



Effects of Warming and Elevated CO₂ on Stomatal Conductance and Chlorophyll Fluorescence of C₃ and C₄ Coastal Wetland Species

Kerrie M. Sendall^{1,2}  · Cyd M. Meléndez Muñoz¹ · Angela D. Ritter¹ · Roy L. Rich³ · Genevieve L. Noyce³ · J. Patrick Megonigal³

Received: 6 September 2023 / Accepted: 11 January 2024 / Published online: 19 March 2024
© The Author(s) 2024

Abstract

Coastal wetland communities provide valuable ecosystem services such as erosion prevention, soil accretion, and essential habitat for coastal wildlife, but are some of the most vulnerable to the threats of climate change. This work investigates the combined effects of two climate stressors, elevated temperature (ambient, + 1.7 °C, + 3.4 °C, and 5.1 °C) and elevated CO₂ (eCO₂), on leaf physiological traits of dominant salt marsh plant species. The research took place at the Salt Marsh Accretion Response to Temperature eXperiment (SMARTX) at the Smithsonian Environmental Research Center, which includes two plant communities: a C₃ sedge community and a C₄ grass community. Here we present data collected over five years on rates of stomatal conductance (g_s), quantum efficiency of PSII photochemistry (F_v/F_m), and rates of electron transport (ETR_{max}). We found that both warming and eCO₂ caused declines in all traits, but the warming effects were greater for the C₃ sedge. This species showed a strong negative stomatal response to warming in 2017 and 2018 (28% and 17% reduction, respectively in + 5.1 °C). However, in later years the negative response to warming was dampened to < 7%, indicating that *S. americanus* was able to partially acclimate to the warming over time. In 2022, we found that sedges growing in the combined + 5.1 °C eCO₂ plots exhibited more significant declines in g_s , F_v/F_m , and ETR_{max} than in either treatment individually. These results are important for predicting future trends in growth of wetland species, which serve as a large carbon sink that may help mitigate the effects of climate change.

Keywords Climate warming · *Distichlis spicata* · Elevated CO₂ · *Schoenoplectus americanus* · *Spartina patens* · Stomatal conductance

Introduction

Considerable research has been devoted to understanding the effects of elevated atmospheric CO₂ and climate warming on physiological responses of plants and the resulting effects on growth and survival (e.g., Drake et al. 1997; Ward and Strain 1999; Anderson et al. 2001; Ainsworth and Rogers 2007; Reich et al. 2018). Experiments investigating the impact of elevated CO₂ (eCO₂) have shown enhanced

photosynthetic rates (A), reductions in stomatal conductance (g_s), and increased water use efficiency (WUE) in a variety of species (Knapp 1993; Owensby et al. 1993; Jackson et al. 1994; Garcia et al. 1998; Ainsworth and Rogers 2007; Xu et al. 2013), which generally leads to an increase in plant productivity (Drake and Leadley 1991; Jacob et al. 1995; Drake et al. 1996). In cold climates limited by growing season temperatures, experimental warming of air and soil can positively affect gas-exchange rates and plant productivity due to enhanced metabolic rates early in spring and an increase in the length of the growing season (Ibáñez et al. 2010; Reich et al. 2018; May et al. 2020). However, during droughts or dry periods of the growing season, any positive effects of warming can be dampened or even eliminated by soil water limitation due to low precipitation and/or high rates of evapotranspiration (Reich et al. 2018; Wilschut et al. 2022). While the individual effects of warming and eCO₂ are relatively well-understood, few manipulative studies have

✉ Kerrie M. Sendall
ksendall@rider.edu

¹ Department of Biology and Behavioral Neuroscience, Rider University, Lawrenceville, NJ, USA

² Department of Biology, Georgia Southern University, Statesboro, GA, USA

³ Smithsonian Environmental Research Center, Edgewater, MD, USA

directly assessed their interactive effects on plant communities, despite model analyses suggesting that these factors will interact and affect species in ways that are not necessarily predictable given the results of single-factor experiments (e.g., Luo et al. 2008).

The magnitude and direction of plant physiological responses to variation in environmental conditions are species-specific and often differ significantly depending on whether a species uses the C₃ or C₄ photosynthetic pathway. Warmer conditions tend to favor C₄ species over C₃ species since C₄ species concentrate CO₂ around Rubisco and diminish O₂ competition around its active site, thus largely eliminating photorespiration (Long 1999; Sage et al. 1999). When well-watered, C₄ plants have lower g_s , and higher A and WUE than C₃ plants (Ripley et al. 2010; Taylor et al. 2011), and have been shown to maintain high photosynthetic rates even under conditions of low resource availability such as limited water or soil nitrogen (Knapp and Medina 1999). In both temperate climates and the tropics, C₄ grasses dominate in permanent and seasonally waterlogged environments where woody plant establishment and maintenance cannot occur (Piedade et al. 1994; Long 1999). However, plants growing in tidal wetlands often deal with salinity stress, as well as periods of both flooded and relatively dry conditions depending on the time of year. Stomata tend to exhibit similar responses to drought and salinity, with declines in g_s occurring with both higher aridity and salt stress making it difficult to predict how plants growing in salt marshes will respond physiologically to inundation under brackish conditions (Chaves 1991; Wang et al. 2003).

Elevated atmospheric CO₂ conditions tend to stimulate photosynthetic rates (Sage 1994; Jacob et al. 1995; Sage and Cowling 1999). However, this stimulation of A tends to be limited when plants are in suboptimal conditions such low nutrient status (Sage 1994). WUE of both C₃ and C₄ species increases under e CO₂ conditions through reduced g_s , but the effects are much more pronounced for C₃ plants (Wang et al. 2001). Previous work in Free-Air CO₂ Enrichment (FACE) experiments saw a decrease in g_s of 22% on average, while declines of approximately 40% were found greenhouse and chamber experiments (Curtis and Wang 1998; Morison and Lawlor 1999; Ainsworth and Rogers 2007). This reduction in g_s is common in response to e CO₂ (Medlyn et al. 2001) and may impact photosynthetic rates by increasing the barrier to CO₂ diffusion into the leaf (Bernacchi et al. 2003). Additionally, because of the decline in g_s under e CO₂ there is also a decline in transpiration and heat loss, causing leaf temperatures to rise (Kim et al. 2008; Šigut et al. 2015). Because of this, the combination of high temperatures and e CO₂ may have an antagonistic effect and exaggerate heat damage to the photosynthetic apparatus due to the decline in latent heat lost as water vapor in response the decline in g_s (Jiahong et al. 2009; Warren et al. 2011).

This study took place in a brackish marsh that is dominated by the C₃ sedge *Schoenoplectus americanus* and two C₄ grasses, *Spartina patens* and *Distichlis spicata*. A well-established limitation of working with the dominant plant species in many salt marsh habitats, in particular sedges such as *S. americanus*, is that gas exchange is not easily measured with commonly-used physiological instruments (more details in Materials and Methods section). Due to this limitation, we chose to focus our efforts on making relatively simple *in situ* measurements of stomatal conductance and chlorophyll fluorescence variables (e.g., electron transport rate, quantum efficiency of PSII photochemistry) which can be used make indirect inferences about plant photosynthetic productivity and water use efficiency. For example, stomata adjust their rates of conductance in response to changes in atmospheric CO₂ concentrations, soil water availability, temperature, and light (Lu and Zeiger 1994; Hetherington and Woodward 2003; Perez-Martin et al. 2009; Hubbard et al. 2013; Šigut et al. 2015), and many studies have found positive correlations between g_s , A , and accumulation of biomass (Cornish et al. 1991; Franks 2006; Kattge et al. 2009; Cernusak et al. 2011; Drake et al. 2013). Likewise, when plants experience environmental stress (e.g., salinity, heat stress), they often exhibit reduced photosynthesis and electron transport rates (ETR) to avoid damage caused by excess absorbed energy (Kato et al. 2003; Adams et al. 2004), while the quantum efficiency of PSII photochemistry (F_v/F_m) tends to decline (Björkman and Demmig 1987; Posch and Bennett 2009), leading to positive correlations between these traits (Wong et al. 2014; Yang et al. 2017).

This light-induced inhibition of photosynthetic machinery occurs whenever light exceeds the amount of energy needed to drive photosynthetic processes (Murata et al. 2007; Guidi et al. 2019). Salinity, high temperatures, low soil nutrient status, and other abiotic plant stressors can affect the point at which light becomes excessive, causing accelerated PSII photoinhibition compared to unstressed plants (Adir et al. 2003; Melis 1999). A decline in the F_v/F_m ratio is considered to be a good indicator of photoinhibition, which may result from damage to the PSII reaction centers or an increase in the rate of energy dissipation (Öquist et al. 1992). PSII photoinhibition has been shown to slow down ETR and prevent reactive oxygen species (ROS) from forming, preventing damage to the PSII reaction centers (Tikkanen et al. 2014). Recent research also suggests that abiotic stress directly inhibits the repair of PSII reaction centers after light-induced damage occurs (Kangasjärvi et al. 2012; Nishiyama and Murata 2014). Thus, the extent of damage depends on the balance between photodamage caused by the generation of ROS and PSII repair mechanisms (Demmig-Adams et al. 2012).

The goal of this study was to directly assess the interactive effects of warming and e CO₂ on the plasticity of leaf

physiological traits related to A and WUE, and thus plant growth and survival. We compared physiological responses of dominant salt marsh species exposed to ambient air and soil temperatures or heated to 1.7, 3.4, and 5.1 °C above ambient, as well as the response of the C_3 sedge to ambient and elevated carbon dioxide levels. We tested the following hypotheses:

- (1) Rates of g_s will be positively correlated with F_v/F_m , ETR_{max} , and saturating light ($PPFD_{sat}$), with higher values attributable to increased CO_2 availability when stomata are open and lower values related to photoinhibition and oxidative stress caused by a reduction in evaporative heat loss when stomata are closed.
- (2) C_3 sedges growing under eCO_2 will have reduced rates of g_s , which will reduce evapotranspiration and lead to heat stress, consequently affecting the point at which light becomes excessive and leading to reduced ETR and F_v/F_m .
- (3) Both C_3 and C_4 plant communities will experience reductions in g_s , ETR, and F_v/F_m in response to warming, but the response of the C_3 sedge will be more pronounced due to the need for C_3 plants to close stomata to minimize water loss under high temperatures.
- (4) The most significant declines in g_s , ETR, and F_v/F_m will occur in sedges grown under 5.1 °C above ambient + eCO_2 conditions.

