Estuaries and Coasts (2021) 44:558–576
https://doi.org/10.1007/s12237-020-00837-7

SPECIAL ISSUE: SEAGRASSES TRIBUTE TO SUSAN WILLIAMS

Scaling up: Predicting the Impacts of Climate Change on Seagrass Ecosystems

Richard C. Zimmerman[1]

Received: 24 April 2020 / Revised: 27 August 2020 / Accepted: 10 September 2020 / Published online: 10 October 2020

Abstract

Since Susan Williams and I started our scientific careers in the mid-1970s, seagrass science has been transformed from a largely descriptive field to an increasingly quantitative and predictive endeavor that requires a mechanistic understanding of environmental influence on metabolic networks that control energy assimilation, growth, and reproduction. Although the potential impacts of environment on gene products are myriad, important phenotypic responses are often regulated by a few key points in metabolic networks where externally supplied resources or physiological substrates limit reaction kinetics. Environmental resources commonly limiting seagrass productivity, survival, and growth include light, temperature, and CO_2 availability that control carbon assimilation and sucrose formation, and regulate stress responses to environmental change. Here I present a systems approach to quantify the responses of seagrasses to shifts in environmental factors that control fundamental physiological processes and whole plant performance in the context of a changing climate. This review shows that our ability to understand the past and predict the future trajectory of seagrass-based ecosystems can benefit from a mechanistic understanding of the responses of these remarkable plants to the simultaneous impacts of ocean acidification, climate warming, and eutrophication that are altering ecosystem function across the globe.

Keywords Ocean acidification · Ocean warming · Carbon dioxide · Scaling up · Prediction · Metabolic theory · Energy balance · Energy flow

Homage to Susan

Susan Williams was driven by her joy in exploring the natural world, her concern for environmental integrity, and her strong motivation to develop a mechanistic understanding of marine ecology. Her particular fondness for marine plants, especially seagrasses, led her to explore the physiology of these remarkable organisms and their function within subtidal ecosystems. Susan's work on nutrient interactions and epiphytes (Hughes et al. 2004; Williams and Ruckelshaus 1993), seagrass population genetics (Williams and Davis 1996; Williams and Orth 1998), human exploitation of marine ecosystems (Coleman and Williams 2002), and biological invasions (Lodge et al. 2006; Williams and Smith 2007) helped formulate some of the most highly influential papers published on the existential crisis facing seagrass ecosystems today (Orth et al. 2006; Waycott et al. 2009).

At the heart of Susan's science, however, was a desire to understand the past and predict the future, beginning with her first investigations into seagrass photosynthesis. The systems perspective she developed, under the influence of C. Peter McRoy, laid the groundwork for her scientific contributions that continue to impact our thinking today. For example, her M.S. thesis, subsequently published as Williams and McRoy (1982), adopted the macroscopic perspective of Odum (2007) to emphasize the similarity of photosynthetic performance among six species of North American seagrasses that were only distantly related across four taxonomic families (den Hartog and Kuo 2006; Waycott et al. 2006). From that early beginning, Susan made a number of important contributions to our understanding of nutrient dynamics (Williams and Ruckelshaus 1993), trophic transfer and the role of herbivores in structuring shallow water benthic communities (Heck et al. 2008; Thayer et al. 1984), patterns of reproduction and population genetics in marine macrophytes (Williams 2001), and

Communicated by Kenneth L. Heck

✉ Richard C. Zimmerman
rzimmerm@odu.edu

[1] Department of Ocean, Earth & Atmospheric Sciences, Old Dominion University, Norfolk, VA, USA

species invasions (Williams 2007; Williams and Grosholz 2008). Susan also focused heavily on the existential threat to coastal marine ecosystems from human impacts, and particularly climate change, which requires a systems-level perspective to understand and predict the scales over which climate will impact living marine systems (Harley et al. 2006).

Since Susan and I began our scientific careers in the mid-1970s, seagrass science has been transformed from a descriptive field emphasizing natural history to an increasingly quantitative, and predictive, endeavor that requires mechanistic understanding of environmental influences on metabolic networks within and among species that control energy assimilation, growth, and reproduction of these remarkable marine plants (Brown et al. 2004). At the turn of the last century, Duarte (1999) criticized seagrass research for being demographically unbalanced in terms of its practitioners and taxonomically unbalanced in terms of its subjects. Perhaps most critically, he found the research to be dominated by descriptive efforts that made little or no attempt to synthesize results or derive general relationships that could be used in a predictive sense for the management of seagrass ecosystems. The remainder of this essay will explore the extent to which we have begun to achieve that predictive understanding of seagrass ecology, particularly in the last 20 years, and to identify opportunities for continued progress in the near future. I will frame this discussion using the systems perspective pioneered by H.T. Odum and focus on ecological energetics to illustrate a path for scaling up from laboratory experiments on individual leaves to whole plant carbon balance, and how that mechanistic knowledge can help us predict climate impacts on seagrass ecosystems that can be tested across the submarine landscape as we march deeper into the Anthropocene.

The Evolution of Our Climate and Our Scientific Thinking

As I write this in August 2020, the monthly average concentration of CO_2 in our atmosphere now hovers above 415 ppm, a level not experienced on Earth in nearly 20 million years (Thomas 2008; Zhang et al. 2013). Of perhaps even greater concern, the acceleration in anthropogenic CO_2 release has been following the "business as usual scenario" (IPCC 2014), exponentially increasing the concentration of CO_2 in the atmosphere at a rate of 0.024 $year^{-1}$ (Fig. 1a). Not coincidentally, the rate of growth in overall scientific knowledge as measured by the annual number of peer-reviewed publications—another anthropogenic product—has increased exponentially at a similar rate of 0.029 $year^{-1}$ since at least 1980 (Bornmann and Mutz 2015). Remarkably, scientific knowledge of seagrasses has grown more than twice as fast as the general scientific literature, with the number of publications increasing at an exponential rate of 0.069 $year^{-1}$ since the mid-1970s when *Estuaries & Coasts* published its first issue under the original name *Estuaries*. My estimate undoubtedly represents a lower bound on the true growth in seagrass publications, as it was based on a simple search query to the *Web of Science* with the words "seagrass OR zostera OR eelgrass OR thalassia OR turtlegrass OR posidonia OR neptune grass OR phyllospadix OR surfgrass" listed in the title or as a topic descriptor. Nonetheless, it retrieved > 12,000 published documents since 1920, distributed across > 100 disciplines. The diversity of investigations is illustrated by the tree map showing the distribution of seagrass publications in the top 25 disciplines ranging across Marine & Freshwater Biology to Biodiversity & Conservation to Genetics (Fig. 1b). These publications provide an ever-growing foundation for developing a predictive understanding of the biology of seagrasses and their environmental significance at scales ranging from molecules to ecosystems.

Despite the prodigious growth in quantitative knowledge about seagrasses across multiple disciplines and scales, and the compilation of that knowledge in several excellent books along the way (e.g., McRoy and Hellfrich 1977; Phillips and McRoy 1980; Hemminga and Duarte 2000; Short and Coles 2001; Larkum et al. 2006; Larkum et al. 2018), seagrass ecosystems continue to suffer local insults from resource extraction, coastal exploitation, waste dumping, and now global impacts from climate warming, sea level rise, and ocean acidification. Collectively, these forces are creating a global crisis that threatens the survival of seagrass meadows, as well as shellfish reefs and coral reefs that create essential habitat for coastal ecosystems worldwide (Lotze et al. 2006; Orth et al. 2006; Waycott et al. 2009).

The global implications of these habitat losses are dire, but sustained local/regional efforts to improve and maintain water quality based on sound science have produced encouraging results. Recognition that seagrasses were relatively weak competitors for light compared with their algal counterparts (e.g., Borum 1983; Bulthius 1983), and that seagrass light requirements could be approximated by the Secchi depth (Dennison 1987; Duarte 1991), provided a management tool linking seagrass survival to water transparency and nutrient loading into coastal waters (Batiuk et al. 2000). Improving water transparency has been important in the recent recovery of submerged aquatic vegetation (SAV) in the Chesapeake Bay, USA (Schulte et al. 2009; Lefcheck et al. 2018), as well as in Tampa and Sarasota Bays, USA (Greening et al. 2011;Greening et al. 2016; Sherwood et al. 2017; Tomasko et al. 2018), and in Europe (de los Santos et al. 2019).

Although the examples cited above demonstrate that a relatively simple measure of light availability could be used to manage water quality improvements that are key to seagrass restoration, the long-term survival of coastal ecosystems remains threatened by global-scale pollution of our atmosphere

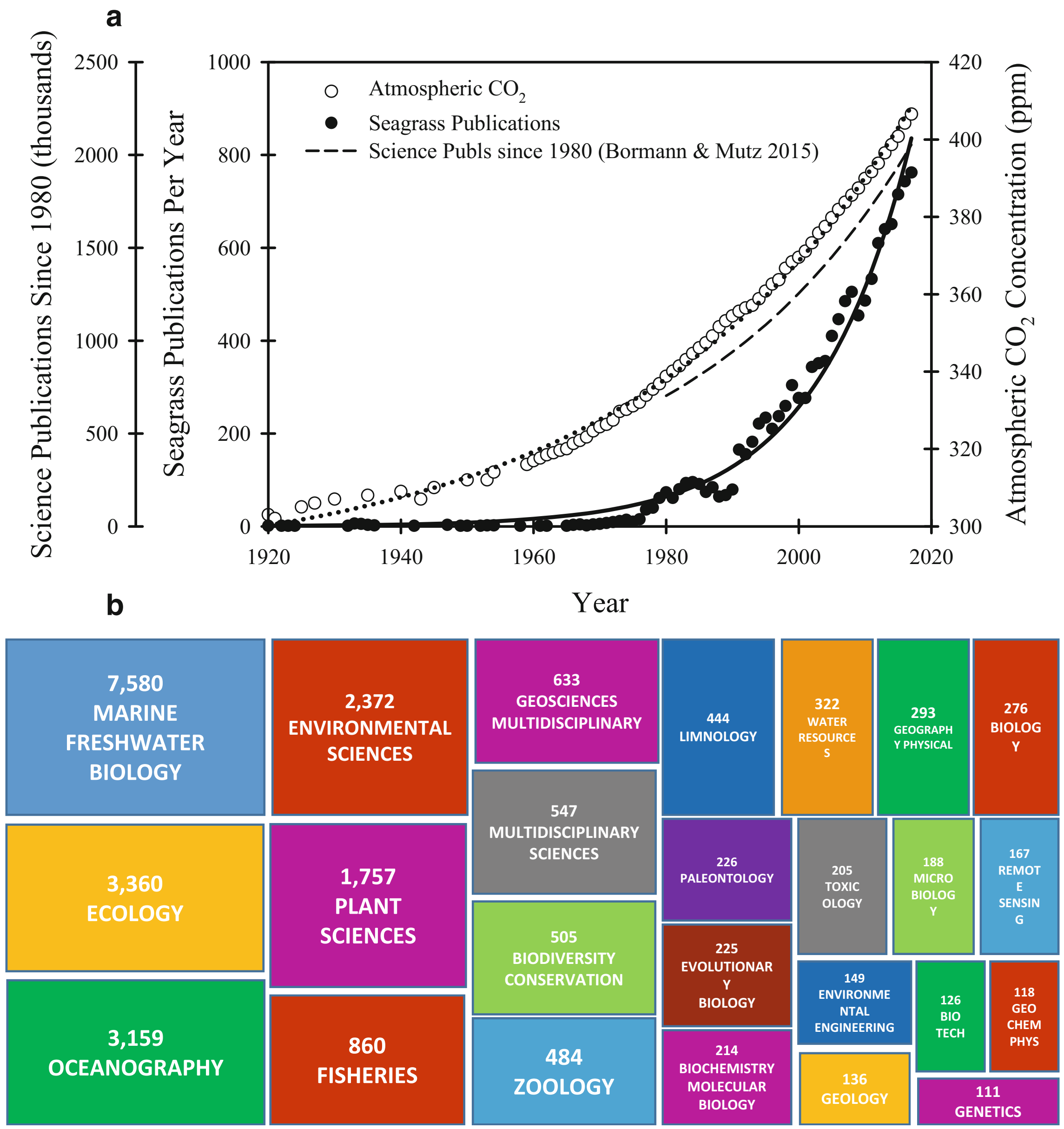


Fig. 1 (a) Rates of increase in (i) the annual average concentration of atmospheric CO_2 at the Mauna Loa Observatory, (ii) modern science publications since 1980 from Bornmann and Mutz (2015), and (iii) seagrass publications obtained from the *Web of Science*. Curves represent non-linear least-squares fit to the data using the simple exponential model ($Y = Y_o\ e^{kT}$) where k represents the intrinsic rate of increase and T represents time (years). The intrinsic rates of increase (k) for atmospheric CO_2, modern science, and seagrass science are 0.024 year^{-1}, 0.029 year^{-1}, and 0.069 year^{-1}, respectively. (b) Tree map of the subject categories generated from the *Web of Science* search. Numeric values indicate the number of seagrass publications in each category, out of the 12,000 “hits”

with greenhouse gases that generate climate-changing impacts not manageable at the scale of local watersheds. Perhaps more important than rising mean water temperature, the frequency and duration of extreme heat events are likely to grow (Lau and Nath 2012), threatening the survival of coastal ecosystems including coral reefs (Hughes et al. 2017) and seagrass meadows (Moore and Jarvis 2008; Thomson et al. 2015; Short et al. 2016), particularly when combined with poor water quality (Moore et al. 2012; Hall et al. 2016).

