *Thalassia testudinum* (Clarke and Kirkman 1989; Williams 1990). If disturbances occur more frequently than recolonization can take place, all seagrasses may be lost from an area. Intense storm events may also result in temporary or permanent loss of seagrasses through increased water column turbidity (Davis and Carey 1981) or by complete burial (Onuf and Quammen 1983). Reduction or elimination of tidal freshwater SAV by scouring, turbidity from sediment resuspension and runoff, and burial from sedimentation has also been documented (Bilby 1977; Rybicki and Carter 1986; Johnstone and Robinson 1987).

Far less studied, but of potentially equal importance, are the chronic impacts of storm disturbance on coastal SAV. Following erosion of patches to mineral sediments by intense wind and wave disturbance, shifts in community composition can occur because of the varying resource requirements of individual species (Williams 1990). However, storm disturbances other than intense erosion events can also influence resource availability. For example, relatively small amounts of sediment deposition can cause gradual changes in the sedimentary environment across broad zones and can be a result of frequent, minor storms. By changing the availability of sediment nutrient resources, such chronic disturbance could also influence community pattern. To improve our ability to predict responses of coastal SAV to overall increases in storm disturbance, we studied the role of chronic physical disturbance in patterns of seagrass distribution and abundance in coastal Louisiana.

Responses to Overwash Disturbance

We used a combination of field observations and field experiments to relate seagrass distribution and abundance to physical factors associated with storm disturbance and to test the effects of disturbance-induced environmental conditions on observed patterns. Our investigations focused on an extensive seagrass bed in Chandeleur Sound that is protected from the Gulf of Mexico by a low-relief barrier island chain, the Chandeleur Islands. Storms regularly overwash the islands and deposit sandy, shoreface sediments in the seagrass community, but erosion and uprooting of vegetation are rare (Fig. 2-10).

From surveys of a series of 16 shore-normal transects across the seagrass bed, we were able to relate seagrass community structure to dominant environmental characteristics. We placed transects randomly within one of two disturbance regimes, in zones of frequent island overwash or in relatively protected zones behind emergent marsh. Although we found no difference in the frequency of occurrence of any species between the two disturbance regimes, we found that the average percent cover of



Figure 2-10. The seagrass ecosystem of Chandeleur Sound, Louisiana, showing seagrass beds and areas of storm overwash.

Thalassia was highest in protected zones whereas that of *Syringodium* was highest in overwashed zones. The nature of the sedimentary environment was related to overwash frequency; regardless of the dominant seagrass species, sediments within the overwashed zones were characterized by a higher proportion of sand and lower availability of inorganic nitrogen than were sites within the protected zones. By identifying those environmental characteristics associated with the highest percent coverage of each seagrass species, we were then able to determine the conditions contributing to patch dominance. Patches dominated by *Syringodium* were indeed associated with sandy sediments, whereas patches dominated by *Thalassia* were found in sediments of high organic content and low proportion of sand. Our subsequent growth experiments showed that *Thalassia* grows more rapidly in the relatively nutrient-rich sediments found in protected areas, whereas *Syringodium* shows no difference in growth between habitats. Presumably patches dominated by *Syringodium* are more prevalent in overwashed areas because of reduced competition from *Thalassia*.

These studies indicate that seagrass community organization can indeed be controlled in part by frequent and relatively minor overwash sediment deposition, either directly as in the case of *Thalassia* or indirectly as in the case of *Syringodium*. Therefore, by increasing deposition of sandy beach and offshore sediments in seagrass beds, a rise in the frequency of low intensity storms would alter community structure. We expect the chronic effects of increased sediment deposition from storm-generated waves to parallel the acute effects, causing an ultimate shift in community composition to early colonizing species.

Conclusions

Effects of Elevated Dissolved Inorganic Carbon

Photosynthesis

Photosynthesis was likely to increase with increased concentrations of dissolved carbon dioxide for a number of plant species and for most plant species during periods of rapid growth and/or warmer temperatures. The sole exceptions appeared to be for plants growing in environments high in dissolved carbon dioxide. The macrophyte species from the environments tested, however, seemed unlikely to increase photosynthesis in response to increased concentrations of dissolved bicarbonate and may be inhibited by such increases which raise pH and decrease available dissolved carbon dioxide. This effect may have been, in part, an experimental artifact arising from a rapid experimental increase in bicarbonate concentration and pH in plants primarily adapted to using free carbon dioxide.