Materials and Methods

Site and species descriptions

Our experiment was located in the Smithsonian's Global Change Research Wetland (GCRew), which is part of the tidal, brackish Kirkpatrick Marsh that runs along the western shore of the Chesapeake Bay, United States (38°53' N, 76°33' W). Flood frequency varies across the high marsh site, but the soils are typically saturated to within 5 to 15 cm of the soil surface. Two plant communities largely dominate the site: the first is a C_3 sedge community that consists primarily of *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller, while the second is primarily comprised of two C_4 grasses, *Spartina patens* (Aiton) Muhl and *Distichlis spicata* (L.) Greene. The higher elevation areas of the marsh that flood during 10 to 20% of high tides are dominated by the C_4 grass community, whereas the lower elevation areas that flood during 30 to 60% of high tides are dominated by the C_3 sedge community. These species are rhizomatous perennials that reproduce sexually by seed and via vegetative sprouting from rhizomes. Aboveground biomass dies back each winter and is replaced by new growth each spring.

Experimental design

The Salt Marsh Accretion Response to Temperature eXperiment (SMARTX) was established within the GCRew site in 2016 (Noyce et al. 2019). The experiment consists of six replicate transects, three located in the C_3 sedge community and three located in the C_4 grass community. Each transect consists of four 2 × 2 m plots: an unheated ambient plot, and plots that are heated to 1.7, 3.4, and 5.1 °C above ambient. Each plot is surrounded by a 0.2 m buffer to minimize edge effects and transects were positioned in the marsh to have similar plant composition along their length. Experimental warming of soil and plant-surface temperatures is carried out using vertical resistance cables belowground (which warm to a soil depth of 1.5 m) and infrared heaters aboveground. Four to six 1,000-W heaters (FTW-1000, Mor Electric Heating Assoc. Inc., Comstock Park, MI) are installed within each heated plot. Concurrent above- and belowground warming provides a more realistic treatment than does either in isolation since growing season soil temperatures are likely to mirror changes in air temperature. To maintain the temperature gradient across plots, we used integrated microprocessor-based feedback control to generate a fixed temperature differential from ambient for each plot. We began warming on June 1, 2016 and have continued 365 days per year since the initial start date.

In the C_3 sedge community, there are six additional 2-m-diameter plots, each consisting of an open-top, elevated carbon dioxide (eCO_2) chamber. Three chambers are at ambient temperatures and three are warmed to 5.1 °C above ambient, using the vertical resistance cables and infrared heaters described above. Target atmospheric CO_2 concentrations of 750 to 800 ppm are maintained within each chamber using K30 sensors (CO2Meter Inc., Ormond Beach, FL) with continuous feedback control. CO_2 concentrations are manipulated only during daylight hours of each growing season: 2017 from April 11–November 30, 2018 from April 26–December 6, 2019 from April 23–November 18, 2020 from April 14–December 11, 2021 from April 20–November 27, and 2022 from April 26–November 28.

Across the duration of the experiment, the species composition in one of the C_4 -dominated transects transitioned into a mix of both C_3 *S. americanus* and C_4 *S. patens* and *D. spicata* as the C_3 sedge encroached into the plots. Thus, in 2019 and later, we measured both plant types in these four plots.

Stomatal Conductance

A well-established limitation of working with the dominant plant species in the GCRew site is that they do not lend themselves to leaf-level gas-exchange measurements with commonly-used physiological equipment such as the

LI-6400 (LI-COR, Lincoln, NE). This is particularly true of the C_3 sedge, which typically reacts to being enclosed in the LI-6400 leaf chamber with complete stomatal closure, and therefore it can take upward of 60 min to make a single measurement. Due to these limitations, we chose to focus our efforts on making relatively simple, *in situ* measurements of instantaneous stomatal conductance (g_s) with a non-destructive, hand-held SC-1 leaf porometer (Decagon Devices, Pullman, WA). From these measurements, we can make indirect assumptions about plant photosynthetic productivity and water use efficiency since these traits are linked to the dynamic range of stomatal conductance (Drake et al. 2013). For example, the upper limit of rates of CO_2 assimilation for plants growing in high light and under low evaporative demand conditions is most often determined by maximum rates of stomatal conductance.

Similar to most leaf physiological equipment, the SC-1 porometer is designed for use with broadleaved plants, so it was necessary to flatten a portion of the triangular cross-section of each C_3 sedge shoot prior to measuring. To determine if this minor shoot damage, or repeated measurements of the same shoot over subsequent days of measuring, had any effect on g_s , a set of preliminary measurements were made over a two-week period in 2017. We found no significant differences between measurements made immediately following the flattening of shoots and shoots that were sampled repeatedly over the preliminary testing period ($p > 0.05$).

Rates of g_s were measured between the hours of 08:00 and 14:00 on warm, sunny days across the growing seasons of 2017–2019 and 2021–22 (the COVID-19 pandemic prevented measurements from being made in 2020). Measurement dates varied from year to year, but generally they spanned a period of eight weeks per summer. Only 2017 measurements occurred over a shorter time period of three weeks. Prior to the start of measurements each year, we systematically designated three physiological sampling areas per plot (hereafter referred to as clusters), so as to minimize the number of shoots subjected to this minimal shoot damage, as well as to avoid portions of the plant biomass being used by other researchers. Each daily set of measurements utilized plants growing in one of the three clusters, and we alternated to the next cluster on the subsequent measurement date. In C_3 plots, three shoots per cluster were randomly chosen for measurement each day, with g_s measured on the top third of the shoot while avoiding any insect damage or sections that were senescing. In C_4 plots, three measurements per cluster were made by selecting 3–5 blades of grass and laying them side-by-side to fill the chamber of the porometer. We varied the plant community and transect where measurements began each day to ensure that different plants were measured in the late morning/early afternoon to account for any mid-day depression or other factors that could affect physiological traits.

Chlorophyll Fluorescence

Maximum Quantum Efficiency of PSII Photochemistry

In 2018, we used a FluoroPen FP 110 (Photon System Instruments, Drásov, Czech Republic) to make rapid, non-destructive measurements of chlorophyll fluorescence. Measurements were made between the pre-dawn hours of 01:00 and 05:00, typically following warm, sunny days. Following similar sampling protocols as above, we randomly chose three C_3 shoots per cluster each measurement day, or made three C_4 measurements by selecting 3–5 blades to lay side-by-side to fill the leaf clip of the FluoroPen, to measure the maximum quantum efficiency of PSII photochemistry (F_v/F_m).

$$F_v/F_m = \frac{F_m - F_o}{F_m} \quad (1)$$

where F_o is the minimum fluorescence yield of dark-adapted leaves and F_m is the maximum dark-adapted fluorescence yield when a saturating light pulse of $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ is applied to the leaf (Schreiber and Bilger 1993). The difference between F_o and F_m is the variable fluorescence, F_v . The value of F_v/F_m is highly consistent for unstressed C_3 leaves, with values of approximately 0.83, and has been shown to correlate well with the maximum quantum yield of photosynthesis (Demmig and Björkman 1987). Several studies have observed F_v/F_m values of 0.80–0.81 for C_4 plants under typical growth conditions where plants may be under minimal light or water stress (Jiang et al. 2011; Romanowska et al. 2017), so we assume that C_4 plants also have an optimum F_v/F_m of approximately 0.83. Plants growing under limiting conditions such as heat stress, salinity stress, or drought stress, tend to exhibit lower values of F_v/F_m due to photoinhibition, or inactivation damage of PSII (Long et al. 1994).

Light-Response Curves

In 2019 and 2021–22, we measured light-response curves using a light curve program of the FluoroPen FP 110. We randomly chose one C_3 shoot per cluster each measurement day, or made one C_4 measurements by selecting 3–5 blades to lay side-by-side to fill the leaf clip of the FluoroPen. Leaves were dark-adapted for 20–40 min, then exposed to actinic light intensities of 0, 100, 200, 300, 500, and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in successive 30 s steps. The initial measurement of the dark-adapted leaf at $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic active radiation (PPFD) is the equivalent of the pre-dawn F_v/F_m measurements described in the previous section. At each stepwise increase in light

intensity, the effective quantum yield of PSII ($\Delta F/F'_m$) was measured.

$$\Delta F/F'_m = \frac{F'_m - F}{F'_m} \quad (2)$$

where F is the fluorescence yield of the light-adapted sample, F'_m is the maximum light-adapted fluorescence yield when a saturating light pulse of $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ is superimposed on the current light intensity level of the light curve program.

The apparent rate of photosynthetic electron transport of PSII (ETR) was calculated as:

$$\text{ETR} = \Delta F/F'_m * \text{PPFD} * 0.5 * 0.84 \quad (3)$$

where the 0.5 value assumes equal excitation of both PSII and PSI photosystems and the 0.84 value is the ETR correction factor, which accounts for the proportion of incident light that is absorbed by the photosystems. We chose to use the empirical mean reflection factor of 0.84 (Ehrlinger 1981) because no specific reflection factors were known for the species in this study, and no anatomical structures that would affect this value such as trichomes or waxy cuticles were present.