The climate would be warming even faster if the oceans did not absorb about 26% of the anthropogenic CO_2 released each year. However, that absorbed CO_2 is the primary driver of ocean acidification (OA) that raises additional concerns for the future of marine ecosystems (Doney et al. 2009; Kroeker et al. 2010; Saba et al. 2019). Although the impacts of CO_2 absorption on the chemistry of the open ocean is now unmistakable (Dore et al. 2009), the direct impacts of atmospheric CO_2 absorption on coastal and estuarine environments can be difficult, if not impossible, to distinguish from the impacts of eutrophication (Duarte et al. 2013; Saba et al. 2019). Often fueled by eutrophication, high rates of metabolic activity in coastal and estuarine waters produce diel fluctuations in $p\mathrm{CO}_2$ and pH that are orders of magnitude greater than those driven by the global anthropogenic CO_2 signal, potentially making estuarine waters sources, rather than sinks, of CO_2 to the atmosphere (Short et al. 2016; Najjar et al. 2018). Furthermore, watershed processes deliver variable amounts of alkalinity to the receiving waters that alter the effect of CO_2 absorption on pH, dissolved inorganic carbon (DIC) concentration, and carbonate alkalinity (Cai 2011).

Coastal aquatic habitats are among the most diverse on earth, creating a significant challenge for assimilating sufficient information to understand the intricate responses of even the dominant species to climate change. However, the relatively simple morphology, life history, and ease of experimental manipulation in the lab and field make seagrasses top candidates for developing predictive models of the integrated, whole organism responses to light availability, climate warming, and ocean acidification that can incorporate patterns of gene expression, metabolic acclimation, and energy balance required to predict the ecological success and spatial distribution of these ecosystem engineers into the Anthropocene. Codifying our broad knowledge about seagrasses into predictive models can also help guide the direction of investigations into other organisms and their interactions with seagrasses, thereby broadening our predictive understanding of ecosystem function (Kroeker et al. 2011; Waldbusser and Salisbury 2014; Koweek et al. 2018).

From Tissue Segments

Seagrass metabolism is easily measured in the laboratory by quantifying the rate of O_2 and/or DIC flux, in combination with variable fluorescence, from small tissue segments incubated in well-stirred, sealed chambers (Fig. 2a). Furthermore, many constituents of leaves, rhizomes, and roots are easily extracted, enabling detailed investigations of the genome (Olesen et al. 2016), the transcriptome (Gu et al. 2012), and the metabolome (Davey et al. 2016). Although laboratory conditions under which these reductionist measures are performed can be unrealistic ecologically, they provide essential data to parameterize functional relationships between, e.g., photosynthesis and irradiance (Williams and McRoy 1982), the metabolic O_2 demand of below-ground tissues (Zimmerman et al. 1989; Kraemer and Alberte 1993), the light intensity and duration required to sustain metabolic carbon balance as measured by ratios of photosynthesis to respiration, or P:R, (Dennison and Alberte 1982), the effect of temperature on photosynthesis and respiration (Evans et al. 1986; Zimmerman et al. 1989), and understanding functional differences across species (Invers et al. 2001) and populations (Zayas-Santiago et al. 2020).

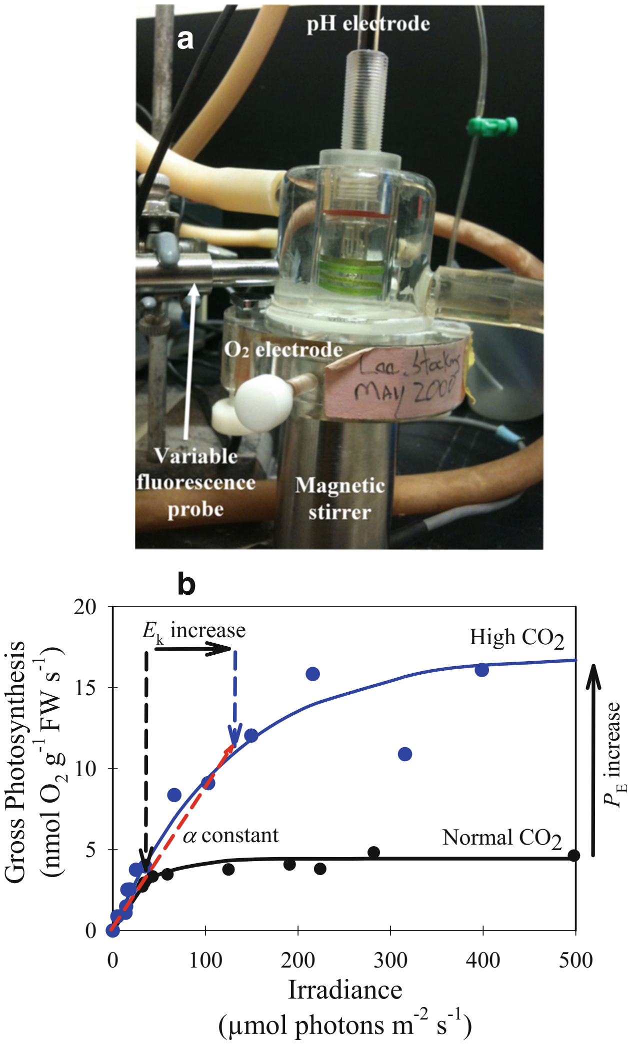


Fig. 2 (a) Seagrass leaf segment enclosed in an incubation chamber for simultaneous measurement of polarographic O_2 (embedded in the base), pH/dissolved inorganic carbon (electrode protruding through the cap), and variable fluorescence (sensor outside the chamber). Temperature is controlled by the water jacket surrounding the incubation chamber and illumination at a constant flux is provided by an artificial lamp (not shown). Reprinted with permission from (Celebi 2016). (b) Photosynthesis vs. irradiance (P vs. E) curves at normal ($\mathrm{pCO}_2 = 400$ μatm, total $\mathrm{CO}_2 = 2$ mmol kg^{-1} SW, pH 8) and elevated CO_2 ($\mathrm{pCO}_2 = 24$ μatm, total $\mathrm{CO}_2 = 3$ mmol kg^{-1} SW, pH 6.5) performed by the author on *Thalassia testudinum* leaves using the polarographic O_2 system illustrated in Fig. 2a. Incubation temperature was 25 °C and salinity was 36 (PSS-78, Lewis 1980). Data were fit to the exponential function of Webb et al. (1974) using the iterative curve fitting tool (CFTOOL) implemented in *Matlab* ®. Red line indicates the initial slope (α) of the light-limited portion of the P vs. E curve. CO_2-driven increases in the light saturation threshold (E_k) and light-saturated rate of photosynthesis (P_E) are indicated by the arrows

The effect of CO_2 on leaf photosynthesis (Sand-Jensen and Gordon 1984; Beer 1989; Durako 1993; Zimmerman et al. 1995; Beer and Koch 1996; Invers et al. 2001) helps limit seagrass colonization depths to the ~10% isolume

(Dennison 1987; Duarte 1991; Onuf 1991; Zimmerman et al. 1991). Photosynthesis vs. irradiance (*P* vs. *E*) curves measured on seagrass leaves at different CO_2 concentrations under controlled laboratory conditions reveal the interaction between light, which provides the energy to drive photosynthesis, and CO_2 availability, the chemical substrate required by Rubisco for carbon fixation (Fig. 2b). Photosynthesis is insensitive to CO_2 concentration at low light intensity because CO_2 availability exceeds the energetic capacity for its assimilation, as revealed by the constant initial slope (α) of the *P* vs. *E* relationship. However, the light-saturated photosynthetic capacity (P_E) of the seagrass leaf is strongly regulated by CO_2, making P_E a hyperbolic function of substrate concentration and permeability, or flow (McPherson et al. 2015). Because α is unaffected by CO_2 availability, the light intensity required to saturate photosynthesis (E_k) also increases with CO_2 availability. Thus, light and CO_2 represent independent, but potentially co-limiting drivers of photosynthesis (Saito et al. 2008) such that the impact of ocean acidification on seagrass performance will depend strongly on the light environment in which the plants are grown.

In contrast, photosynthesis of most marine autotrophs exhibits little response to ocean acidification because CO_2-concentrating mechanisms, including those associated with pyrenoids in algal chloroplasts and carboxysomes in cyanobacteria, effectively facilitate the extraction CO_2 from bicarbonate, which is 140 times more abundant in seawater than free CO_2, thereby maintaining a CO_2-rich environment around Rubisco (Raven et al. 1995; Raven and Beardall 2014). The resulting higher rates of light-saturated photosynthesis generate more favorable *P*:*R* ratios that enable marine algae to colonize depths that extend to the 1% isolume. In addition to elevating seagrass light requirements, carbon limitation of seagrass photosynthesis reduces the effect of temperature on photosynthesis but not on respiration, limiting the ability of seagrasses to maintain positive daily carbon balance as summer temperatures rise (Barber and Behrens 1985; Evans et al. 1986; Zimmerman et al. 1989). Although the positive effect of CO_2 on leaf photosynthesis and sucrose formation suggests that ocean acidification may increase thermal tolerance of eelgrasses by raising *P*:*R* in a warming climate (Zimmerman et al. 1995), differences among species in the power of CO_2 to stimulate leaf photosynthesis suggest that some species, e.g., *Zostera marina*, will benefit more from ocean acidification than others, e.g., *Posidonia oceanica* (Invers et al. 2001).

Short-term laboratory studies have also improved our understanding of carbon isotope fractionation in seagrass leaves and its sensitivity to light availability (McPherson et al. 2015), allowing the relatively easy measurement of leaf $\delta^{13}C$ to provide an index of light availability in seagrass populations (Hu et al. 2012; Lapointe et al. 2020) and its relation to standing biomass in light limited estuaries (Ruesink et al. 2015).

Taken together, the laboratory studies of tissue segment metabolism and chemical composition, in conjunction with knowledge of leaf optical properties (Cummings and Zimmerman 2003; Enríquez 2005), radiative transfer processes controlling water column transparency (Gallegos 2001; Lee et al. 2005), and plant canopy architecture (Zimmerman 2003b), have enabled the creation of multi-parameter bio-optical models that predict the integrated effects of temperature, light, and dissolved gas concentrations on whole plant carbon balance (Zimmerman 2006; Zimmerman et al. 2015) (Fig. 3a). The interactions produced by these models are strongly nonlinear, resulting in a complex response surface in which the

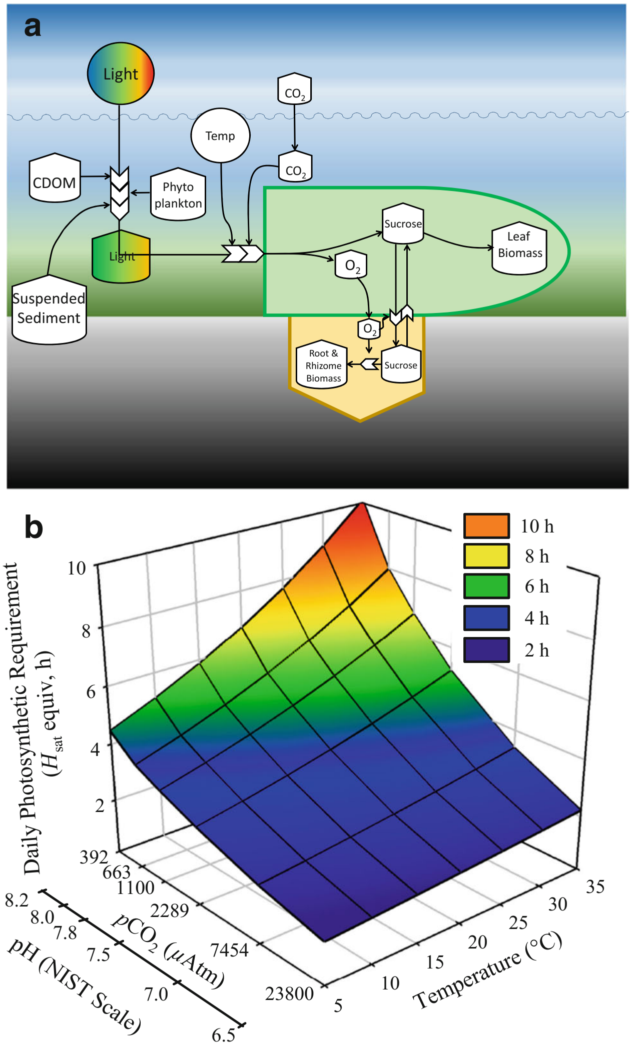


Fig. 3 (a) Conceptual diagram illustrating the interaction between light, temperature, and CO_2 availability on photosynthesis and growth of seagrasses, based on the short-term laboratory experiments. Symbols are after Odum (1983). (b) Interactive effects of temperature and CO_2 enrichment on the daily photosynthetic requirement to maintain positive whole-plant carbon balance in *Zostera marina*. With sufficient light availability, the "CO_2 fertilization effect" associated with coastal acidification can offset the deleterious effects of elevated temperatures. Reprinted with permission from Zimmerman et al. (2015)

photosynthesis (expressed here as hours of light-saturated photosynthesis, H_{sat}) required to balance daily carbon demand for metabolism increases exponentially with temperature at present-day ocean CO_2 levels, but decreases dramatically as CO_2 concentration increases/pH decreases (Fig. 3b).