Phytoplankton from saline environments, even if only brackish, did not respond to increased carbon dioxide concentrations, probably because photosynthesis was saturated by available concentrations of bicarbonate. Freshwater

phytoplankton did respond to increases in both dissolved carbon dioxide and dissolved bicarbonate on most occasions, except for one environment high in dissolved carbon. Even for the latter site, photosynthesis was increased on occasion.

Finally, benthic microalgal photosynthesis did not respond to increases in either dissolved carbon dioxide or dissolved bicarbonate. However, in highly autotrophic sediments in waters with low total inorganic carbon or low dissolved carbon dioxide, this community may respond as did freshwater phytoplankton.

Growth

Increased carbon dioxide did not increase production of plant biomass for either *Halodule wrightii* or *Vallisneria americana* subjected to a short-term, late-season enrichment; however, it did increase the biomass of seagrass epiphytes and did alter the allocation of macrophyte biomass, increasing the relative proportion of belowground biomass in both species. Increased carbon dioxide also increased the relative proportion of carbon to nitrogen in leaf tissues of the freshwater species. In addition, growth under increased carbon dioxide did not cause photosynthesis to acclimate to higher concentrations for either species.

Predictions for SAV Communities Under Elevated Dissolved Inorganic Carbon

Community composition will shift towards species which are less efficient users of bicarbonate, and shifts in the relative importance of primary producer groups are possible. Phytoplankton and epiphyte responses may be detrimental to both growth and survival of submersed species, particularly in eutrophic waters where nutrient limitations to algal growth are alleviated. Responses may favor SAV species whose ecological requirements are compatible with enhanced production of phytoplankton and/or epiphytes.

Benthic microalgal production is likely to be inhibited by enhanced production of phytoplankton, epiphytes, and macrophytes due to shading effects.

Shifts in the allocation of biomass to belowground plant tissues will have important consequences for other species using SAV habitats. For example, species such as wintering redhead ducks which feed primarily on belowground tissues of *Halodule wrightii* may find an expanded food base, while species such as juvenile shrimp may find a reduction in the cover they need for survival.

Increases in the relative concentration of carbon to nitrogen in plant tissues will make for poorer quality forage for grazing species such as wintering waterfowl. Decomposition processes will likely be slowed as organic matter becomes more refractory, decreasing the amount of production by higher trophic levels dependent on detrital food chains. Higher tissue/detrital carbon-to-nitrogen ratios may also alter the cycling of other critical nutrients such as nitrogen, with largely unknown effects for these

ecosystems. This alteration may also happen to phytoplankton communities, but no research has been conducted on this aspect to date. Other possible effects on macrophytes include alteration of plant morphology, increased biomass, accelerated growth, and compression of life history.

Effects of Increased Salinity Caused By Elevated Sea Level

Based on the responses of mature plants to short-term salinity increases, we conclude that macrophyte species which tolerate high salinities are generally weak competitors at lower, less physiologically stressful salinities. Species that tend to dominate the community at low salinities are excluded from waters of higher salinity by physiological intolerance to abiotic conditions.

In systems that experience a salinity increase from freshwater to oligohaline (0.5-5‰) conditions, consequent changes in SAV community structure will be highly influenced by the competitive abilities of both existing species and new recruits. Strong competitors such as *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Heteranthera dubia* are predicted to dominate Gulf of Mexico systems at low salinity.

Changes in SAV community structure in mesohaline (5-18‰) systems subjected to salinity increase will be strongly governed by the salinity tolerance of existing species and new recruits. Salt-tolerant species such as *Potamogeton pectinatus* and *Ruppia maritima* will likely dominate systems at high salinity.

The ecological value of SAV systems is a function of both primary and secondary production. Therefore, although important wildlife food plants such as *Ruppia maritima* and *Potamogeton pectinatus* may actually be enhanced by salinity increase within the mesohaline range, future habitat value will depend also on responses of other trophic levels such as macroinvertebrates. In some instances a rise in salinity may eliminate nuisance species such as *Hydrilla verticillata* and *Myriophyllum spicatum*.

Effects of Increased Storm Disturbance on Seagrass Systems

Increased deposition of sandy shoreface sediments in seagrass beds results in a higher proportion of large-sized particles in the substrate and lower availability of inorganic nitrogen. Seagrass beds protected from frequent overwash deposition are dominated by *Thalassia testudinum*, a climax seagrass species with a high nitrogen demand, while *Syringodium filiforme* dominates areas subject to frequent overwash deposition, presumably because of reduced competition from *Thalassia testudinum*. Therefore, increased deposition of sandy sediments caused by increased storm disturbance will likely cause a shift in seagrass community composition to early colonizing species (*Syringodium filiforme*, *Halodule wrightii*) with relatively low nutrient demands.