The $\Delta F/F'_m$ versus PPFD curves were mathematically fitted using a double exponential decay function, as provided by SigmaPlot (SPSS Inc., San Rafael, CA):

$$f(x) = m + ae^{-bx} + ce^{-dx} \quad (4)$$

where a , b , c , d , and m are independent parameters. To determine the cardinal points of the light response curves, ETR versus PPFD data were fit using a single exponential function in SigmaPlot:

$$f(x) = a(1 - e^{-bx}). \quad (5)$$

From the results of Eq. 5, cardinal points can be determined with $a = \text{ETR}_{\text{max}}$ and PPFD_{sat} is reached at $0.9\text{ETR}_{\text{max}}$ (Rascher et al. 2000).

Statistical Analyses

Mixed effects analyses of variance (ANOVAs) were used to determine the treatment effects on stomatal conductance and chlorophyll fluorescence traits. Models included the following independent variables: year, plant community, warming treatment, CO_2 treatment, and all 2- and 3-way interactions among variables. Plot was added to each model as a random effect with each plot having a unique identifying number. We ran multiple models for each measured trait because not all plant types were measured in all growing seasons; C_3 sedges were measured in 2017–19 and 2021, C_4 grasses were measured in 2018–19 and 2021–22, and

C_3 sedges encroaching into the C_4 plots were measured in 2019 and 2021–22. Additionally, the $e\text{CO}_2$ treatment is only present in the C_3 sedge community, so a separate model was used to look at the interactive effects of warming and CO_2 on the sedge community. In all cases, we used the fullest model possible, meaning some measurements were used in more than one analysis. For example, *S. americanus* measurements made in the warming treatment (under ambient CO_2 conditions) were included in analyses comparing C_3 and C_4 plants responses to warming, as well as in analyses comparing C_3 plant responses under ambient and elevated CO_2 . ANOVA tables and fixed effect results for each model are provided. Bivariate relationships among traits were analyzed using linear regressions with all analyses conducted in JMP statistical analysis software (JMP 15.0, SAS Institute, Cary, NC, USA).

Results

Environmental Conditions

Since the experiment began in 2016, mean growing season air temperature has not differed dramatically among years, though 2018 and 2019 averaged approximately 0.5°C higher than other years (Table 1). Precipitation regime, however, has varied from year to year, with 2018 and 2022 being wetter and other years receiving 35% less rain on average (Table 1). Water depth and salinity also differed by year, but

Table 1 Growing season (May–September) environmental conditions of measurement years calculated using SERC Meteorological Data (Chitra-Tarak et al. 2019). Temperature means \pm SE were calculated using the daily average of ambient plots from 08:00 to 08:00 so we could investigate the effects of temperature for the 24-h period prior to measurements beginning. Precipitation is the total rainfall received from May through September. Water depth and salinity means \pm SE were calculated using the daily average of ambient plots in each plant community

Year	Mean air temp $^\circ\text{C}$	Total precip (cm)	Plant community	Mean water depth (cm)	Mean water salinity (PSU)
2017	23.1 ± 0.24	46.2	C_3	47.1 ± 0.13	21.6 ± 0.03
			C_4	53.2 ± 0.13	8.1 ± 0.01
2018	24.1 ± 0.17	78.6	C_3	51.1 ± 0.28	10.8 ± 0.02
			C_4	57.3 ± 0.36	7.1 ± 0.02
2019	23.9 ± 0.20	39.3	C_3	49.5 ± 0.08	7.9 ± 0.01
			C_4	56.8 ± 0.12	6.7 ± 0.02
2021	23.4 ± 0.24	47.3	C_3	45.2 ± 0.10	9.4 ± 0.01
			C_4	53.7 ± 0.15	7.6 ± 0.02
2022	23.3 ± 0.22	67.2	C_3	51.2 ± 0.14	9.0 ± 0.04
			C_4	54.8 ± 0.15	8.0 ± 0.03

neither measure was significantly related to the total amount of precipitation that fell.

Stomatal Conductance

Rates of g_s varied significantly across year and plant community (C_3 , C_4 , and C_3 encroaching into C_4 plots) in all statistical models ($P < 0.001$, Table 2 and Fig. 1). Interestingly, rates of g_s were 15–20% higher on average for *S. americanus* sedges encroaching into the higher elevation C_4 plots compared to sedges in the lower elevation C_3 plots in 2019 and 2021, but rates were similar across elevations in 2022. Rates of g_s of C_3 sedges encroaching into the C_4 plots were negatively affected by warming, ($P < 0.01$, Table 2 and Fig. 1), with a generally similar negative effect across all years of the experiment as indicated by the weak Year x Warming treatment interaction terms in models including those measurements. Stomatal conductance in the C_4 grasses were affected least by the warming treatment, and in some cases seemed to exhibit a modest positive response to the +1.7 and +3.4 °C treatments (Fig. 1).

Warming also had a significant negative effect on g_s of *S. americanus* growing in the C_3 plots, whether the sedges were growing under ambient or elevated CO_2 (eCO_2) conditions ($P < 0.05$, Table 2 and Fig. 1). However, the eCO_2 treatment caused a significant reduction in g_s of 15% on

average for C_3 *S. americanus*, with a similar decline regardless of whether they were growing under ambient or +5.1 °C warming in 2018, 2019, and 2021 ($P < 0.001$, Table 2 and Fig. 1). It was only in 2022 that the most significant reduction in g_s was observed in sedges growing in the warmed x eCO_2 interaction plots (Fig. 1).

Chlorophyll Fluorescence

F_v/F_m measured during pre-dawn hours in 2018 was unaffected by both warming and eCO_2 (Appendix Table 5 and 6). Values of F_v/F_m for C_3 sedges were similar to values reported for unstressed leaves (approximately 0.83; Demmig and Björkman 1987), while values for C_4 grasses were slightly lower, indicating very mild stress. However, it appears that if plants were under any type of heat, light, salinity, or inundation stress during the day in these plots, they were able to successfully recover overnight.

In 2019–2022, when F_v/F_m was measured on dark-adapted leaves during daylight hours, we found that the C_3 sedges showed the least amount of stress on average (F_v/F_m values were closest to the 0.83 known value for unstressed leaves; F_v/F_m growing season average = 0.79), followed by the C_3 sedges encroaching into C_4 plots (F_v/F_m average = 0.77), and the C_4 grasses showed the highest degree of stress (F_v/F_m average = 0.67). We observed a

Table 2 Mixed effect ANOVA results for stomatal conductance measurements made from 2017–2022 in the Salt Marsh Accretion Response to Temperature eXperiment (SMARTX). Four analyses

Plant community	Years measured	Habitat	Source of variance	F	df	P
C_3 sedges	2017–2022	Ambient CO_2	Year	113.25	4	< 0.001
			Warming treatment	4.59	3	0.0183
			Year x Warming	3.75	12	< 0.001
C_3 sedges C_4 grasses	2018–2022	Ambient CO_2	Year	61.72	3	< 0.001
			Community	4902.51	1	< 0.001
			Warming treatment	9.32	3	0.0008
			Year x Community	83.46	3	< 0.001
			Year x Warming	0.69	9	0.7119
			Community x Warming	8.74	3	0.0011
			Yr x Comm x Warming	1.38	9	0.1926
C_3 sedges C_3 encroaching in C_4 plots	2019–2022	Ambient CO_2	Year	108.40	2	< 0.001
			Community	28.21	1	0.0007
			Warming treatment	12.29	3	0.0022
			Year x Community	21.38	2	< 0.001
			Year x Warming	0.65	6	0.6475
			Community x Warming	0.25	3	0.2530
			Yr x Comm x Warming	0.39	9	0.8859
C_3 sedges	2018–2022	Ambient and Elevated CO_2	Year	119.03	3	< 0.001
			CO_2	57.98	1	< 0.001
			Warming treatment	14.17	1	0.0054
			Year x CO_2	3.40	3	0.0171
			Year x Warming	3.93	3	0.0083
			CO_2 x Warming	0.17	1	0.6895
			Yr x CO_2 x Warming	1.73	3	0.1588

were run since not all plant communities were measured in all four years. $P < 0.05$ are indicated in bold

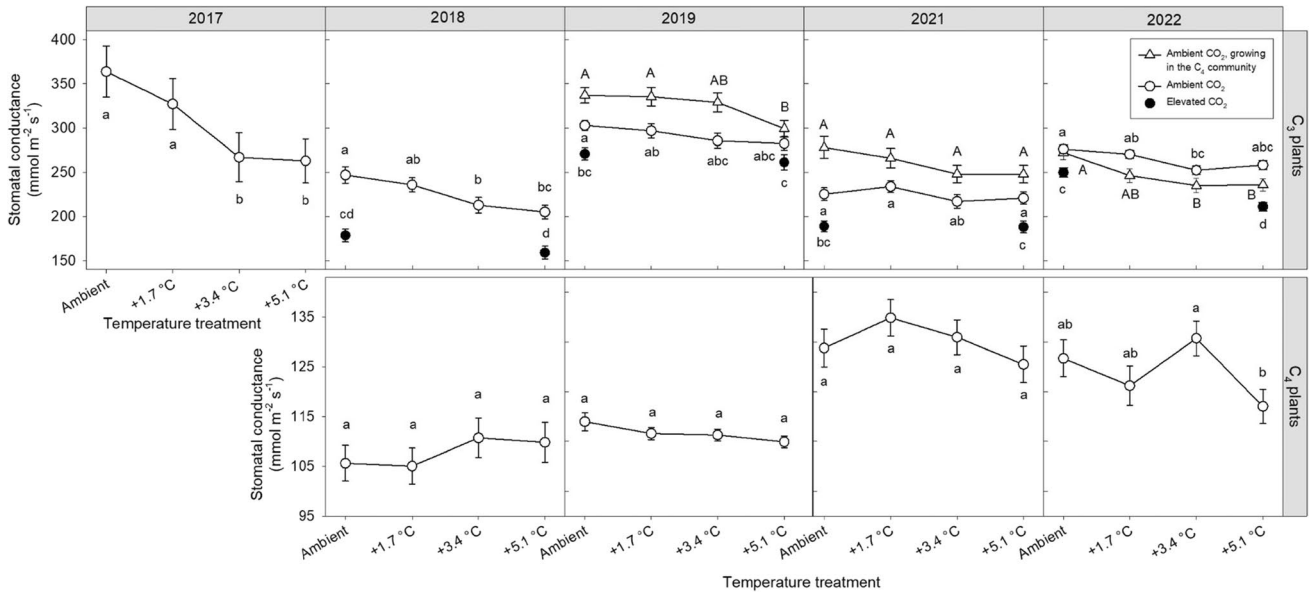


Fig. 1 Changes in stomatal conductance in response to warming and CO₂ measured in 2017–2019 and 2021–2022 ($n=273, 1756, 1733, 2443, \text{ and } 2058$, respectively). Open circles represent plants growing under ambient CO₂, closed circles represent plants growing under elevated CO₂, open triangles represent C₃ sedges that began encroaching into C₄ plots beginning in 2019, and error bars repre-

sent \pm 1 SE. Note the difference in y-axis scale between the C₃ and C₄ plant communities. Letters show results of Tukey–Kramer HSD tests looking for warming and CO₂ effects within each measurement year; capital letters in the top row show results for C₃ sedges growing in C₄ plots and lowercase letters show results for C₃ sedges in C₃ plots. ANOVA results are provided in Table 2