To Whole Plants

The ability to cultivate seagrasses in laboratory aquaria and mesocosms provides a pathway for mapping predictions and validating models derived from metabolic measurements using tissue segments (described above) onto the integrated long-term performance of whole plants. Aquaria and mesocosms also permit experimental manipulation over a broader range of treatments than might be experienced at any one location in the field, permitting accurate quantification of the metabolic response curve to environmental drivers such as light, temperature, and CO_2 availability. Results from these experiments allow functional relationships to be quantified by "drawing the line" rather just testing for significant differences among treatments (Brown et al. 2004; Cottingham et al. 2005; Palacios and Zimmerman 2007; Zimmerman et al. 2017).

Whole-plant experiments with numerous seagrass species typically yield significantly enhanced rates of leaf photosynthesis and sugar accumulation after brief exposures to elevated CO_2 in laboratory aquaria (Table 1). Although the strength of the whole-plant response should be expected to vary depending on species (Invers et al. 2001), the duration of exposure, light intensity, temperature, and nutrient regimes can also play a major roles in elucidating performance features that might be impacted by ocean acidification. For example, growth of *Amphibolis antarctica, Halophila uninervis*, and *Thalassia hemprichii*, but not *Cymodocea serrulata*, responded positively to increased CO_2 availability in as little as 2 to 4 weeks (Burnell et al. 2014; Ow et al. 2015). However, a separate 2-week experiment showed that growth of *C. serrulata* responded positively to both light and CO_2 availability, while *H. uninervis* only exhibited a positive growth response to light availability (Ow et al. 2016). The different species responses reported above may have resulted from differences in carbon allocation strategies to shoots, roots/rhizomes, and reproduction among species/populations that suggests a genetic component. However, experimental periods that barely encompass one plastochron interval (~2 weeks) for leaf initiation may simply be too short to manifest significant long-term impacts on whole plant morphology and performance. Extending the experimental exposure period is likely to produce important responses not observed in short-term studies.

A 21-day experiment with *T. hemprichii* produced a significant positive effect of CO_2 enrichment on leaf photosynthesis and soluble carbohydrate accumulation that generated a 30% increase in leaf growth (Jiang et al. 2010). A 28-day experiment with *Cymodocea nodosa* revealed that ocean acidification improved ammonium assimilation and helped maintain a positive carbon balance in the face of a temperature-induced increase in respiration (Egea et al. 2018). A 45-day aquarium experiment with *Z. marina* demonstrated that tripling the rate of leaf photosynthesis by CO_2 enrichment reduced the daily period of irradiance-saturated photosynthesis required for plants to maintain positive whole carbon balance from 7 to 2.7 h (Zimmerman et al. 1997). The 3-fold increase in light-saturated leaf photosynthesis stimulated by CO_2 enrichment allowed plants growing under a daily 4-h photoperiod to perform like plants growing under a 12-h daily photoperiod in unenriched seawater, verifying the stoichiometric impact of CO_2 on whole plant carbon balance predicted from experiments on individual leaves. Plants grown under the 4-h photoperiod without CO_2 enrichment slowly consumed internal carbon reserves, decreased their growth rates, and expired after 45 days. The square-wave nature of illumination employed in this experiment was unrealistic ecologically and should not be interpreted to imply an equivalent response to a 3-fold reduction in natural light intensity in the field. However, this experiment did facilitate the calculation of daily carbon budgets for each treatment, quantitatively linking the CO_2-stimulated increase in leaf photosynthesis to daily photosynthetic carbon gain by the leaves and the determination of carbon budgets, growth, and survival of whole plants.

An 8-week experiment performed with *Halodule wrightii* and *Ruppia maritima* under mesohaline conditions (salinity ≅ 20 (PSS-78, Lewis 1980)) in outdoor aquaria found no effect on species composition, plant morphology, tissue C or N content, or rapid light curve parameters measured using variable fluorescence (Guerrero-Meseguer et al. 2020). However, rapid light curves produced by variable fluorescence instruments can be insensitive to CO_2 limitation of photosynthesis if alternate pathways for photochemical quenching (e.g., photorespiration) and non-photochemical quenching (e.g., xanthophyll cycling) are active. Although soluble sugar concentrations were not reported, $\delta^{13}C$ values of above- and below-ground tissues were significantly reduced under CO_2 enrichment, which is consistent with model predictions of CO_2-stimulated photosynthesis and its impact on stable isotope composition (McPherson et al. 2015).

A 14-week manipulation revealed positive impacts on shoot density and thermal tolerance of *T. hemprichii*, in addition to the positive impacts on mobile carbon reserves and leaf growth rates (Liu et al. 2020). This study further showed that seagrass metabolism had a positive impact on the growth of the reef coral *Pocillopora damicornis* when co-located in the same aquaria.

A year-long CO_2 enrichment experiment with *Zostera marina* from California using outdoor aquaria illuminated by natural sunlight (Palacios and Zimmerman 2007)

Table 1 Summary list of CO_2 enrichment experiments employing whole plants ranging from 1 week to 20 months duration, and indications of their basic findings. Positive impacts of CO_2 enrichment are indicated by "+," negative impacts are indicated by "−," "NS" indicates no significant effect, and "nr" indicates the results were not reported

Experimental context	Species	Experimental duration	Photosynthesis or ETR	Tissue chemistry	Leaf growth	Shoot density	Flowering	Light requirements	Thermal tolerance	Source
Laborataory Aquaria	*Amphibolis antarctica*	1 week	+	+	+	NS	nr	NS	nr	Burnell et al. 2014
	Cymodocea cerrulata	2 weeks	+	+	NS	NS	nr	+	nr	Ow et al. 2015
	Cymodocea cerrulata	2 weeks	+	+	+	NS	nr	NS	NR	Ow et al. 2016
	Cymodocea nodosa	4 weeks	nr	+	NS	NS	nr	nr	NS	Egea et al. 2018
	Haludule uninervis	2 weeks	+	+	+	NS	nr	+	nr	Ow et al. 2015
	Haludule uninervis	2 weeks	+	+	NS	NS	nr	NS	NR	Ow et al. 2016
	Halodule wrightii	8 weeks	NS	NS,+	NS	NS	NS	nr	nr	Guerrero-Meseguer et al. 2020
	Ruppia maritima	8 weeks	NS	NS, +	NS	NS	NS	nr	nr	Guerrero-Meseguer et al. 2020
	Thalassia hemprichii	2 weeks	+	+	+	NS	nr	+	nr	Ow et al. 2015
	Thalassia hemprichii	3 weeks	+	+	+	nr	nr	NS	nr	Jiang et al. 2010
	Thalassia hemprichii	14 weeks	nr	+	+	+	nr	nr	+	Liu et al. 2020
	Zostera marina	6 weeks	+	+	+	+	nr	+*	nr	Zimmerman et al. 1997
	Zostera marina	12 months	nr	+	+	+	+	NS	nr	Palacios and Zimmerman 2007
	Zostera marina	20 months	nr	+	+	+	+	NS	+	Zimmerman et al. 2017
	Zostera marina	20 months	+	+	nr	nr	nr	nr	nr	Celebi 2016
	Zostera marina	20 months	+	+	+	nr	nr	nr	nr	Zayas-Santiago et al. 2020
In situ manipulations	*Thalassia testudinum*	6 months	nr	+	NS	NS	nr	nr	nr	Campbell and Fourqurean 2013
	Posidonia oceanica	4 months	NS	NS	NS	NS	nr	nr	nr	Cox et al. 2016
Natural experiments	*Posidonia oceanica*	N/A	nr	nr	nr	+	nr	nr	nr	Hall-Spencer et al. 2008
	Cymodocea nodosa	N/A	+	nr	nr	NS	nr	nr	nr	Apostolaki et al. 2014
	Cymodocea rotundata	N/A	nr	+	+	+	nr	nr	nr	Takahashi et al. 2016
	Cymodocea serrulata	N/A	nr	nr	nr	+	nr	nr	nr	Takahashi et al. 2016
	Halodule uninervis	N/A	nr	nr	nr	+	nr	nr	nr	Takahashi et al. 2016
	Halophila ovalis	N/A	nr	nr	nr	−**	nr	nr	nr	Takahashi et al. 2016
	Thalassia hemprichii	N/A	nr	nr	nr	−**	nr	nr	nr	Takahashi et al. 2016
	Syringodium isoetifolium	N/A	nr	nr	nr	−**	nr	nr	nr	Takahashi et al. 2016

*Although Zimmerman et al. (1997) reported a positive effect of CO_2 on plants grown under short daily photoperiods, plants were exposed to photosynthesis-saturating intensities and these results should not be interpreted as demonstrating an increase in the shade tolerance under elevated CO_2

**Negative impacts on understory seagrasses reported by Takahashi et al. (2016) from increased competition for light and/or nutrients by canopy-forming species whose size and abundance increased with CO_2

demonstrated a number of long-term effects not evidenced in the shorter-duration experiments described above. Prolonged exposure to CO_2 enrichment under light repletion yielded a transient period of significantly higher rates of leaf growth and sugar accumulation during spring that subsequently gave way to a summer period of enhanced rhizome growth, vegetative proliferation, and flowering shoot production that increased the population size going into the subsequent winter. Thus, CO_2 enrichment facilitated survival of the clone and/or population in ways that were not evident in short-term experiments focused on individual shoots. This experiment also confirmed the inability of high CO_2 to stimulate plant growth or survival under light limitation, as predicted from laboratory experiments with leaf segments (Fig. 2b).

A 20-month experiment demonstrated that CO_2 stimulation of primary production enhanced the survival, growth, subsequent vegetative proliferation, and flowering shoot production of *Zostera marina* from the Chesapeake region despite being exposed to a prolonged period of summer heat stress (Zimmerman et al. 2017) (Fig. 4). The experiment also demonstrated quantitative equivalency in the effect of CO_2 on shoot proliferation, size, growth, and sugar accumulation with model predictions based on metabolic carbon balance derived from short-term laboratory experiments on individual leaves (Zimmerman et al. 2015). Thus, rather than acting in a neutral fashion, or as an independent stressor, CO_2 availability appears to serve as a quantitative antagonist able to counter the negative impact of warm summer temperatures on eelgrass growth and survival when light is not a limiting factor.

Long-term experiments encompassing the annual cycle of ambient temperature and light availability also provide mechanistic insight into acclimation processes not evident in short-term experiments. Quantifying the positive impact of CO_2 availability on flowering shoot production required an experimental duration of at least a full year (Palacios and Zimmerman 2007; Zimmerman et al. 2017). Long-term exposure to CO_2 enrichment also reduced the content of photosynthetic pigments without decreasing light harvesting efficiency or photosynthetic capacity (Celebi 2016), in a manner similar to photoacclimation (Cummings and Zimmerman 2003; Dattolo et al. 2014). The photoacclimation-like response to CO_2 availability can be explained by the stimulation of Calvin Cycle activity that also suppresses photorespiration and promotes Photosystem II (PSII) activity, leading to a buildup of O_2 in the chloroplast stroma (Fig. 5). The resulting formation of reactive oxygen species (ROS), along with over-reduction of the plastoquinone (PQ) pool derived from increased PSII activity, likely reduces the expression of light harvesting complex genes via regulatory pathways common among higher plants (Pfannschmidt and Yang 2012), leading to the photoacclimation-like response to elevated CO_2.