Table 3 Mixed effect ANOVA results for maximum quantum efficiency of PSII photochemistry (F_v/F_m) measurements made from 2019–2022 on dark-adapted leaves in the Salt Marsh Accretion

Response to Temperature eXperiment (SMARTX). Two analyses were run since the elevated CO₂ treatment is only in the C₃ community. $P < 0.05$ are indicated in bold, $P < 0.10$ are italicized

Plant community	Years measured	Habitat	Source of variance	<i>F</i>	df	<i>P</i>
C ₃ sedges	2019–2022	Ambient CO ₂	Year	8.17	2	0.0003
C ₃ encroaching in C ₄ plots			Community	350.5	2	< 0.001
C ₄ grasses			Warming treatment	4.56	3	0.0202
			Year x Community	2.03	4	0.0795
			Year x Warming	0.35	6	0.9101
			Community x Warming	1.28	6	0.2961
			Yr x Comm x Warming	1.08	12	0.3742
C ₃ sedges	2019–2022	Ambient and Elevated CO ₂	Year	3.51	2	0.0307
			CO ₂	0.25	1	0.6296
			Warming treatment	10.3	2	0.0110
			Year x CO ₂	4.80	2	0.0086
			Year x Warming	4.43	2	0.0124
			CO ₂ x Warming	0.23	1	0.6443
			Yr x CO ₂ x Warming	0.59	2	0.5529

significant decline in F_v/F_m with warming in all plant communities in $a\text{CO}_2$, indicating higher levels of plant stress under warmer growing conditions ($P < 0.05$, Table 3 and Fig. 2). The $e\text{CO}_2$ treatment had no effect on C₃ sedges in 2019 and 2021, and did not appear to cause any form of additional plant stress (Table 3 and Fig. 2). However, in 2022, F_v/F_m was significantly reduced in the $e\text{CO}_2$ treatment indicating a higher level of stress in these plants (Year x CO₂ interaction $P < 0.01$).

ETR_{max} and PPFD_{sat} varied significantly across year and plant community (C₃, C₄, and C₃ encroaching into C₄ plots) in all statistical models ($P < 0.001$, Table 4, Appendix Table 7). Rates of ETR_{max} and PPFD_{sat} were 20–30% higher in 2019 than in 2021 and 2022, and were also 20–30% higher in the C₃ sedges than in the C₄ grasses in all years (Fig. 3). In the ETR_{max} model that included all three plant communities, we found a significant negative effect of warming ($P < 0.05$), and in the model solely for the C₃ sedge community, we

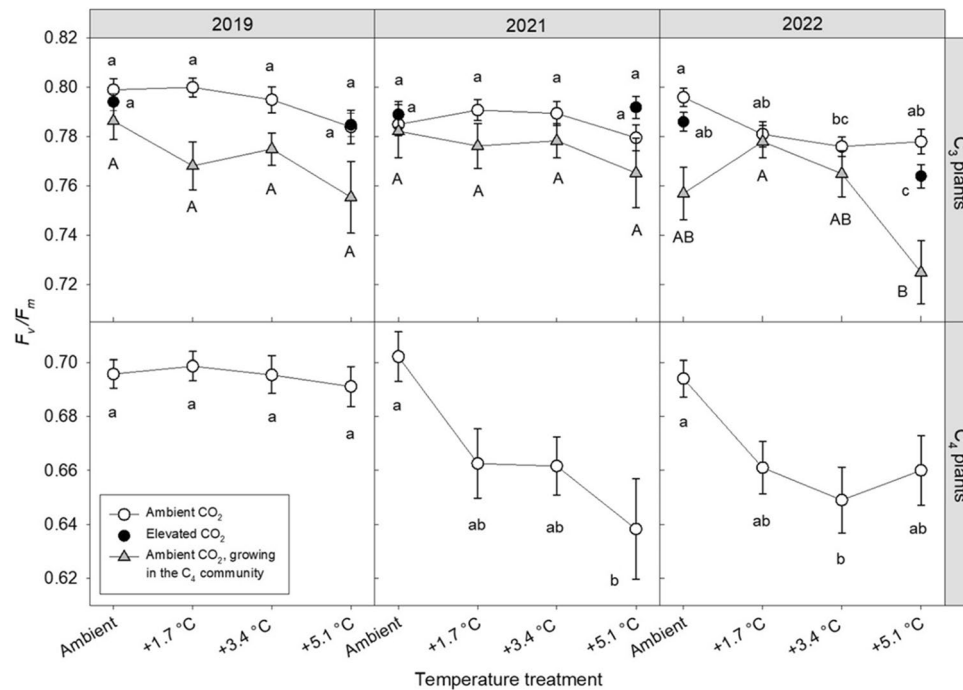


Fig. 2 Changes in maximum quantum efficiency of PSII photochemistry (F_v/F_m) in response to warming and CO_2 measured in 2019, 2021, and 2022 on dark-adapted leaves ($n=328, 580, \text{ and } 664$, respectively). Open circles represent plants growing under ambient CO_2 , closed circles represent plants growing under elevated CO_2 , open triangles represent C_3 sedges that began encroaching into C_4 plots beginning in 2019, and error bars represent ± 1 SE. Note the dif-

ference in y-axis scale between the C_3 and C_4 plant communities. Letters show results of Tukey–Kramer HSD tests looking for warming and CO_2 effects within each measurement year; capital letters in the top row show results for C_3 sedges growing in C_4 plots and lowercase letters show results for C_3 sedges in C_3 plots. ANOVA results are provided in Table 3

Table 4 Mixed effect ANOVA results for the apparent rate of maximum photosynthetic electron transport of PSII (ETR_{max}) measurements made in 2019 and 2021–22 in the Salt Marsh Accretion

Response to Temperature eXperiment (SMARTX). Two analyses were run since the elevated CO_2 treatment is only in the C_3 community. $P < 0.05$ are indicated in bold

Plant community	Years measured	Habitat	Source of variance	F	df	P
C_3 sedges	2019–2022	Ambient CO_2	Year	317.64	2	< 0.001
C_3 encroaching in C_4 plots			Community	174.22	2	< 0.001
C_4 grasses			Warming treatment	4.31	3	0.0185
			Year x Community	9.46	4	< 0.001
			Year x Warming	0.89	6	0.5038
			Community x Warming	0.88	6	0.5177
			Yr x Comm x Warming	1.64	12	0.0739
C_3 sedges	2019–2022	Ambient and Elevated CO_2	Year	175.05	2	< 0.001
			CO_2	49.64	1	< 0.001
			Warming treatment	13.21	1	0.0036
			Year x CO_2	1.65	2	0.1938
			Year x Warming	2.29	2	0.1021
			CO_2 x Warming	0.01	1	0.9873
			Yr x CO_2 x Warming	0.74	2	0.4760

found that both $+5.1\text{ }^\circ\text{C}$ warming and eCO_2 caused significant declines in electron transport of PSII ($P < 0.01$, Figs. 2, 3 and 4). $PPFD_{sat}$ was unaffected by warming in all plant communities, but did decline significantly in C_3 sedges

grown under eCO_2 conditions ($P < 0.001$, Fig. 4, Appendix Table 7). Across all years and plant communities, we found significant positive relationships between g_s and F_v/F_m , ETR_{max} , and $PPFD_{sat}$ (Figs. 5 and 6).