To Populations

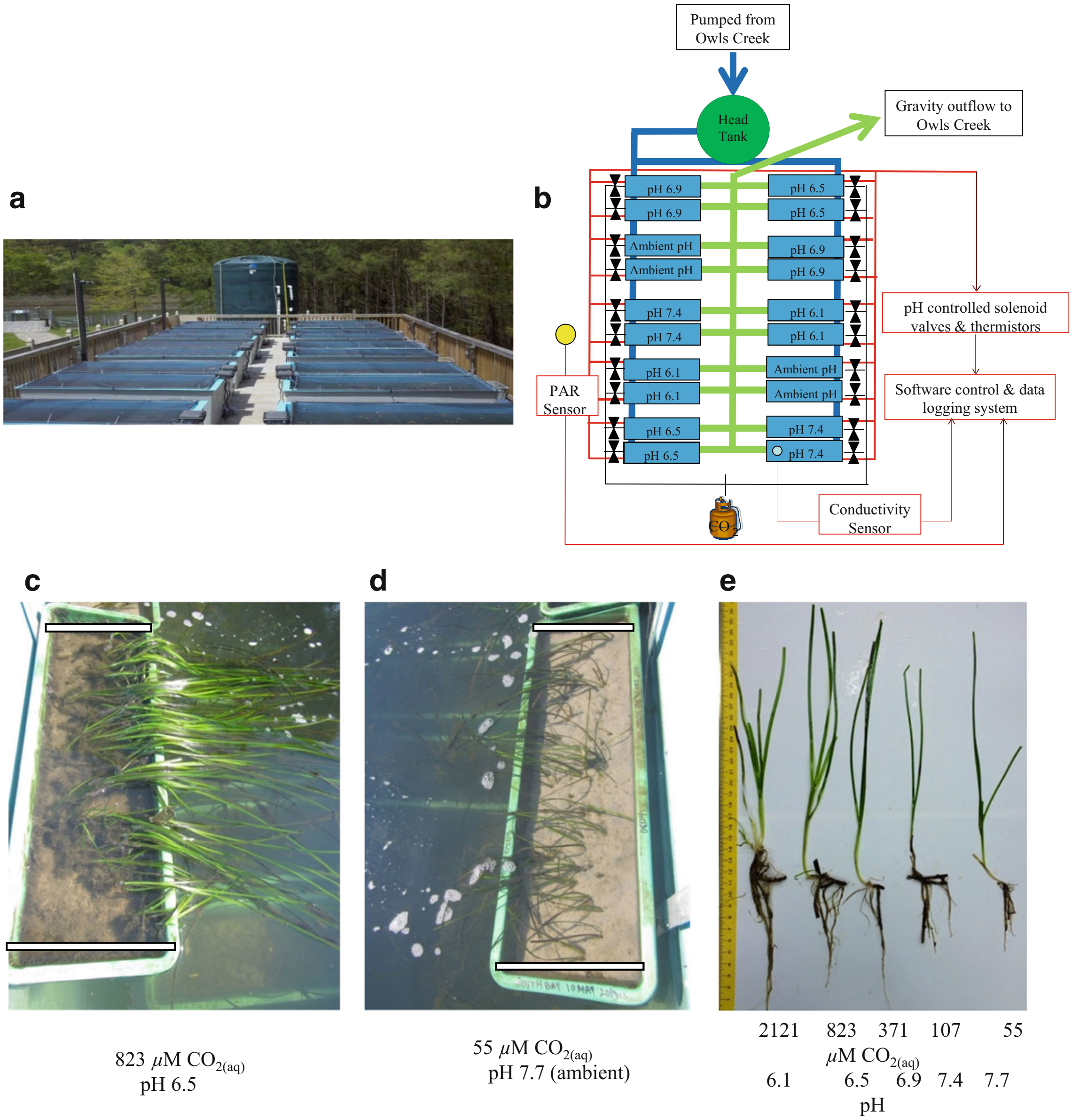
Similar responses of many seagrass species to light, temperature, and CO_2 availability suggest that a common metabolic wiring scheme (e.g., Figs. 3A and 5) may be useful for exploring genetic differences in the responses of seagrasses to environmental stress. Reduced genetic diversity can affect population growth and individual fitness in eelgrass populations (Williams 2001; Hughes et al. 2004) and resilience of whole populations to climate warming (Ehlers et al. 2008). Nonetheless, these population-level differences in eelgrass performance appear to have genetic bases in the regulation of principal metabolic pathways involved in carbon metabolism and storage that can be tracked at the level of the transcriptome (Salo et al. 2015), as well as the metabolome (Zayas-Santiago et al. 2020) and may be common among many seagrass species (Ruocco et al. 2017). Continued application of advanced omics technologies offers to improve our mechanistic understanding of species- and population-level responses to environmental change (Procaccini et al. 2012).

To Natural Seagrass Meadows

The laboratory experiments described above demonstrated that CO_2 can stimulate seagrass productivity, in conjunction with light availability, and is capable of buffering the negative effects of temperature stress on whole plant metabolism. However, ocean acidification represents a persistent environmental press likely to have cascading impacts on nutrient utilization, competitive interactions, and trophic relationships that are difficult to simulate in laboratory mesocosms. Consequently, ecosystem-scale experiments need to be performed in seagrass meadows to test many of the predictions emanating from models based on the leaf- and aquarium-scale experiments described above.

Free-Air CO_2 Enrichment (FACE) experiments performed in terrestrial ecosystems have shown that long-term (years) exposure to elevated CO_2 stimulates photosynthetic carbon gain, net primary production, and improves nitrogen and water use efficiency at both the leaf and canopy scales (Leakey et al. 2009). Long-term FACE experiments also enable realistic investigations into the effects of climate change on community dynamics and trophic transfer. However, logistical and engineering challenges have yet to enable similar long-term Free-Ocean CO_2 Enrichment (FOCE) experiments in natural marine ecosystems (Gattuso et al. 2014).

Nonetheless, there have been a few attempts to conduct ocean acidification experiments *in situ* using enclosures and diffusers placed in natural seagrass meadows. An *in situ* enclosure experiment conducted for 6 months in a shallow *Thalassia testudinum* meadow demonstrated a positive impact of elevated CO_2 on non-structural carbohydrates allocated to



823 μM $CO_{2(aq)}$
pH 6.5

55 μM $CO_{2(aq)}$
pH 7.7 (ambient)

2121 823 371 107 55
μM $CO_{2(aq)}$
6.1 6.5 6.9 7.4 7.7
pH

Fig. 4 (a) Experimental climate change facility at the Virginia Aquarium & Marine Science Center showing the 20 fiberglass tanks (3 m^3 each), CO_2 control units mounted on each aquarium, and the large head tank. (b) Schematic diagram of the experimental system, illustrating the experimental aquaria (blue rectangles), water inflow (blue lines) and outflow (green lines), CO_2 supply delivery system (tank black lines) with pH-controlled valves (black hourglass symbols), and environmental monitoring system (red lines and rectangles). Eelgrass growing at (c) 823µM $CO_{2(aq)}$, pH 6.5 and (d) 55 µM $CO_{2(aq)}$, pH 7.7 (ambient) after 6-month growth in the experimental chambers in October 2013. White bars at the top and bottom of the pictures are 20-cm long. (e) Differences in eelgrass shoot size across the CO_2 gradient in October 2014. Reprinted with permission from Zimmerman et al. (2017)

rhizomes and carbon content of leaves, relative to nitrogen and phosphorus, but did not demonstrate an increase in plant size, growth rate, or shoot density within the enriched plots (Campbell and Fourqurean 2013). The authors suggest that structural CO_2 responses may require experimental periods longer than 6 months in this species, and at scales beyond small groups of short shoots in seagrasses, such as *T. testudinum*, that maintain extensive horizontal rhizomatous interconnections and only propagate new short shoots at the meristematic tips of horizontal rhizomes. They also noted that self-shading by the dense leaf canopy used in their study may have resulted in low light levels that attenuated the growth and morphological responses to CO_2.

A subtidal enclosure system deployed in a *P. oceanica* meadow produced no measurable impact on epiphyte abundance, leaf biometrics, or variable fluorescence after 4 months of elevated pCO_2 (Cox et al. 2016). As with *T. testudinum*, *P. oceanica* may require longer experimental periods, larger plot sizes, and some appreciation of self-shading effects by intact plant canopies to fully evaluate the impacts of pCO_2

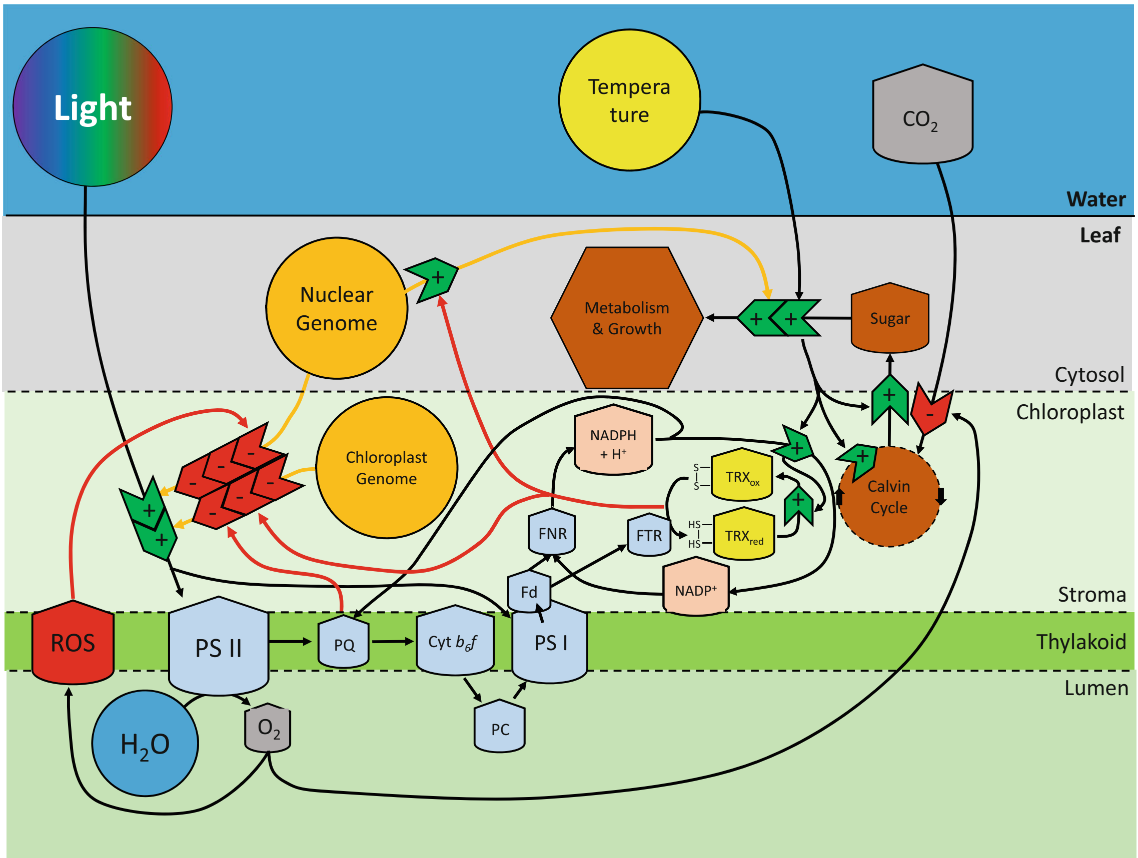


Fig. 5 Interacting effects of light, temperature and CO_2 availability on acclimation and growth. The scheme depicts (i) the light-dependent but temperature-independent photochemistry involved in light harvesting and photosynthetic electron transport through the thylakoid membrane, (ii) the enzyme, temperature, and CO_2-dependent dark reactions coupled to each other by the Calvin Cycle, NADPH, and the ferredoxin-thioredoxin oxidoreductase system (FTS and TRX). Black arrows indicate energy/carbon flow. Red arrows indicate regulatory feedbacks on chloroplast and nuclear gene expression (orange arrows) that control metabolic processes. CO_2 required for Calvin cycle enhances photosynthetic electron flow by stimulating the NADP+/NADPH cycle, over-reducing the plastoquinone (PQ) and thioredoxin (TRX) pools, thereby downregulating production of the Photosystem II (PS II) light harvesting complex that contains most of the photosynthetic pigments. Temperature effects illustrated here are acutely sub-lethal and do not consider enzyme deactivation or protein denaturation. After Pfannschmidt and Yang (2012)

on this exceptionally long-lived species. However, the lack of a dramatic CO_2 effect is also consistent with the observation that CO_2 enrichment produces a rather modest increase in leaf photosynthesis of *P. oceanica* relative to other species, particularly *Z. marina* and *Phyllospadix torreyi* (Invers et al. 2001).

An open (enclosure-free) FOCE experiment performed for 6 weeks using underwater diffusers caused the levels of protective phenolic acids to decrease in the leaves of *Ruppia maritima* and *Potamogeton amplifolius* in the mesohaline portion of the Chesapeake Bay, suggesting downregulation of the shikimic acid/phenylproprenoid pathway in response to CO_2 enrichment (Arnold et al. 2012), in striking contrast to what is often observed in terrestrial plants (Goverde et al. 1999). A similar CO_2-induced downregulation of shikimate pathway intermediates was observed in *Z. marina* (Zayas-Santiago et al. 2020), suggesting that this unusual response, relative to terrestrial plants, may be shared among aquatic vascular plants. The loss of chemical defenses in response to elevated CO_2 may also make the leaves of submerged aquatic vegetation more vulnerable to leaf grazers, and to opportunistic pathogens such as the *Labyrinthula* complex often held responsible for wasting disease.

Volcanic submarine CO_2 seeps have served as natural laboratories to explore the potential impact of ocean acidification on seagrass ecosystems. Surveys along the natural CO_2 gradient in Ischia, Italy, revealed increased leaf density and productivity of *P. oceanica* in the high CO_2 zone (Hall-Spencer et al. 2008), consistent with predictions from leaf segment and whole plant experiments described above. Despite the reduced abundance of gastropod grazers in the high CO_2 area at Ischia, epiphyte loads remained low on the plants growing in the CO_2 enrichment zone (Hall-Spencer et al. 2008). The loss of some invertebrate taxa in the extreme low pH zones appeared to be compensated by increases in populations of small acidification-tolerant taxa, particularly crustacean mesograzers responsible for controlling epiphyte abundance, despite the overall reductions in ecosystem diversity and food web complexity (Kroeker et al. 2011).

C. nodosa plants growing in a high CO_2 region near Volcano Italy exhibited higher rates of photosynthetic electron transport under light saturation and were depleted in $\delta^{13}C$ relative to an adjacent control plot (Apostolaki et al. 2014), as predicted from the laboratory experiments cited above. These plants also possessed reduced polyphenol concentrations in leaves (Arnold et al. 2012), consistent with the results from the diffuser experiment described above. However, the CO_2-stimulated increase in photosynthetic capacity did not translate into increased biomass, perhaps because of nutrient limitation, grazing, or low light availability (Apostolaki et al. 2014).