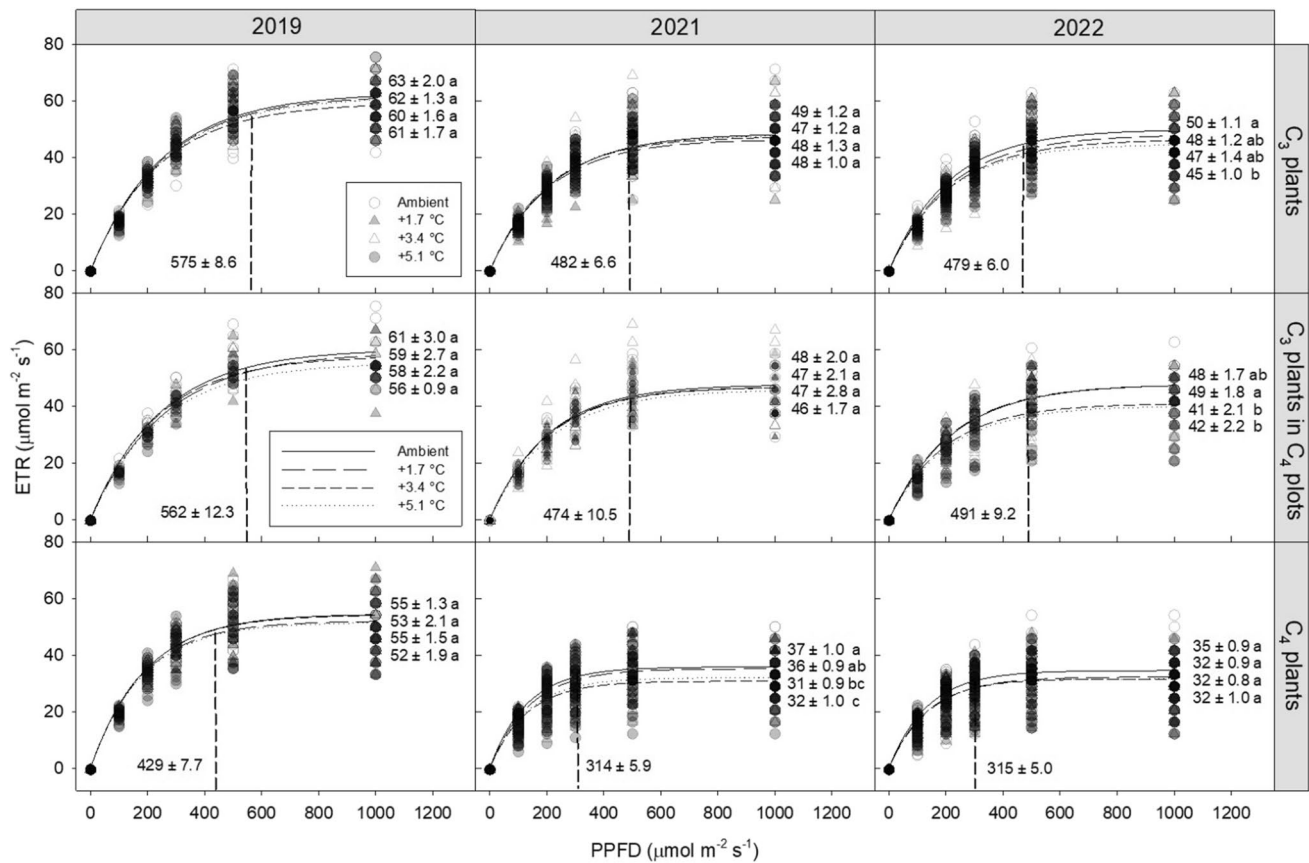


Fig. 3 Light response curves of C_3 *S. americanus* and C_4 grasses measured in 2019, 2021, and 2022. Plants were dark-adapted for 30+ minutes prior to measurements. The top row of panels represents C_3 plants, the middle row of panels show C_3 plants encroaching into C_4 plots, and the bottom row of panels is C_4 plants. Open circles/solid lines represent ambient temperatures, closed triangles/long dashed lines are +1.7 °C above ambient, open triangles/short dashed lines are +3.4 °C above ambient, and closed circles/dotted lines are +5.1 °C above ambient. The numbers to the right of the fitted

curves give the maximum rate of electron transport ($ETR_{max} \pm SE$) for each warming treatment and the dashed vertical lines show $PPFD_{sat} \pm SE$ (i.e., PPFD at 90% of ETR_{max}). Only one $PPFD_{sat}$ value (left of vertical dashed line) is shown for each plant community in a given year because there was no significant effect of warming; ANOVA results are provided in Table 4 and Appendix Table 7. Letters show results of Tukey–Kramer HSD tests looking for warming effects for each community within a measurement year

Discussion

In support of our hypotheses we found that both experimental warming and eCO_2 caused reductions in stomatal conductance (g_s), maximum electron transport rates (ETR_{max}), the light level at which ETR saturates ($PPFD_{sat}$), and the maximum quantum efficiency of PSII photochemistry (F_v/F_m ; Table 2, 3, 4 and Figs. 1, 2, 3 and 4), and that these traits were positively correlated with one another (Figs. 5 and 6). These declines were not always significant when post hoc Tukey–Kramer HSD analyses were run within a given year, but the trends in data were consistent. The hypothesis that the sedge would experience more severe declines in these traits than the grasses (hypothesis 3) was supported at the start of the experiment as the C_3 sedge showed a strong negative stomatal response to warming in 2017 and 2018 (28% and 17% reduction, respectively in +5.1 °C). However,

in 2019, 2021, and 2022, the negative response to warming was dampened to <7% reduction in all years, indicating that *S. americanus* was able to partially acclimate to the warming treatments over time (Fig. 7). These plant responses suggest that future climate conditions have the potential to negatively affect gas-exchange rates in both C_3 and C_4 salt marsh communities, but the long-term negative impacts on plant growth and survival have may be mitigated through physiological adjustments or genetic selection (Vahsen et al. 2023).

Elevated CO_2 caused declines in the physiological traits of *S. americanus* as hypothesized (hypothesis 2). However, in contrast to hypothesis 4, the declines under eCO_2 conditions were similar for plants in 2018–2021 regardless of whether they were growing in the ambient or +5.1 °C temperature treatment (Figs. 1, 2, and 4). It was only in 2022 that sedges growing in the combined +5.1 °C x eCO_2 plots exhibited more significant declines in g_s , F_v/F_m , and ETR_{max}

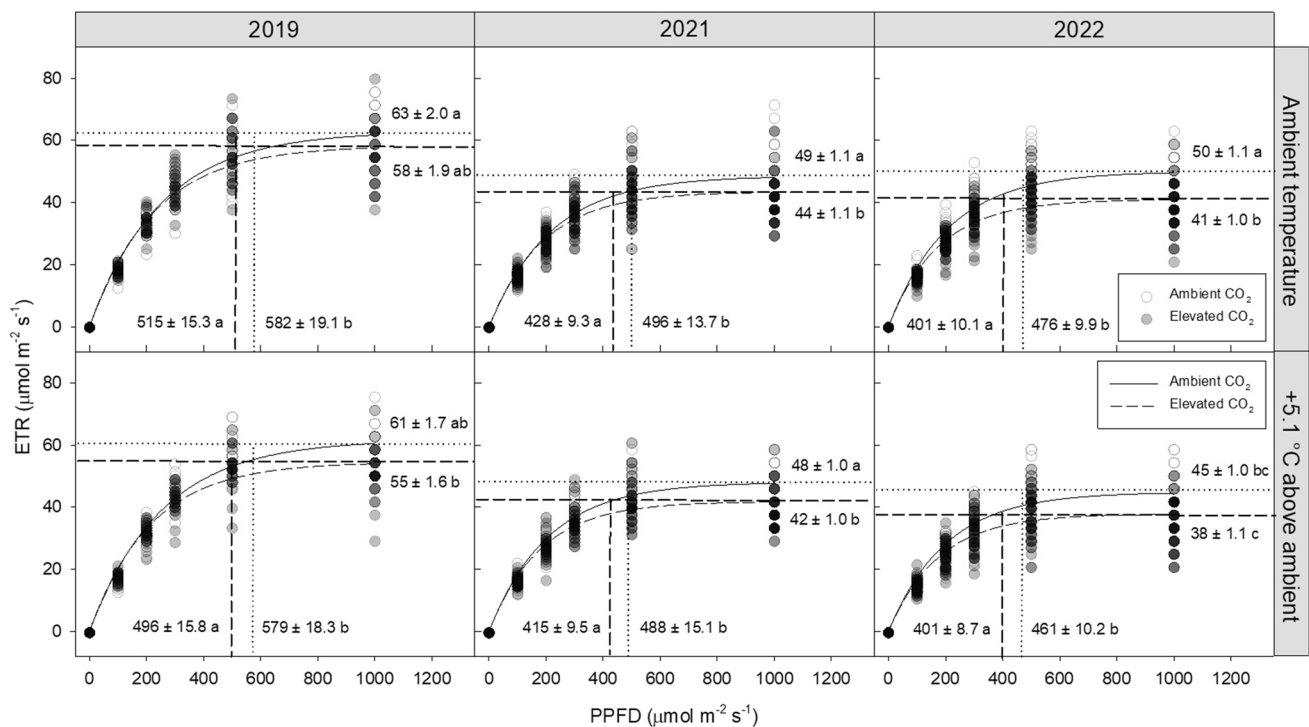


Fig. 4 Light response curves of C_3 *S. americanus* growing under warming and eCO_2 treatments in 2019, 2021 and 2022. Plants were dark-adapted for at least 30 min prior to the start of measurements. The top row of panels represents plants growing under ambient temperatures and the bottom row of panels represents plants growing in $+5.1$ °C above ambient. Symbols refer to the CO_2 treatment: open circles/solid line fits represent ambient CO_2 (aCO_2) and closed circles/dashed line fits are elevated CO_2 (eCO_2). The numbers at the

dotted horizontal lines give the maximum rate of electron transport ($ETR_{max} \pm SD$) of aCO_2 plants and the numbers at the dashed horizontal lines give $ETR_{max} (\pm SD)$ of eCO_2 plants. The dotted vertical lines show $PPFD_{sat}$ (i.e., PPFD at 90% of ETR_{max}) of aCO_2 plants and the numbers at the dashed horizontal lines give $PPFD_{sat}$ of eCO_2 plants. ANOVA results are provided in Table 4 and Appendix Table 7. Letters show results of Tukey–Kramer HSD tests looking for warming and CO_2 effects within each measurement year