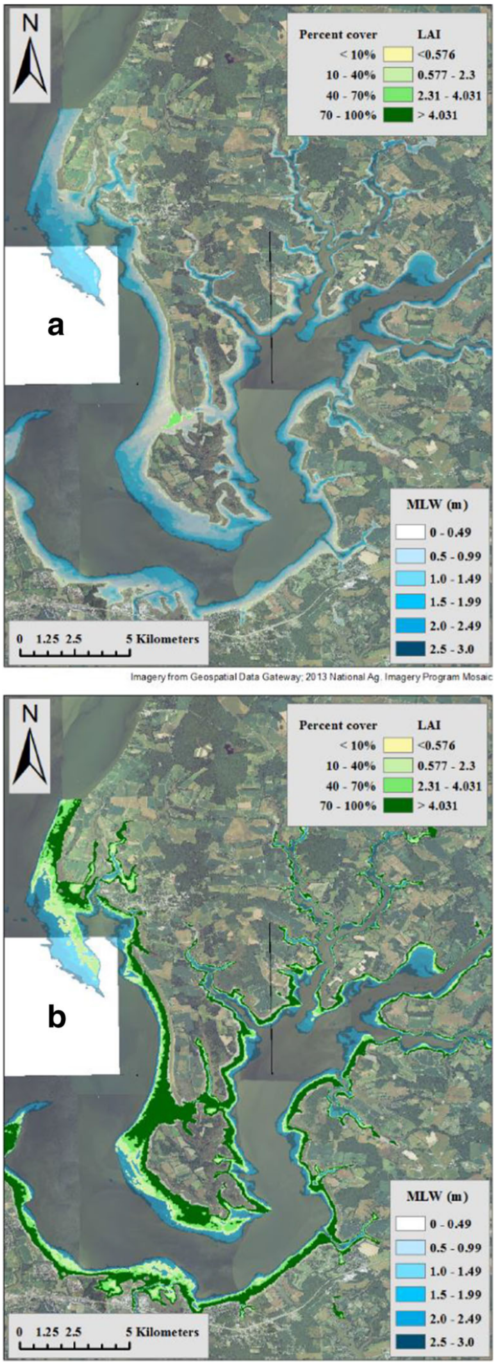
A series of shallow volcanic vents in Papua New Guinea were used to examine the impacts of CO_2 enrichment on multi-species seagrass communities (Takahashi et al. 2016). Overall seagrass cover and biomass increased, while leaf $\delta^{13}C$ decreased with CO_2 across the sites. However, the CO_2 subsidy appeared to favor canopy-forming species (*Cymodocea serrulata*, *Cymodocea rotundata*, and *Halodule uninervis*) over understory species (*Halophila ovalis*, *Thalassia hemprichii*, and *Syringodium isoetifolium*), suggesting that competitive hierarchies for light and-or nutrients among seagrasses may be altered in a high CO_2 world.

To Predictions of Future Impacts

Taken together, the whole-plant experiments and field observations summarized above help validate the effects of light, temperature, and CO_2 availability on metabolic carbon balance initially quantified by experiments with tissue segments, leading to the conclusion that seagrasses are likely to benefit from a high CO_2 world. Quantifying that benefit in the context of other environmental variables (e.g., light, temperature, epiphytes) requires formal translation of the experimental findings into functional responses so that their linked behaviors can be explored in silico. For example, laboratory measurements of individual leaf metabolism, as described above, often produce light intensities required to saturate photosynthesis that are 2 to 4 times lower than those estimated from whole canopy incubations performed in the field (Fourqurean and Zieman 1991; Herzka and Dunton 1997). However, by incorporating explicit geometric corrections for leaf orientation, the angular distribution of submarine irradiance and canopy self-shading, the bio-optical model *GrassLight* exploits data derived from laboratory measurements of individual leaf segments to accurately reproduce the higher light saturation thresholds for whole plant canopies often reported from field incubations (Hu et al. 2012; Zimmerman 2003b).

GrassLight also exhibits some expertise in predicting the distribution and density of *Z. marina* across the submarine landscape in response to water quality (Zimmerman 2006; del Barrio et al. 2014). In particular, this modeling approach was used to evaluate the relative contributions phytoplankton vs. suspended sediments and detritus on the density and distribution of seagrasses (Zimmerman 2003a). Sensitivity of SAV distributions to light availability in the Chesapeake Bay is illustrated by *GrassLight* simulations performed for the Chester River MD estuary. A model simulation using average concentrations of phytoplankton (20 mg m^{-3} Chl *a*) and suspended particulate matter (30 mg L^{-1}) measured in the Chester River by the Chesapeake Bay Program (www.ChesapeakeBay.net) produced a very small region of SAV habitat along the north shore of Eastern Neck Island (Fig. 6a) that is consistent with observational maps of SAV distribution generated by the Virginia Institute of Marine Science SAV Program (http://web.vims.edu/bio/sav/index.html). Reducing the suspended loads to 10 mg m^3 Chl *a* and 10 mg L^{-1} total suspended matter (TSM) dramatically increased the potential habitation zone and vegetation density throughout the lower regions of the river (Fig. 6b), enabling one to quantitatively predict potential gain in habitat area and vegetation density from incremental improvements in water quality. This capability allows the effects of water quality improvements on SAV distribution in upper Chesapeake Bay, as well as the determination of Chl *a* and TSM levels required to achieve SAV restoration goals, to be explored in silico in ways that enhance our ability to protect and manage submerged aquatic vegetation.

When properly constrained and parameterized to reproduce local conditions accurately, simulation models such as *GrassLigh*t offer predictive insights into the performance of eelgrass meadows that can inform our understanding of ecosystem responses to future climate change (Zimmerman et al. 2015). With respect to the Chesapeake region, our results suggest that ocean acidification projected for the next century will stimulate photosynthesis sufficiently to offset the negative effects of mean temperature increases on eelgrass survival, even in the presence of typical epiphyte loads that compete for light and chemical resources, at least in light-replete environments (Fig. 7). Additionally, the reduced temperature sensitivity exhibited by eelgrass growing in the relatively clean coastal lagoons of the DelMarVa Peninsula relative to Chesapeake Bay populations in those simulations suggests that improved water quality may also reduce the effects of thermal stress on populations growing near their southern limits, even in the absence of CO_2-stimulated photosynthesis. This prediction of increased thermal tolerance is supported by independent field observations who reported that, after accounting for temperature differences (~ 1 °C) between the sites, eelgrass thriving in the coastal bays received at least 100% of their light requirements 24% of the time, while less robust meadows in the lower Chesapeake Bay only met this requirement 6% of the time. (Moore et al. 2012). Consequently, eelgrass populations in the coastal bays have been expanding at a rate of 66% $year^{-1}$ since 2005, while



Imagery from Geospatial Data Gateway; 2013 National Ag. Imagery Program Mosaic

Fig. 6 *GrassLight* simulations of SAV distribution and density at the mouth of the Chester River, MD, a tidal estuary on the eastern shore of the Chesapeake Bay. Blue shading represents local bathymetry obtained from the NOAA Environmental Data Center (https://maps.ngdc.noaa.gov). Green colors represent potential SAV distribution and density, based on water quality conditions used in the simulation. (a) Simulated SAV distribution for mean water quality conditions in the Chester River (20 mg m^{-3} Chl *a*, 30 mg L^{-1} TSM). (b) Simulated SAV distribution for 10 mg m^{-3} Chl *a*, 10 mg L^{-1} TSM

corresponding populations in the Chesapeake Bay experienced a 2% expansion and two significant die-offs in 2005 and 2010 that did not occur in the coastal lagoon populations. Thus, without an increase in available light, Chesapeake Bay populations may be severely reduced or eliminated, while the proximity to clearer Atlantic waters may enable coastal lagoon populations to thrive even as the climate warms. These findings should provide further incentive to improve coastal water quality in support of SAV habitat restoration goals in spite of projected climate warming.

Unlike seagrasses, numerous marine organisms, especially those that precipitate limestone shells, are likely to suffer in an increasingly hot and sour sea. However, given that seagrasses often share the submarine landscape with calcareous organisms, including corals and oysters, there is a potential for seagrasses to increase seawater pH by photosynthetic uptake of CO_2, thereby improving local conditions for other organisms (Unsworth et al. 2012). By linking models originally developed for different purposes, we can broaden the ecological relevance of our mechanistic understanding of seagrass performance. *GrassLight* was combined with a fluid mechanical box model to evaluate the potential for a temperate eelgrass meadow to modify local water chemistry on hourly-to-monthly time scales in the context of providing ecosystem services to adjacent oyster populations (Koweek et al. 2018). The combined models showed that the ability of a seagrass meadow to mitigate ocean acidification for adjacent oyster populations could be predicted from depth-averaged net production, seawater residence time, and the carbonate chemistry of the source water, and represents an important step in defining the ability of seagrass meadows to provide important biogeochemical services to other components of the coastal ecosystem. Partly as a result of that effort, originally organized by Susan Williams, the *GrassLight* model is currently being integrated with the *Eco-Oyster* model of Kellogg et al. (2018) to identify ecologically relevant thresholds required for successful oyster restoration and aquaculture operations and evaluate the potential for seagrass meadows to provide a management tool for mitigating the impacts of OA on oyster populations in the Chesapeake Bay (Fig. 8).

Although numerous lines of evidence provided above indicate that seagrasses are likely to benefit from ocean acidification when applied as a continuous press, light intensities must be sufficient for photosynthesis to take advantage of the more abundant CO_2 substrate. Consequently, these submerged plant systems remain vulnerable to extreme events generated by heat waves and nuisance algal blooms that create acutely toxic conditions, even in the presence of elevated CO_2, and which may occur with increasing frequency as we march deeper into the Anthropocene (Plus et al. 2003; Rask et al. 2000; Seddon et al. 2000). Rapid seagrass die-offs occurred throughout Florida Bay from 1987 to 1992, and again in 2015 when reduced O_2 solubility resulting from elevated temperature and salinity combined with high turbidity to limit seagrass photosynthesis, leading to oxygen stress and sulfide intrusion that resulted in plant death (Borum et al. 2005; Hall et al. 2016).

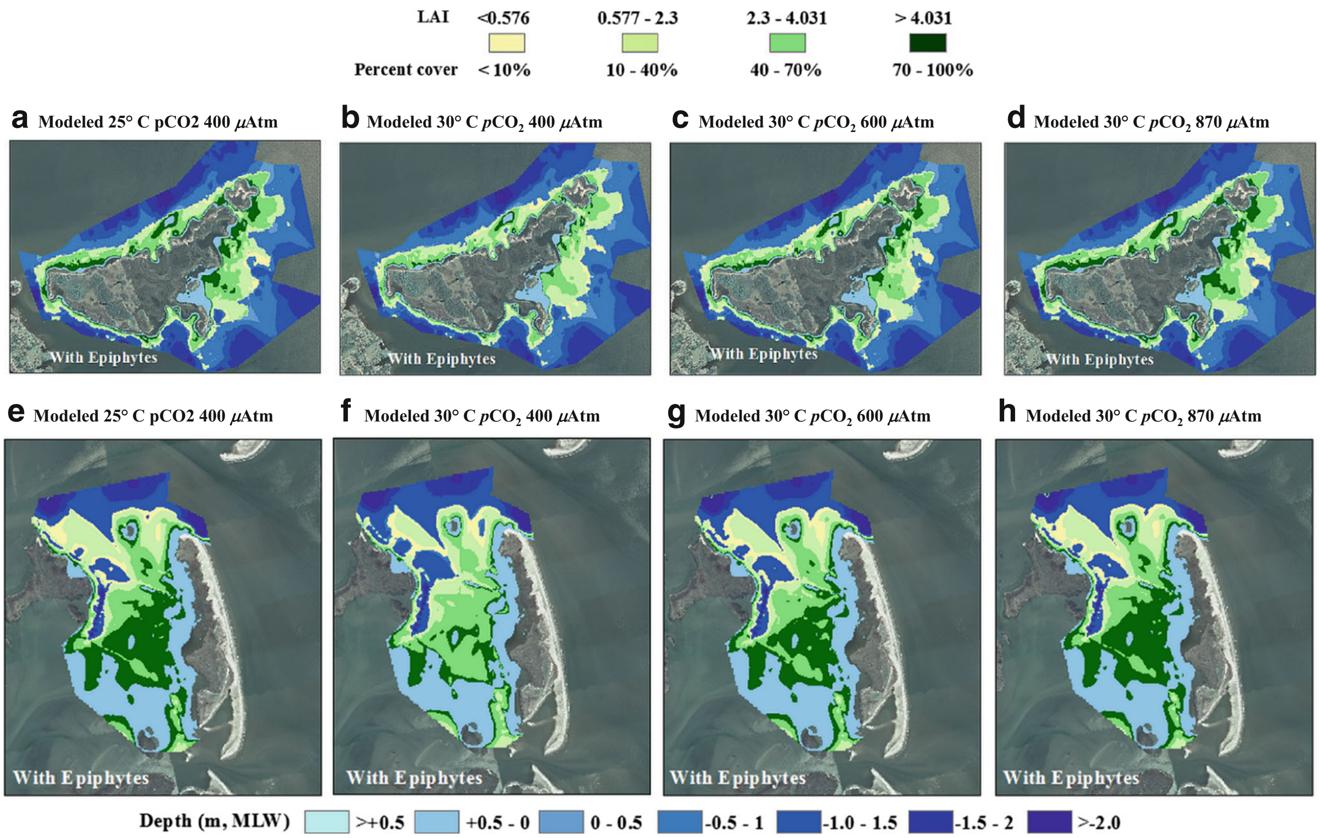


Fig. 7 Combined effects of ambient temperature and pCO_2 on the distribution and density of eelgrass (tan to green colors) across the submarine landscape overlaid on the digital elevation model (blue colors) at Goodwin Islands at the mouth of the York River in Chesapeake Bay (a–d) and South Bay (e–h), a coastal lagoon on the DelMarVa Peninsula. Conditions for each simulation are indicated on the plots. Unvegetated light blue areas close to shore represent intertidal regions shallower than 0 MLW, which we considered too shallow for successful eelgrass colonization. Density classes were selected to match the classes defined by the Virginia Institute of Marine Science SAV Program (http:/web.vims.edu/bio/sav/). Reprinted with permission from Zimmerman et al. (2015)

To a View from Space

Advances in computational power and image rendering now enable the computer simulations described above to generate highly textured maps of seagrass distribution across the submarine landscape at a level of detail that is virtually impossible to validate by on-the-ground sampling (Fig. 9). Spatial assessment of model predictions such as those illustrated above will be enabled by analysis of remote sensing imagery that is becoming increasingly capable of mapping seagrass distribution and density across the submarine landscape. Radiometrically uncalibrated aerial photography has been used with considerable success to map the relative abundance (e.g., percent cover) of SAV in shallow coastal environments (Kendrick et al. 2000; http://web.vims.edu/bio/sav/index.html). However, radiometrically calibrated aerial and orbiting imagers are now capable of mapping seagrass distributions at spatial scales approaching 1 m (Coffer et al. 2020; Kovacs et al. 2018). In addition to facilitating quantitative retrievals of seagrass habitat across images, radiometric calibration permits the application of radiative transfer algorithms capable of retrieving absolute density and biomass from the imagery (Fig. 9) at spatial resolutions that can be matched to model predictions on a pixel-by-pixel basis (Dierssen and Zimmerman 2003; Hill et al. 2014). Thus, the science of seagrass ecology is rapidly approaching a point where mathematical models can provide the “glue” linking laboratory experiments to field observations across scales ranging from individual leaves to whole plants and genomes to predict the behavior of entire meadows, and observe those changes from space.

And Finally, Understanding the Past as a Key to Predicting the Future

The mechanistic understanding of seagrass performance obtained by the studies described above, combined with numerous well-tuned adaptations for a submerged aquatic existence, underscores the curious fact that seagrasses have retained so much capacity for photosynthesis even though natural availability of CO_2 limits the realized activity well below its physiological scope. Some of this excess capacity may reflect the terrestrial origins of seagrasses and/or their evolution in a seawater environment that was considerably richer in dissolved CO_2 than it is today. Seagrasses first appeared in the fossil

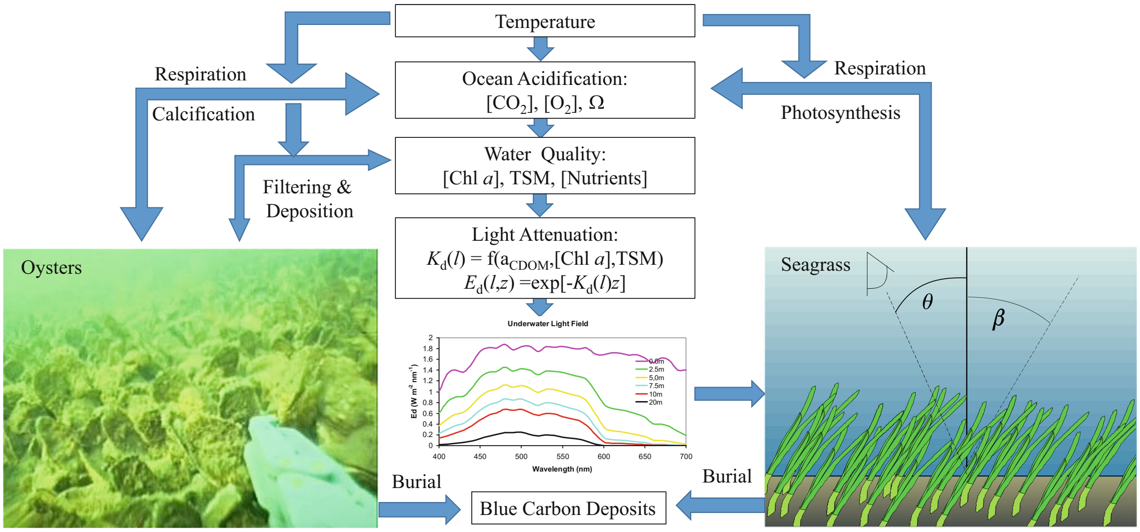


Fig. 8 Conceptual diagram showing coupling between the *EcoOyster* and *GrassLight* models. The objective of this effort is to explore, in silico, the mutual ecosystem service feedbacks provided by co-locating eelgrass and oysters to buffer potential negative impacts of ocean acidification and eutrophication. Eelgrass metabolism raises estuarine pH and O_2 concentration to facilitate oyster growth and calcification. Oysters filter the water, removing phytoplankton and suspended sediments, thereby increasing light transmission to benthic plants and their photosynthesis. Oyster respiration also generates CO_2 that stimulates eelgrass photosynthesis. This ongoing work is being performed in collaboration with Virginia Institute of Marine Sciences colleagues Emily B. Rivest and Mark Brush. Oyster photo: www.bayjournal.com

record about 90 million years ago (den Hartog and Kuo 2006) and the pH of ocean surface waters may have been as low as 7.4, suggesting that dissolved CO_2 concentrations may have been more than double the current level for a considerable portion of their evolutionary history (Spivack et al. 1993). High concentrations of dissolved CO_2 would allow seagrasses to compete more effectively with algae without the need to develop an efficient carbon concentrating mechanisms. Thus, the low photosynthetic performance of modern seagrasses in natural waters, their excess capacity for processing that carbon into sucrose and growth, and their present vulnerability to eutrophication and light competition from algae may be the combined consequences of their descent from terrestrial plants that lost CO_2-concentrating pyrenoids in the chloroplasts, their evolutionary origins in CO_2-rich environments, and relatively recent (< 100 years) anthropogenic impacts on coastal biogeochemical processes that have severely reduced water column transparency and light availability.

The experimental results and model relationships described above omit many details and therefore are certainly wrong in some aspects. However, consistency in the experimental findings and field observations reported here provides some confidence that model predictions based on this growing body of knowledge are broadly correct, even though the models themselves represent an incomplete simplification of reality (Box 1979). They also strongly support the argument that metabolic theory, which can predict how the rates of resource uptake from the environment and the allocation of that resource to survival, growth, and reproduction, controls ecological processes at all levels of organization from individuals to the biosphere (Brown et al. 2004). Although not a "theory of everything," the focus on metabolism laid out in this essay provides a pathway for making explicit, quantitative, and ecologically important predictions from first principles of physics and chemistry that are ultimately regulated in living organisms by gene expression. As a

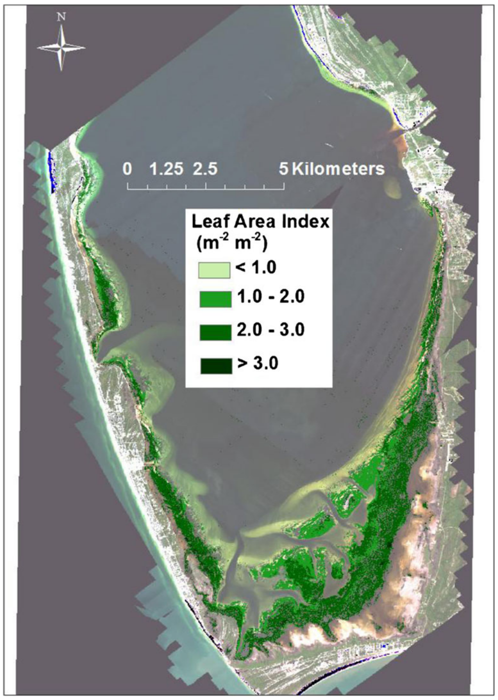


Fig. 9 Distribution of seagrass leaf area index (LAI) across St. Josephs' Bay, FL, USA, obtained from calibrated hyperspectral imagery. Reproduced with permission from Hill et al. (2014)

consequence, our ability to quantify the flow of energy and cycling of materials through seagrasses allows us to develop a mechanistic understanding of seagrass performance at scales ranging from molecules to ecosystems, an effort to which Susan Williams contributed mightily, and certainly appreciated. The following quote perhaps summarizes it best:

"If the bewildering complexity of human knowledge…..is to be retained and well used, unifying concepts are needed to consolidate the understanding of systems of many kinds and to simplify the teaching of general principles"

– Howard T. Odum (1994)

Acknowledgments Many thanks for the insight, guidance, and creativity of mentors, collaborators, and students who helped articulate and demonstrate the ideas presented here, especially James Kremer, Randall Alberte, Steve Ackleson, Olga Invers, Sherry Palacios, Heidi Dierssen, Victoria Hill, David Ruble, Billur Celebi, Meredith McPherson, and Carmen Zayas-Santiago, as well as numerous colleagues for providing lively discussions that helped formulate these ideas over the years. A special thank you to Robert Howarth and Ken Heck for initially suggesting this review and for their patience during its longer-than expected gestation. Dedicated to the memory of Susan Williams.

Funding Financial support for the preparation of this manuscript was provided by the National Science Foundation (OCE-1635403), the Ocean Biology and Biogeochemistry Program of the National Aeronautics and Space Administration (NNX17AH01G), and the Ocean Acidification Program of the National Oceanic and Atmospheric Administration (NA18NOS4780177).

Compliance with Ethical Standards

Disclaimer Any opinions, conclusions, recommendations, and especially the errors expressed in this essay are those of the author and do not necessarily reflect the views of my mentors, colleagues, students, or the funding agencies.

References

Apostolaki, E.T., S. Vizzini, I.E. Hendriks, and Y.S. Olsen. 2014. Seagrass ecosystem response to long-term high CO_2 in a Mediterranean volcanic vent. *Marine Environmental Research* 99: 9–15.

Arnold, T., C. Mealey, H. Leahey, A.W. Miller, J.M. Hall-Spencer, M. Milazzo, and K. Maers. 2012. Ocean acidification and the loss of phenolic substances in marine plants. *PLoS One* 7: e35107.

Barber, B.J., and P.J. Behrens. 1985. Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* banks ex König and *Syringodium filiforme* Kützing. *Aquatic Botany* 22: 61–69.

Batiuk, R., P. Bergstrom, M. Kemp, E. Koch, L. Murray, J. Stevenson, R. Bartleson, V. Carter, N. Rybicki, J. Landwehr, C. Gallegos, L. Karrh, M. Naylor, D. Wilcox, K. Moore, S. Ailstock, and M. Teichberg. 2000. *Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: a second synthesis*, 217. Annapolis: Chesapeake Bay Program Office.

Beer, S. 1989. Photosynthesis and respiration of marine angiosperms. *Aquatic Botany* 34: 153–166.

Beer, S., and E. Koch. 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. *Marine Ecology Progress Series* 141: 199–204.

Bornmann, L., and R. Mutz. 2015. Growth rates of modern science: a bibliometric analysis based on the number of publications and cited references. *Journal of the Association for Information Science and Technology* 66: 2215–2222.

Borum, J. 1983. The quantitative role of macrophytes, epiphytes and phytoplankton under different nutrient conditions on Rosskilde Fjord, Denmark. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 35–40.

Borum, J., O. Pedersen, T.M. Greve, T.A. Frankovich, J.C. Zieman, J.W. Fourqurean, and C.J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology* 93: 148–158.

Box, G.E.P. 1979. Robustness in the strategy of scientific model building. In *Robustness in statistics*, ed. R.L. Launer and G.N. Wilkinson, 201–236. Academic press.

Brown, J., J. Gillooly, A. Allen, V. Savage, and G. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Bulthius, D.A. 1983. Effects of *in situ* light reduction on density and growth of the seagrass *Heterozostera tasmanica* (martens ex Aschers.) den Hartog in Western port, Victoria, Australia. *Journal of Experimental Marine Biology and Ecology* 67: 91–103.

Burnell, O.W., S.D. Connell, A.D. Irving, J.R. Watling, and B.D. Russell. 2014. Contemporary reliance on bicarbonate acquisition predicts increased growth of seagrass *Amphibolis antarctica* in a high-CO_2 world. *Conservation Physiology* 2: 1–11.

Cai, W.-J. 2011. Estuarine and coastal ocean carbon paradox: CO_2 sinks or sites of terrestrial carbon incineration? *Annual Review of Marine Science* 3: 123–145.

Campbell, J., and J. Fourqurean. 2013. Effects of *in situ* CO_2 enrichment on the structural and chemical characteristics of the seagrass *Thalassia testudinum*. *Marine Biology* 160: 1465–1475.

Celebi, B. 2016. Potential impacts of climate change on photochemistry of *Zostera marina* L., Ph.D. Dissertation, Old Dominion University Norfolk.

Coffer, M., B. Schaeffer, R. Zimmerman, V. Hill, J. Li, K. Islam, and P. Whitman. 2020. Performance across WorldView-2 and RapidEye for reproducible seagrass mapping. *Remote Sensing of Environment* In Press.

Coleman, F.C., and S.L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology & Evolution* 17: 40–44.

Cottingham, K., J. Lennon, and B. Brown. 2005. Knowing when to draw the line: designing more informative ecological experiments. *Frontiers in Ecology and the Environment* 3: 145–152.