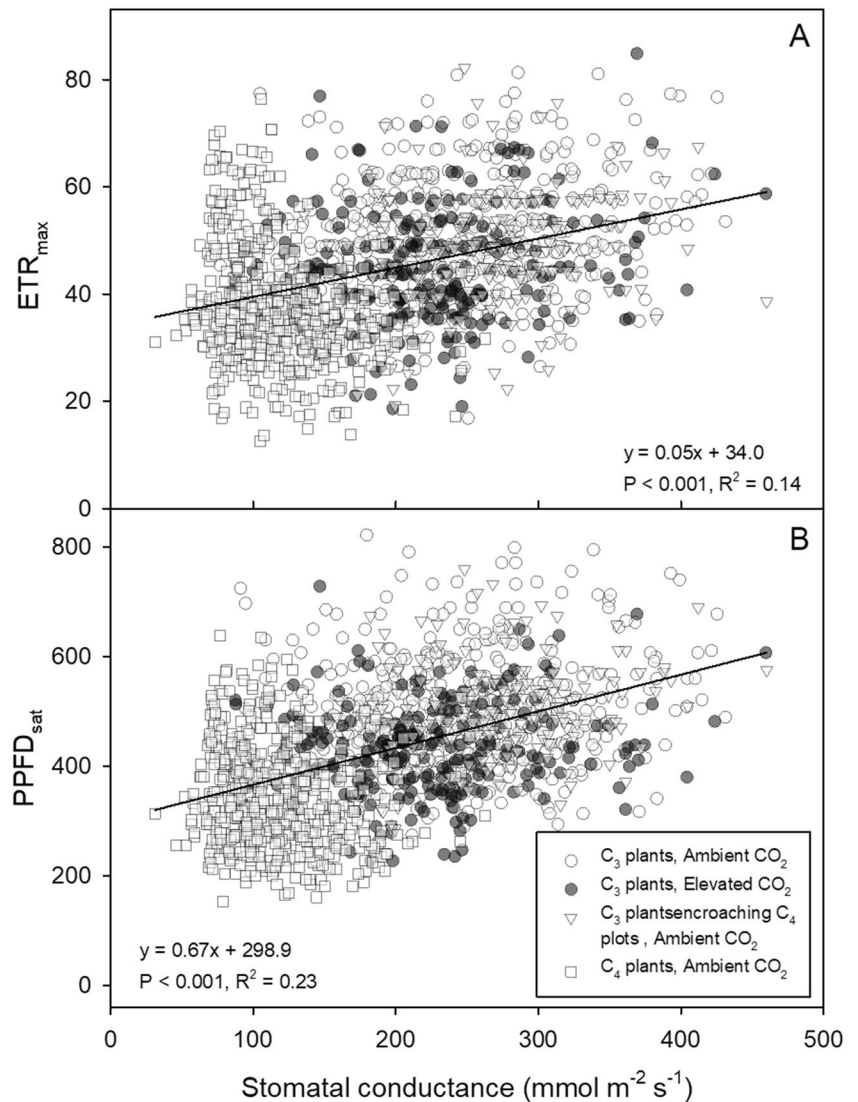
than in either treatment individually (Figs. 1, 2, and 4). In this case, it seems that long-term responses can also exacerbate the negative impacts of warming and eCO_2 on the processes we measured.

We were surprised to discover that mean annual variation in plant traits and species-specific responses to warming and eCO_2 treatments across years were not dependent on growing season average environmental conditions (Table 1). For example, prior research has shown that plants adjust rates of stomatal conductance in response to annual average changes in environmental conditions such as soil water availability and temperature (Perez-Martin et al. 2009; Šigut et al. 2015), and long-term records from our study site suggest that plant productivity is positively correlated to precipitation (Drake et al. 2013). As such, we expected years with relatively low precipitation to be associated with overall declines in physiological traits and more significant drops in g_s and other traits in response to warming. While plants that experience prolonged exposure to extreme growth conditions may acclimate or adapt to those conditions, as suggested by the decline in the negative response of *S. americanus* g_s to warming over time (Fig. 7), plants also exhibit

short-term sensitivity to changes in their environment on the scale of hours to weeks. For example, grassland species have been shown to increase rates of g_s and photosynthesis in response to increased soil water content over a 3-month period (Volk et al. 2000), and sedge species showed patterns of g_s and photosynthesis that were related to diurnal and seasonal variability in leaf temperature and vapor pressure deficit (Koch and Rawlik 1993; Gebauer et al. 1998). We suspect that environmental factors occurring over short periods early in the growing season set the development of the plant traits we measured, a topic that is beyond the scope of the current study.

While our statistical model that included both plant communities found a reduction in g_s response to the warming treatment ($P < 0.001$, Table 2), the C_3 sedges showed a more consistent negative response to warming than the C_4 grasses when Tukey–Kramer HSD tests were run within year (Fig. 1). This result is not surprising given that warmer growing conditions tend to favor C_4 species over C_3 species due to the elimination of photorespiration in C_4 species which concentrate CO_2 around Rubisco, eliminating O_2 competition for its active site (Osmond et al. 1982; Long

Fig. 5 Relationships between stomatal conductance and (A) maximum photosynthetic electron transport of PSII (ETR_{max}) and (B) saturating photosynthetically active radiation ($PPFD_{sat}$). Measurements were made in 2019, 2021, and 2022 ($n = 1544$)

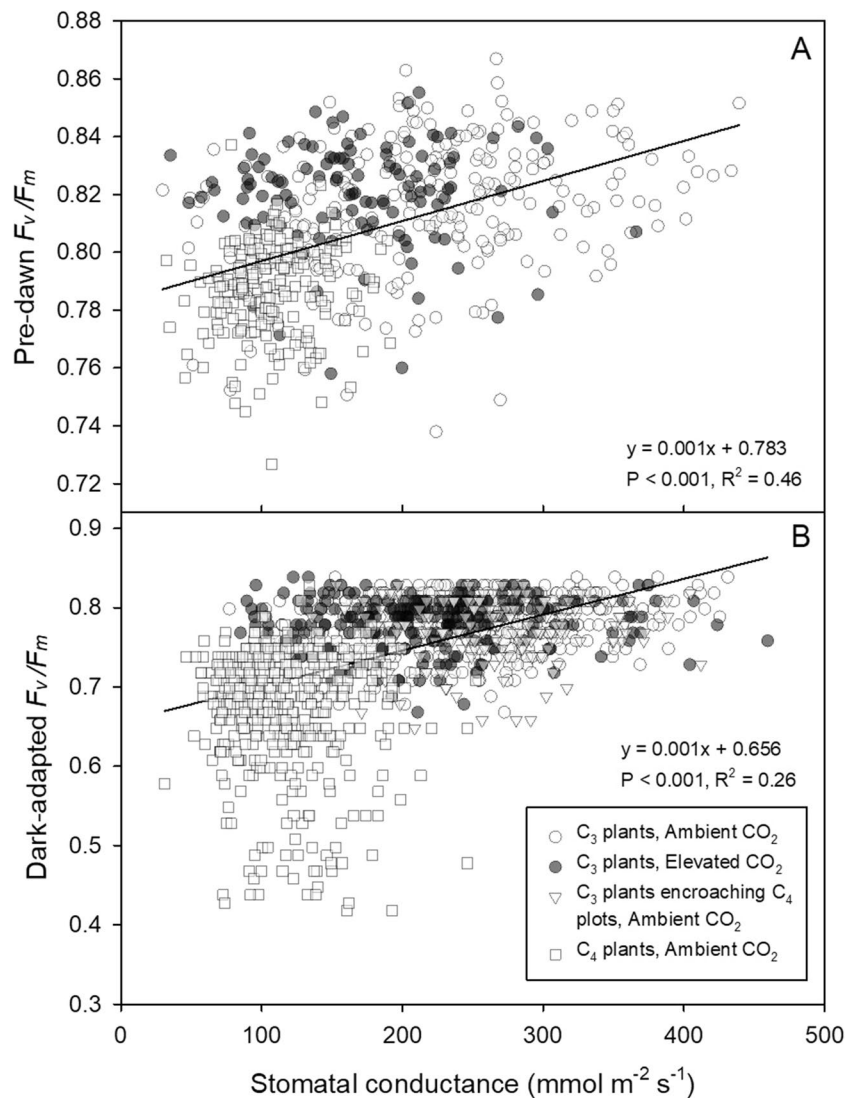


1999; Taylor et al. 2014). Since many prior studies have found a positive correlation between g_s and photosynthesis (Franks 2006; Kattge et al. 2009; Cernusak et al. 2011), it is likely that the C₃ sedges in this habitat would exhibit stronger negative gas exchange and growth responses to future climate warming compared to the C₄ grasses, but could eventually acclimate and become more similar to the C₄ response. Furthermore, a study of four tropical tree species exposed to higher than optimal temperatures showed that photosynthetic rates were limited by g_s , rather than traits associated with enzymatic control of photosynthetic capacity (maximum carboxylation rate V_{cmax} ; maximum electron transport rate J_{max}) (Slot and Winter 2017). However, while we observed a large decline in g_s associated with warming during the first two years of the experiment, the C₃ sedges seemed to acclimate to the warming treatment in later years and declines in g_s were greatly reduced (Fig. 7). This could alleviate potential reductions in gas-exchange rates and plant

growth associated with higher growth temperatures (Kattge and Knorr 2007; Gunderson et al. 2010), allowing both C₃ sedges and C₄ grasses to remain successful under future climate warming.

Despite the relatively minimal decline of g_s of C₄ grasses and the acclimation of C₃ sedges in response to warming after 2019, we observed a negative effect of warming on ETR_{max} and F_v/F_m in 2022 for C₃ sedges, and in both 2021 and 2022 for C₄ grasses (Figs. 2 and 3). We expected g_s and ETR_{max} to follow similar patterns because stomatal closure prevents water loss via transpiration, but yields excess light energy that can damage photosynthetic machinery via the generation of reactive oxygen species (Cruz de Carvalho 2008). Thus, we assumed that during years when the warming treatments caused the most severe declines in g_s , we would also observe significant declines in ETR_{max} . Similarly, we assumed that g_s and F_v/F_m would follow similar patterns because as transpiration declines with stomatal closure,

Fig. 6 Quantum efficiency of PSII photosynthesis (F_v/F_m) in relation to stomatal conductance. Pre-dawn measurements (panel A) were made in 2018 between the hours of 01:00 and 05:00 ($n = 566$) and dark-adapted measurements (panel B) were made in 2019–2022 between the hours of 08:00 and 14:00 ($n = 1434$)



plants cannot release heat and therefore suffer increased leaf temperatures (Kim et al. 2006; Šigut et al. 2015). Since reductions in F_v/F_m are indicative of higher levels of plant stress (Demmig and Bjorkman 1987), we thought that heat damage and/or damage to the photosynthetic machinery caused by reactive oxygen species would lead to reductions in this leaf trait. Nonetheless, while we did not observe expected similarities in plant responses to warming when averaged over growing seasons, we did find that these traits were positively correlated when data were pooled across years and plant communities (Figs. 5 and 6), and that lower g_s was observed in plants that had lower ETR_{max} and were under a higher degree of stress (e.g., lower F_v/F_m).