Cox, T.E., F. Gazeau, S. Alliouane, I.E. Hendriks, P. Mahacek, A. Le Fur, and J.P. Gattuso. 2016. Effects of *in situ* CO_2 enrichment on structural characteristics, photosynthesis, and growth of the Mediterranean seagrass *Posidonia oceanica*. *Biogeosciences* 13: 2179–2194.

Cummings, M., and R. Zimmerman. 2003. Light harvesting and the package effect in *Thalassia testudinum* Koenig and *Zostera marina* L.: optical constraints on photoacclimation. *Aquatic Botany* 75: 261–274.

Dattolo, E., M. Ruocco, C. Brunet, M. Lorenti, C. Lauritano, D. D'Esposito, P. De Luca, R. Sanges, S. Mazzuca, and G. Procaccini. 2014. Response of the seagrass *Posidonia oceanica* to different light environments: insights from a combined molecular and photophysiological study. *Marine Environmental Research* 101: 225–236.

Davey, P.A., M. Pernice, G. Sablok, A. Larkum, H.T. Lee, A. Golicz, D. Edwards, R. Dolferus, and P. Ralph. 2016. The emergence of molecular profiling and omics techniques in seagrass biology; furthering our understanding of seagrasses. *Functional & Integrative Genomics* 16: 465–480.

de los Santos, C.B., D. Krause-Jensen, T. Alcoverro, N. Marbà, C.M. Duarte, M.M. van Katwijk, M. Pérez, J. Romero, J.L. Sánchez-Lizaso, G. Roca, E. Jankowska, J.L. Pérez-Lloréns, J. Fournier, M. Montefalcone, G. Pergent, J.M. Ruiz, S. Cabaço, K. Cook, R.J. Wilkes, F.E. Moy, G.M.-R. Trayter, X.S. Arañó, D.J. de Jong, Y. Fernández-Torquemada, I. Auby, J.J. Vergara, and R. Santos. 2019. Recent trend reversal for declining European seagrass meadows. *Nature Communications* 10: 3356.

del Barrio, P., N.K. Ganju, A.L. Aretxabaleta, M. Hayn, A. García, and R.W. Howarth. 2014. Modeling future scenarios of light attenuation and potential seagrass success in a eutrophic estuary. *Estuarine, Coastal and Shelf Science* 149: 13–23.

den Hartog, C., and J. Kuo. 2006. Taxonomy and biogeography of seagrasses. In *Seagrasses: biology, ecology and conservation*, ed. A. Larkum, R. Orth, and C. Duarte, 1–23. Dordecht: Springer.

Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27: 15–26.

Dennison, W.C., and R.S. Alberte. 1982. Photosynthetic respones of *Zostera marina* L. (eelgrass) to *in situ* manipulations of light intensity. *Oecologia* 55: 137–144.

Dierssen, H., and R. Zimmerman. 2003. Benthic ecology from space: seagrass net primary production across the Bahamas banks. *Marine Ecology-Progress Series* 1–15.

Doney, S., V. Fabry, R. Feeley, and J. Kleypas. 2009. Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science* 1: 169–192.

Dore, J.E., R. Lukas, D.W. Sadler, M.J. Church, and D.M. Karl. 2009. Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proceedings of the National Academy of Sciences* 106: 12235–12240.

Duarte, C. 1991. Seagrass depth limits. *Aquatic Botany* 40: 363–377.

Duarte, C. 1999. Seagrass ecology at the turn of the millennium: challenges for the new century. *Aquatic Botany* 65: 7–20.

Duarte, C., I. Hendricks, T. Moore, Y. Olsen, A. Steckbauer, L. Ramajo, J. Carstensen, J. Trotter, and M. McCulloch. 2013. Is ocean acidification an open-ocean syndrome? Understanding the drivers and impacts of pH variability in coastal ecosystems. *Estuaries and Coasts* 36: 221–236.

Durako, M. 1993. Photosynthetic utilization of $CO_{2(aq)}$ and HCO_3^- in *Thalassia testudinum* (Hydrocharitacae). *Marine Biology* 115: 373–380.

Egea, L.G., R. Jiménez-Ramos, J.J. Vergara, I. Hernández, and F.G. Brun. 2018. Interactive effect of temperature, acidification and ammonium enrichment on the seagrass *Cymodocea nodosa*. *Marine Pollution Bulletin* 134: 14–26.

Ehlers, A., B. Worm, and T. Reusch. 2008. Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine Ecology Progress Series* 355: 1–7.

Enríquez, S. 2005. Light absorption efficiency and the package effect in the leaves of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 289: 141–150.

Evans, A.S., K.L. Webb, and P.A. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany* 24: 185–197.

Fourqurean, J.W., and J.C. Zieman. 1991. Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 69: 161–170.

Gallegos, C. 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. *Estuaries* 24: 381–397.

Gattuso, J., W. Krirkwood, J. Barry, E. Cox, F. Gazeau, L. Hansson, I. Hendricks, D. Kline, P. Mahacek, S. Martin, P. McElhany, E. Peltzer, J. Reeve, D. Roberts, V. Saderne, K. Tait, S. Widdicombe, and P. Brewer. 2014. Free-ocean CO_2 enrichment systems (FOCE): present status and future developments. *Biogeosciences* 11: 4057–4072.

Goverde, M., A. Bazin, J.A. Shykoff, and A. Erhardt. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO_2 and plant genotype. *Functional Ecology* 13: 801–810.

Greening, H.S., L. Cross, and E. Sherwood. 2011. A multiscale approach to seagrass recovery in Tampa, Florida. *Ecological Restoration* 29: 82–93.

Greening, H., A. Janicki, and E. Sherwood. 2016. Seagrass recovery in Tampa Bay, Florida (USA). In *The wetlands book*, ed. C. Finlayson, G. Milton, R. Prentice, and N. Davidson, 1–12. Dortrecht: Springer.

Gu, J., K. Weber, E. Klemp, G. Winters, S. Franssen, I. Wienphal, A. Huylmans, K. Zecher, T. Reusch, E. Bornberg-Bauer, and A. Weber. 2012. Identifying core features of adaptive metabolic mechanisms for chronic heat stress attenuation contributing to system robustness. *Integrative Biology* 4: 480–493.

Guerrero-Meseguer, L., T. Cox, C. Sanz-Lázaro, S. Schmid, L. Enzor, K. Major, F. Gazeau, and J. Cebrian. 2020. Does ocean acidification benefit seagrasses in a mesohaline environment? A mesocosm experiment in the northern Gulf of Mexico. *Estuaries and Coasts* 43: 1377–1393.

Hall, M.O., B.T. Furman, M. Merello, and M.J. Durako. 2016. Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay, USA: initial observations. *Marine Ecology Progress Series* 560: 243–249.

Hall-Spencer, J., R. Rodolfo-Metalpa, S. Martin, E. Ransome, M. Fine, S. Turner, S. Rowley, D. Tedesco, and M.-C. Buia. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454: 96–99.

Harley, C.D.G., A. Randall Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, and S.L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9: 228–241.

Heck, K.L., T.J.B. Carruthers, C.M. Duarte, A.R. Hughes, G. Kendrick, R.J. Orth, and S.W. Williams. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11: 1198–1210.

Hemminga, M., and C. Duarte. 2000. *Seagrass ecology*. Cambridge University Press.

Herzka, S., and K. Dunton. 1997. Seasonal photosynthetic patterns in the seagrass *Thalassia testudinum* in the western Gulf of Mexico. *Marine Ecology Progress Series* 152: 103–117.

Hill, V.J., R.C. Zimmerman, W.P. Bissett, H. Dierssen, and D.D. Kohler. 2014. Evaluating light availability, seagrass biomass, and productivity using hyperspectral airborne remote sensing in Saint Joseph's Bay, Florida. *Estuaries and Coasts* 37: 1467–1489.

Hu, X., D. Burdige, and R. Zimmerman. 2012. $\delta^{13}C$ is a signature of light availability and photosynthesis in seagrass. *Limnology and Oceanography* 57: 441–448.

Hughes, A.R., K.J. Bando, F.R. Laura, and L.W. Susan. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Marine Ecology Progress Series* 282: 87–99.

Hughes, T.P., J.T. Kerry, M. Álvarez-Noriega, J.G. Álvarez-Romero, K.D. Anderson, A.H. Baird, R.C. Babcock, M. Beger, D.R. Bellwood, R. Berkelmans, T.C. Bridge, I.R. Butler, M. Byrne, N.E. Cantin, S. Comeau, S.R. Connolly, G.S. Cumming, S.J. Dalton, G. Diaz-Pulido, C.M. Eakin, W.F. Figueira, J.P. Gilmour, H.B. Harrison, S.F. Heron, A.S. Hoey, J.-P.A. Hobbs, M.O. Hoogenboom, E.V. Kennedy, C.-y. Kuo, J.M. Lough, R.J. Lowe, G. Liu, M.T. McCulloch, H.A. Malcolm, M.J. McWilliam, J.M. Pandolfi, R.J. Pears, M.S. Pratchett, V. Schoepf, T. Simpson, W.J.

Skirving, B. Sommer, G. Torda, D.R. Wachenfeld, B.L. Willis, and S.K. Wilson. 2017. Global warming and recurrent mass bleaching of corals. *Nature* 543: 373.

Invers, O., R. Zimmerman, R. Alberte, M. Perez, and J. Romero. 2001. Inorganic carbon sources for seagrass photosynthesis: an experimental evaluation for bicarbonate use in temperate species. *Journal of Experimental Marine Biology and Ecology* 265: 203–217.

IPCC. 2014. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In , ed. R.K.P.a.L.A. Meyer, vol. 151. Geneva, Switzerland: IPCC.

Jiang, Z., X. Huang, and J. Zhang. 2010. Effects of CO_2 enrichment on photosynthesis, growth and biochemical composition of seagrass *Thalassia hemprechii* (Ehrenb.) Aschers. *Journal of Integrative Plant Biology* 52: 904–913.

Kellogg, M., M. Brush, and J. Cornell. 2018. An updated model for estimating the TMDL-related benefits of oyster reef restoration Harris Creek, Maryland, USA. Virginia Institute of Marine Science, College of William and Mary. https://doi.org/10.25773/7a75-ds48.

Kendrick, G.A., B.J. Hegge, A. Wyllie, A. Davidson, and D.A. Lord. 2000. Changes in seagrass cover on success and Parmelia banks, Western Australia between 1965 and 1995. *Estuarine, Coastal and Shelf Science* 50: 341–353.

Kovacs, E., C. Roelfsema, M. Lyons, S. Zhao, and S. Phinn. 2018. Seagrass habitat mapping: how do Landsat 8 OLI, Sentinel-2, ZY-3A, and Worldview-3 perform? *Remote Sensing Letters* 9: 686–695.

Koweek, D.A., R.C. Zimmerman, K.M. Hewett, B. Gaylord, S.N. Giddings, K.J. Nickols, J.L. Ruesink, J.J. Stachowicz, Y. Takeshita, and K. Caldeira. 2018. Expected limits on the ocean acidification buffering potential of a temperate seagrass meadow. *Ecological Applications* 28: 1694–1714.

Kraemer, G.P., and R.S. Alberte. 1993. Age-related patterns of metabolism and biomass in subterranean tissues of *Zostera marina* L. (eelgrass). *Marine Ecology Progress Series* 95: 193–203.

Kroeker, K.J., R.L. Kordas, R.N. Crim, and G.G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* 13: 1419–1434.

Kroeker, K.J., F. Micheli, M.C. Gambi, and T.R. Martz. 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. *Proceedings of the National Academy of Sciences* 108: 14515–14520.

Lapointe, B.E., L.W. Herren, R.A. Brewton, and P.K. Alderman. 2020. Nutrient over-enrichment and light limitation of seagrass communities in the Indian River Lagoon, an urbanized subtropical estuary. *Science of the Total Environment* 699: 134068.

Larkum, A., R. Orth, and C. Duarte. 2006. *Seagrasses: biology, ecology and conservation*, 691. Dordrecht: Springer.

Larkum, A., G. Kendrick, and P. Ralph. 2018. *Seagrasses of Australia. Structure, ecology and conservation*, 800. Cham, Switzerland: Springer.

Lau, N.-C., and M.J. Nath. 2012. A model study of heat waves over North America: meteorological aspects and projections for the twenty-first century. *Journal of Climate* 25: 4761–4784.

Leakey, A.D.B., E.A. Ainsworth, C.J. Bernacchi, A. Rogers, S.P. Long, and D.R. Ort. 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany* 60: 2859–2876.

Lee, Z.-P., K. Du, and R. Arnone. 2005. A model for the diffuse attenuation coefficient of downwelling irradiance. *Journal of Geophysical Research* 110: 1–10.

Lefcheck, J.S., R.J. Orth, W.C. Dennison, D.J. Wilcox, R.R. Murphy, J. Keisman, C. Gurbisz, M. Hannam, J.B. Landry, K.A. Moore, C.J. Patrick, J. Testa, D.E. Weller, and R.A. Batiuk. 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proceedings of the National Academy of Sciences* 115: 3658–3662.

Lewis, E. 1980. The practical salinity scale 1978 and its antecedents. *IEEE Journal of Oceanic Engineering* OE-5: 3–8.

Liu, P.-J., S.-J. Ang, A.B. Mayfield, and H.-J. Lin. 2020. Influence of the seagrass *Thalassia hemprichii* on coral reef mesocosms exposed to ocean acidification and experimentally elevated temperatures. *Science of the Total Environment* 700: 134464.

Lodge, D.M., S. Williams, H.J. MacIsaac, K.R. Hayes, B. Leung, S. Reichard, R.N. Mack, P.B. Moyle, M. Smith, D.A. Andow, J.T. Carlton, and A. McMichael. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16: 2035–2054.

Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.

McPherson, M.L., R.C. Zimmerman, and V.J. Hill. 2015. Predicting carbon isotope discrimination in eelgrass (*Zostera marina* L.) from the environmental parameters—light, flow, and [DIC]. *Limnology and Oceanography* 60: 1875–1889.

McRoy, C., and C. Hellfrich. 1977. *Seagrass ecosystems: a scientific perspective*. New York: Marcel Delkker.

Moore, K., and J. Jarvis. 2008. Environmental factors affecting summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. *Journal of Coastal Research* 55: 135–147.

Moore, K., E. Shields, D. Parrish, and R. Orth. 2012. Eelgrass survival in two contrasting systems: role of turbidity and summer water temperatures. *Marine Ecology Progress Series* 448: 247–258.

Najjar, R., M. Hermann, R. Alexander, E. Boyer, D. Burdige, D. Butman, W. Cai, E. Canuel, R. Chen, A. Friedrichs, R. Feagin, P. Griffith, A. Hinson, J. Holmquist, X. Hu, W. Kemp, K. Kroeger, A. Mannino, S. McCallister, W. McGillis, M. Mulholland, C. Pilskan, J. Salisbury, S. Signorini, P. St-Laurent, H. Tian, M. Tzortziou, P. Vlahoss, Z. Wang, and R. Zimmerman. 2018. Carbon budget of tidal wetlands, estuaries and shelf waters of Eastern North America. *Global Biogeochemical Cycles* 32: 389–416.

Odum, H. 1994. *Ecological and general systems*. Niowat: University Press of Coloroado.

Odum, H. 2007. *Environment, power and society for the twenty first century. The hierarchy of energy*. New York: Columbia University Press.

Olesen, B., D. Krause-Jensen, and P.B. Christensen. 2016. Depth-related changes in reproductive strategy of a cold-temperate *Zostera marina* meadow. *Estuaries and Coasts* 1–11.

Onuf, C. 1991. Light requirements for *Halodule wrightii*, *Syringodium filiforme*, and *Halophila englemanni* in a heterogeneous and variable environment inferred from long-term monitoring. In *The light requirements of seagrasses. Results and recommendations of a workshop. NOAA Tech. Memo. NMFS-SEFC-287*, ed. J. Kenworthy and D. Haunert, 95–105. Beaufort.

Orth, R., T. Carruthers, W. Dennison, C. Duarte, J. Fourqurean, K. Heck, A. Hughes, G. Kendrick, W. Kenworthy, S. Olyarnik, F. Short, M. Waycott, and S. Williams. 2006. A global crisis for seagrass ecosystems. *BioScience* 56: 987–996.

Ow, Y.X., C.J. Collier, and S. Uthicke. 2015. Responses of three tropical seagrass species to CO_2 enrichment. *Marine Biology* 162: 1005–1017.

Ow, Y.X., S. Uthicke, and C.J. Collier. 2016. Light levels affect carbon utilisation in tropical seagrass under ocean acidification. *PLoS One* 11: e0150352.

Palacios, S., and R. Zimmerman. 2007. Response of eelgrass (*Zostera marina* L.) to CO_2 enrichment: possible impacts of climate change and potential for remediation of coastal habitats. *Marine Ecology Progress Series* 344: 1–13.

Pfannschmidt, T., and C. Yang. 2012. The hidden function of photosynthesis: a sensing system for environmental conditions that regulates plant acclimation responses. *Protoplasma* 249: 125–135.

Phillips, R., and C. McRoy. 1980. *Handbook of seagrass biology: an ecosystem perspective, xiii + 353 p*. New York: Garland STPM Press.

Plus, M., J.-M. Deslous-Paoli, and F. Dagault. 2003. Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany* 77: 121–134.

Procaccini, G., S. Beer, M. Björk, J. Olsen, S. Mazzuca, and R. Santos. 2012. Seagrass ecophysiology meets ecological genomics: Are we ready? *Marine Ecology* 33: 522–527.

Rask, N., M.B. Rasmussen, and J.S. Laursen. 2000. Ålegræs - udbredelse før og nu. *Vand and Miljø* 7: 51–54.

Raven, J.A., and J. Beardall. 2014. CO_2 concentrating mechanisms and environmental change. *Aquatic Botany* 118: 24–37.

Raven, J.A., D.I. Walker, A.M. Johnston, L.L. Handley, and J. Kubler. 1995. Implications of ^{13}C natural abundance measurements for photosynthetic performance by marine macrophytes in their natural environment. *Marine Ecology Progress Series* 123: 193–205.

Ruesink, J., S. Yang, and A. Trimble. 2015. Variability in carbon availability and eelgrass (*Zostera marina*) biometrics along an estuarine gradient in Willapa Bay, WA, USA. *Estuaries and Coasts* 38: 1908–1917.

Ruocco, M., F. Musacchia, I. Olivé, M.M. Costa, I. Barrote, R. Santos, R. Sanges, G. Procaccini, and J. Silva. 2017. Genomewide transcriptional reprogramming in the seagrass *Cymodocea nodosa* under experimental ocean acidification. *Molecular Ecology* 26: 4241–4259.

Saba, G., K. Goldsmith, S. Cooley, D. Grosse, S. Meseck, W. Miller, M. Poach, B. Phelan, R. Rheault, K.St. Laurent, J. Testa, J. Weis, and R. Zimmerman. 2019. Recommended priorities for research on ecological impacts of ocean and coastal acidification in the U.S. mid-Atlantic. *Estuarine, Coastal and Shelf Science* 225: 1–15.

Saito, M.A., T. Goepfert, and J. Ritt. 2008. Some thoughts on the concept of colimitation: Three definitions and the importance of bioavailability. *Limnology and Oceanography* 53: 276–290.

Salo, T., T.B.H. Reusch, and C. Boström. 2015. Genotype-specific responses to light stress in eelgrass *Zostera marina*, a marine foundation plant. *Marine Ecology Progress Series* 519: 129–140.

Sand-Jensen, K., and D.M. Gordon. 1984. Differential ability of marine and freshwater macrophytes to utilize HCO_3^- and CO_2. *Marine Biology* 80: 247–253.

Schulte, D.M., R.P. Burke, and R.N. Lipcius. 2009. Unprecedented restoration of a native oyster metapopulation. *Science* 325: 1124–1128.

Seddon, S., R.M. Connolly, and K.S. Edyvane. 2000. Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany* 66: 297–310.

Sherwood, E., H. Greening, J. Johansson, K. Kaufman, and G. Raulerson. 2017. Tampa Bay (Florida, USA). Documenting seagrass recovery sonce the 1980's and reviewing the benefits. *Southeastern Geographer* 57: 294–319.

Short, F., and R. Coles. 2001. *Global seagrass research methods*. Amsterdam: Elsevier.

Short, F.T., S. Kosten, P.A. Morgan, S. Malone, and G.E. Moore. 2016. Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany* 135: 3–17.

Spivack, A., C. You, and H. Smith. 1993. Foraminiferal boron isotope ratios as a proxy for surface ocean pH over the past 21 My. *Nature* 363: 149–151.

Takahashi, M., S.H.C. Noonan, K.E. Fabricius, and C.J. Collier. 2016. The effects of long-term *in situ* CO_2 enrichment on tropical seagrass communities at volcanic vents. *ICES Journal of Marine Science: Journal du Conseil* 73: 876–886.

Thayer, G.W., K.A. Bjorndal, J.C. Ogden, S.L. Williams, and J.C. Zieman. 1984. Role of larger herbvores in seagrass communities. *Estuaries* 7: 351–376.

Thomas, E. 2008. Descent into the icehouse. *Geology* 36: 191–192.

Thomson, J.A., D.A. Burkholder, M.R. Heithaus, J.W. Fourqurean, M.W. Fraser, J. Statton, and G.A. Kendrick. 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Global Change Biology* 21: 1463–1474.

Tomasko, D., M. Alderson, R. Burnes, J. Hecker, J. Leverone, G. Raulerson, and E. Sherwood. 2018. Widespread recovery of seagrass coverage in Southwest Florida (USA): temporal and spatial trends and management actoins responsible for success. *Marine Pollution Bulletin* 135: 1128–1137.

Unsworth, R., C. Collier, G. Henderson, and L. McKenzie. 2012. Tropical seagrass meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean acidification. *Envrionmental Research Letters* 7: 1–9.

Waldbusser, G.G., and J.E. Salisbury. 2014. Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Annual Review of Marine Science* 6: 221–247.

Waycott, M., G. Procaccini, D. Les, and T. Reusch. 2006. Seagrass evolution, ecology and conservation: a genetic perspective. In *Seagrasses: biology, ecology and conservation*, ed. A. Larkum, R. Orth, and C. Duarte, 25–50. Dortrecht: Springer.

Waycott, M., C.M. Duarte, T. Carruthers, R. Orth, W. Dennison, S. Olyarnik, A. Calladine, J. Fourqurean, K. Heck, A. Hughes, G. Kendrick, W. Kenworthy, F. Short, and S. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377–12381.

Webb, W., M. Newton, and D. Starr. 1974. Carbon dioxide exchange of *Alnus rubra*: a mathematical model. *Oecol.* 17: 281–291.

Williams, S.L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11: 1472–1488.

Williams, S.L. 2007. Introduced species in seagrass ecosystems: status and concerns. *Journal of Experimental Marine Biology and Ecology* 350: 89–110.

Williams, S.L., and C.A. Davis. 1996. Population genetic analyses of transplanted eelgrass (*Zostera marina*) beds reveal reduced genetic diversity in southern California. *Restoration Ecology* 4: 163–180.

Williams, S.L., and E.D. Grosholz. 2008. The invasive species challenge in estuarine and coastal environments: marrying management and science. *Estuaries and Coasts* 31: 3–20.

Williams, S.L., and C.P. McRoy. 1982. Seagrass productivity: the effect of light on carbon uptake. *Aquatic Botany* 12: 321–344.

Williams, S.L., and R.J. Orth. 1998. Genetic diversity and structure of natural and transplanted eelgrass populations in the Chesapeake and Chincoteague Bays. *Estuaries* 21: 118–128.

Williams, S.L., and M.H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74: 904–918.

Williams, S.L., and J.E. Smith. 2007. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annual Review of Ecology, Evolution, and Systematics* 38: 327–359.

Zayas-Santiago, C.C., A. Rivas-Ubach, L.-J. Kuo, N.D. Ward, and R.C. Zimmerman. 2020. Metabolic profiling reveals biochemical pathways responsible for eelgrass response to elevated CO_2 and temperature. *Scientific Reports* 10: 1–11.

Zhang, Y.G., M. Pagani, Z. Liu, S.M. Bohaty, and R. DeConto. 2013. A 40-million-year history of atmospheric CO_2. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 371: 20130096.

Zimmerman, R. 2003a. Appendix M. Final Report. A bio-physical model evaluation of eelgrass distribution and habitat potential in Dumas Bay, WA. In *Puget sound submerged vegetation monitoring project: 2000–2003 monitoring report, 60 pp plus appendices*, ed. H.D. Berry, A.T. Sewell, S. Wyllie-Echeverria, B.R. Reeves, T.F. Mumford, J.R. Skalski, R.C. Zimmerman, and J. Archer. Olympia: Nearshore Habitat Program, Washington State Department of Resources.

Zimmerman, R. 2003b. A biooptical model of irradiance distribution and photosynthesis in seagrass canopies. *Limnology and Oceanography* 48: 568–585.

Zimmerman, R. 2006. Chapter 13. Light and photosynthesis in seagrass meadows. In *Seagrasses: biology, ecology and conservation*, ed. A. Larkum, R. Orth, and C. Duarte, 303–321. Dordrecht: Springer.

Zimmerman, R.C., R.D. Smith, and R.S. Alberte. 1989. Thermal acclimation and whole plant carbon balance in *Zostera marina* L. (eelgrass). *Journal of Experimental Marine Biology and Ecology* 130: 93–109.

Zimmerman, R.C., J.L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn, and R.S. Alberte. 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. *Aquatic Botany* 39: 353–366.

Zimmerman, R., D. Kohrs, D.L. Steller, and R. Alberte. 1995. Carbon partitioning in eelgrass. Regulation by photosynthesis and the response to daily light-dark cycles. *Plant Physiology* 108: 1665–1671.

Zimmerman, R., D. Kohrs, D. Steller, and R. Alberte. 1997. Impacts of CO_2 -enrichment on productivity and light requirements of eelgrass. *Plant Physiology* 115: 599–607.

Zimmerman, R., V. Hill, and C. Gallegos. 2015. Predicting effects of ocean warming, acidification and water quality on Chesapeake region eelgrass. *Limnology and Oceanography* 60: 1781–1804.

Zimmerman, R., V. Hill, B. Celebi, M. Jinuntuya, D. Ruble, M. Smith, T. Cedeno, and W. Swingle. 2017. Experimental impacts of climate warming and ocean carbonation on eelgrass (*Zostera marina* L.). *Marine Ecology Progress Series* 566: 1–15.