It is commonly accepted that C₄ plants have higher photosynthetic rates than C₃ species, which is attributable to different mechanisms of carbon fixation connected to biochemical and anatomical differences that exist between these groups. Because of this, we were surprised to find that the

C₄ grasses in our experiment exhibited lower values of F_v/F_m , ETR_{max} , and $PPFD_{sat}$ compared to the C₃ sedges. However, while the CO₂ concentrating mechanism in C₄ species increases their water use efficiency, studies have shown that stomatal limitation posed by abiotic stressors (e.g., high temperatures or drought) potentially induces a larger reduction in CO₂ uptake in these species (Wand et al. 2001). Comparisons of C₃ and C₄ grass subspecies of *Alloteropsis semialata* showed that the C₄ plants had a lower CO₂ assimilation rate under drought conditions (Ripley et al. 2007). Additionally, Killi et al. (2017) found that drought- and heat-induced declines in F_v/F_m and PSII efficiency were more severe in C₄ species, suggesting that they perform more poorly under stressful conditions, even at temperatures that should favor C₄ species over C₃. Thus, our results support the premise that C₄ species may be inferior competitors under abiotic stress due to a higher susceptibility for photoinhibition (Guidi et al. 2019).

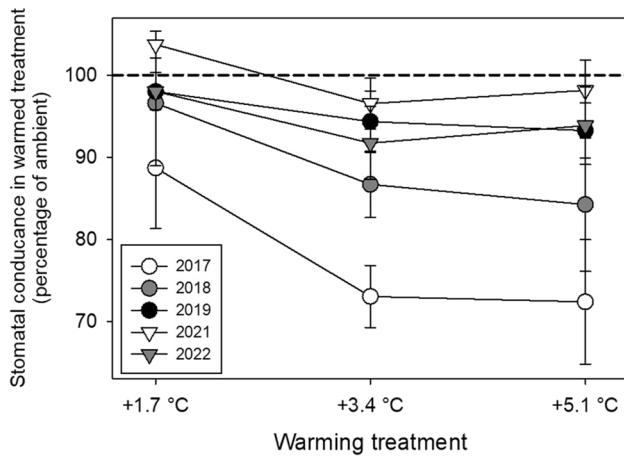


Fig. 7 Stomatal conductance of *S. americanus* in +1.7, +3.4, and +5.1 °C above ambient conditions as a percentage of stomatal conductance in the ambient warming treatment. All data are from ambient CO₂ growth conditions. Data are averaged from measurements made in 2017 (white circles, $n=273$), 2018 (gray circles, $n=1756$), 2019 (black circles, $n=1733$), 2021 (white triangles, $n=2443$), and 2022 (gray triangles, $n=2058$). ANOVA results are provided in Table 2. Symbols represent the mean response to each warming treatment (shown as a percentage of ambient) averaged across transects ($n=3$); error bars represent ± 1 SE

Similar to plant responses to the warming treatment, we found that g_s declined significantly for the C₃ sedge in response to e CO₂ treatment, which again was expected given results of prior studies (Fig. 1; Morison and Lawlor 1999; Medlyn et al. 2001; Ainsworth and Rogers 2007). We also observed significant declines in ETR_{max} in the e CO₂ treatments (Fig. 4). This may seem counterintuitive given the significant increase in net primary production of *S. americanus* to e CO₂ observed in our experiment in 2017 and 2018 (Noyce et al. 2019), as well as prior findings from the same coastal wetland site (Curtis et al. 1989; Drake and Leadley 1991; Jacob et al. 1995; Drake et al. 1996). However, because of the increase in CO₂ supply in e CO₂ treatments, plants tend to have enhanced photosynthetic rates in spite of the limitation of lower g_s (Sage 1994; Kaiser et al. 2017), leading to increased photosynthesis in C₃ plants regardless of whether ETR_{max} is limiting (Stitt 1991; Long and Drake 1992). We found no significant effect of e CO₂ on F_v/F_m in 2019, 2021, and under ambient temperatures in 2022 (Table 4). This may be due to the alleviation of oxidative

stress that would typically be induced by excess light under a CO₂, as higher photosynthetic rates caused by enhanced CO₂ levels would make use of that extra light energy input.

We predicted that the combined +5.1 °C x e CO₂ treatment would have the largest effects on plant physiological traits, particularly for the C₃ sedges, but we only saw evidence for this in 2022 (Figs. 1, 2, and 4). Mean growing season air temperature was not atypical in 2022, while the amount of precipitation that fell indicates that plants would not have been drought-stressed any more than prior years (Table 1). However, we observed significant declines in g_s , ETR_{max} , and F_v/F_m in the combined +5.1 °C x e CO₂ treatment compared to the individual +5.1 °C or e CO₂ treatments. It could be that some of the initial stimulation of plants under e CO₂ is becoming offset by changes in the development of photosynthetic organs as they acclimate (Long and Drake 1992). For example, Jacob et al. (1995) found that e CO₂ led to a 30–58% reduction in Rubisco content and lower carboxylation efficiency in *S. americanus* grown under e CO₂ over eight years of treatment. It is possible that these types of developmental changes could, over time, have led to additive effects of warming and e CO₂ for this species, but more research is required to test this interpretation.

More studies evaluating the interaction of climate stressors are needed to better understand mechanisms driving gas-exchange and growth responses of plant communities. For example, this study is helping to fill in some gaps regarding plant responses to warming and e CO₂, but a recent publication investigating the effects of rising temperatures and CO₂ levels found that most ecosystems are becoming deficient in nutrients such as nitrogen (Mason et al. 2022), which further complicates making predictions about the health of future ecosystems. The GCRew site where this experiment took place is the longest continually running investigation on the effects of e CO₂ on an ecosystem, and research found reduced tissue nitrogen concentrations in e CO₂ treatments over a 28-year period, but particularly in years when precipitation rates were high (Drake et al. 2013). Drake et al. (2013) posits that any decline in nitrogen was driven by a combination of the higher nitrogen demand for growth and transpiration rates (Polley et al. 1999; McDonald et al. 2002). Thus, independent from any changes in photosynthesis or growth, changes in stomatal conductance with warming, e CO₂, or environmental factors such as precipitation will affect broader ecosystem processes such as nutrient availability and recycling.

Appendix 1

Table 5 Mixed effect ANOVA results for maximum quantum efficiency of PSII photochemistry (F_v/F_m) measurements made during pre-dawn hours in 2018 in the Salt Marsh Accretion Response to Temperature eXperiment (SMARTX). Two analyses were run since the elevated CO_2 treatment is only in the C_3 community. $P < 0.05$ are indicated in bold, $P < 0.10$ are italicized

Plant community	Habitat	Source of variance	<i>F</i>	df	<i>P</i>
C_3 sedges	Ambient CO_2	Community	164.3	1	< 0.001
C_4 grasses		Warming treatment	0.81	3	0.5060
		Community x Warming	0.76	3	0.5304
C_3 sedges	Ambient and Elevated CO_2	CO_2	1.09	1	0.3263
		Warming treatment	0.88	1	0.8825
		CO_2 x Warming	2.02	1	0.1925

Table 6 Mean \pm SE maximum quantum efficiency of PSII photochemistry (F_v/F_m) of plants made during pre-dawn hours in 2018 in the Salt Marsh Accretion Response to Temperature eXperiment (SMARTX)

Plant community	CO_2 treatment	Warming Treatment	Mean $F_v/F_m \pm SE$	<i>n</i>
C_3 sedges	Ambient	Ambient	0.821 \pm 0.0020	177
		+1.7 °C	0.813 \pm 0.0028	176
		+3.4 °C	0.816 \pm 0.0025	177
	Elevated	+5.1 °C	0.819 \pm 0.0023	173
		Ambient	0.814 \pm 0.0023	174
		+5.1 °C	0.825 \pm 0.0017	172
C_4 grasses	Ambient	Ambient	0.785 \pm 0.0016	186
		+1.7 °C	0.787 \pm 0.0014	186
		+3.4 °C	0.784 \pm 0.0014	186
		+5.1 °C	0.789 \pm 0.0017	186

Table 7 Mixed effect ANOVA results for saturating photosynthetically active radiation ($PPFD_{sat}$) measurements made in 2019 and 2021–22 in the Salt Marsh Accretion Response to Temperature eXperiment (SMARTX). Two analyses were run since the elevated CO_2 treatment is only in the C_3 community. $P < 0.05$ are indicated in bold

Plant community	Years measured	Habitat	Source of variance	<i>F</i>	df	<i>P</i>
C_3 sedges	2019–2022	Ambient CO_2	Year	106.83	2	< 0.001
C_3 encroaching in C_4 plots			Community	462.75	2	< 0.001
C_4 grasses			Warming treatment	1.74	3	0.2197
			Year x Community	1.62	4	0.1664
			Year x Warming	1.107	6	0.3177
			Community x Warming	0.44	6	0.8464
			Yr x Comm x Warming	1.14	12	0.3236
C_3 sedges	2019–2022	Ambient and Elevated CO_2	Year	70.53	2	< 0.001
			CO_2	213.78	1	< 0.001
			Warming treatment	5.25	1	0.0400
			Year x CO_2	0.10	2	0.9059
			Year x Warming	0.88	2	0.8775
			CO_2 x Warming	0.01	1	0.9197
			Yr x CO_2 x Warming	0.72	2	0.4879

Author Contributions Kerrie Sendall, Patrick Megonigal, Genevieve Noyce, and Roy Rich contributed to the study conception and design. Data collection was performed by Kerrie Sendall, Cyd Meléndez Muñoz, and Angela Ritter. Material preparation and analysis were performed by Kerrie Sendall, Cyd Meléndez Muñoz, and Angela Ritter. The first draft of the manuscript was written by Kerrie Sendall and Patrick Megonigal and Genevieve Noyce commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This material is based upon work supported by the US Department of Energy, Office of Science, Office of Biological and Environmental Research Program (DE-SC0014413, DE-SC0019110, and DE-SC0021112); an institutional grant (award no. NA18OAR4170084) to the Georgia Sea Grant College Program from the National Sea Grant Office, National Oceanic and Atmospheric Administration, United States Department of Commerce; a research grant from the Maryland Native Plant Society; Georgia Southern University; Rider University; and the Smithsonian Institution.

Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adams WW III, Zarter CR, Ebbert V, Demmig-Adams B (2004) Photoprotective strategies of overwintering evergreens. *Bioscience* 54:41–49. [https://doi.org/10.1641/0006-3568\(2004\)054\[0041:PSOOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0041:PSOOE]2.0.CO;2)
- Adir N, Zer H, Shochat S, Ohad I (2003) Photoinhibition: a historical perspective. *Photosynthesis Research* 76:343–370. <https://doi.org/10.1023/A:1024969518145>
- Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant, Cell & Environment* 30:258–270. <https://doi.org/10.1111/j.1365-3040.2007.01641.x>
- Anderson LJ, Maherali H, Johnson HB, Polley HW, Jackson RB (2001) Gas exchange and photosynthetic acclimation over subambient to elevated CO₂ in a C₃–C₄ grassland. *Global Change Biology* 7:693–707. <https://doi.org/10.1046/j.1354-1013.2001.00438.x>
- Bernacchi CJ, Calfapietra C, Davey PA, Wittig VE, Scarascia-Mugnozza GE, Raines CA, Long SP (2003) *New Phytologist* 159:609–621. <https://doi.org/10.1046/j.1469-8137.2003.00850.x>
- Björkman O, Demmig B (1987) Photon yield of O₂ evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. *Planta* 170:489–504. <https://doi.org/10.1007/BF00402983>
- Cernusak LA, Hutley LB, Beringer J, Holtum JAM, Turner BL (2011) Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. *Agricultural and Forest Meteorology* 151:1462–1470. <https://doi.org/10.1016/j.agrformet.2011.01.006>
- Chaves MM (1991) Effects of Water Deficits on Carbon Assimilation. *Journal of Experimental Botany* 42:1–16. <https://doi.org/10.1093/jxb/42.1.1>
- Chitra-Tarak R, McMahon S, Neale P (2019) SERC Meteorological Data. Smithsonian Environmental Research Center. Dataset. <https://doi.org/10.25573/serc.11020646.v2>
- Cornish K, Radin JW, Turcotte EL, Lu Z, Zeiger E (1991) Enhanced Photosynthesis and Stomatal Conductance of Pima Cotton (*Gossypium barbadense* L.) Bred for Increased Yield. *Plant Physiology* 97:484–489. <https://doi.org/10.1104/pp.97.2.484>
- Cruz de Carvalho MH (2008) Drought stress and reactive oxygen species. *Plant Signaling & Behavior* 3156–165. <https://doi.org/10.4161/psb.3.3.5536>
- Curtis P, Wang X (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113:299–313. <https://doi.org/10.1007/s004420050381>
- Curtis PS, Drake BG, Whigham DF (1989) Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ in situ. *Oecologia* 78:297–301. <https://doi.org/10.1007/BF00379101>
- Demmig B, Björkman O (1987) Photon yield of O₂ evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. *Planta* 170:489–504. <https://doi.org/10.1007/BF00402983>
- Demmig-Adams B, Cohu CM, Muller O, Adams WW (2012) Modulation of photosynthetic energy conversion efficiency in nature: from seconds to seasons. *Photosynthesis Research* 113:75–88. <https://doi.org/10.1007/s11120-012-9761-6>
- Drake BG, Leadley PW (1991) Canopy photosynthesis of crops and native plant communities exposed to long term elevated CO₂. *Plant, Cell & Environment* 14:853–860. <https://doi.org/10.1111/j.1365-3040.1991.tb01448.x>
- Drake BG, Peresta G, Beugeling E, Matamala R (1996) Long-term elevated CO₂ exposure in a Chesapeake Bay wetland: ecosystem gas exchange, primary production, and tissue nitrogen. *Plant and Soil* 187:111–118. <https://doi.org/10.1111/gcb.12631>
- Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* 48:609–639. <https://doi.org/10.1146/annurev.arplant.48.1.609>
- Drake PL, Froend RH, Franks PJ (2013) Smaller, faster stomata: scaling of stomatal size, rate of response, and stomatal conductance. *Journal of Experimental Botany* 64:495–505. <https://doi.org/10.1093/jxb/ers347>
- Ehrlinger J (1981) Leaf absorptances of Mohave and Sonoran desert plants. *Oecologia* 49:366–370. <https://doi.org/10.1007/BF00347600>
- Franks PJ (2006) Higher rates of leaf gas exchange are associated with higher leaf hydrodynamic pressure gradients. *Plant, Cell & Environment* 29:584–592. <https://doi.org/10.1111/j.1365-3040.2005.01434.x>
- Garcia RL, Long SP, Wall GW, Osborne CP, Kimball BA, Nie GY, Pinter PJ Jr, Lamorte RL, Wechsung F (1998) Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO₂ enrichment. *Plant, Cell & Environment* 21:659–669. <https://doi.org/10.1046/j.1365-3040.1998.00320.x>
- Gebauer R, Reynolds J, Tenhunen J (1998) Diurnal patterns of CO₂ and H₂O exchange of the Arctic sedges *Eriophorum angustifolium*

- and *E. vaginatum* (Cyperaceae). *American Journal of Botany* 85:592
- Guidi L, Piccolo EL, Landi M (2019) Chlorophyll Fluorescence, Photoinhibition and Abiotic Stress: Does it Make Any Difference the Fact to Be a C₃ or C₄ Species? *Frontiers in Plant Science* 10:1–11. <https://doi.org/10.3389/fpls.2019.00174>
- Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology* 16:2272–2286. <https://doi.org/10.1111/j.1365-2486.2009.02090.x>
- Hetherington AM, Woodward FI (2003) The role of stomata in sensing and driving environmental change. *Nature* 424:901–908. <https://doi.org/10.1038/nature01843>
- Hubbard RM, Rhoades CC, Elder K, Negron J (2013) Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *Forest Ecology and Management* 289:312–317. <https://doi.org/10.1016/j.foreco.2012.09.028>
- Ibáñez I, Primack RB, Miller-Rushing AJ, Ellwood E, Higuchi H, Lee SD, Kobori H, Silander JA (2010) Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B* 365:3247–3260. <https://doi.org/10.1098/rstb.2010.0120>
- Jackson RB, Sala OE, Field CB, Mooney HA (1994) CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* 98:257–262. <https://doi.org/10.1007/BF00324212>
- Jacob J, Greitner C, Drake BG (1995) Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and in situ carboxylase activity in *Scirpus olneyi* grown at elevated CO₂ in the field. *Plant, Cell & Environment* 18:875–884. <https://doi.org/10.1111/j.1365-3040.1995.tb00596.x>
- Jiahong LI, Erickson E, Peresta G, Drake BG (2009) Evapotranspiration and water use efficiency in a Chesapeake Bay wetland under carbon dioxide enrichment. *Global Change Biology* 16:234–245. <https://doi.org/10.1111/j.1365-2486.2009.01941.x>
- Jiang CD, Wang X, Gao H-Y, Shi L, Chow WS (2011) Systemic regulation of leaf anatomical structure, photosynthetic performance, and highlight tolerance in sorghum. *Plant Physiology* 155:1416–1424. <https://doi.org/10.1104/pp.111.172213>
- Kaiser E, Zhou D, Heuvelink E, Harbinson J, Morales A, Marcelis LFM (2017) Elevated CO₂ increases photosynthesis in fluctuating irradiance regardless of photosynthetic induction state. *Journal of Experimental Botany* 68:5629–5640. <https://doi.org/10.1093/jxb/erx357>
- Kangasjärvi S, Neukermans J, Li S, Aro E-M, Noctor G (2012) Photosynthesis, photorespiration, and light signalling in defence responses. *Journal of Experimental Botany* 63:1619–1636. <https://doi.org/10.1093/jxb/err402>
- Kato MC, Hikosaka K, Hirotsu N, Makino A, Hirose T (2003) The excess light energy that is neither utilized in photosynthesis nor dissipated by photoprotective mechanisms determines the rate of photoinactivation in photosystem II. *Plant Cell Physiology* 44:318–325. <https://doi.org/10.1093/pcp/pcg045>
- Kattge J, Knorr W (2007) Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell & Environment* 30:1176–1190. <https://doi.org/10.1111/j.1365-3040.2007.01690.x>
- Kattge J, Knorr W, Raddatz T, Wirth C (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* 15:976–991. <https://doi.org/10.1111/j.1365-2486.2008.01744.x>
- Killi D, Bussotti F, Raschi A, Haworth M (2017) Adaptation to high temperature mitigates the impact of water deficit during combined heat and drought stress in C₃ sunflower and C₄ maize varieties with contrasting drought tolerance. *Physiologia Plantarum* 159:130–147. <https://doi.org/10.1111/pp.12490>
- Kim SH, Sicher RC, Bae H, Gitz DC, Baker JT, Timlin DJ (2006) Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO₂ enrichment. *Global Change Biology* 12:588–600. <https://doi.org/10.1111/j.1365-2486.2006.01110.x>
- Kim HS, Oren R, Hinckley TM (2008) Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation. *Tree Physiology* 28:559–577. <https://doi.org/10.1093/treephys/28.4.559>
- Knapp AK (1993) Gas exchange dynamics in C₃ and C₄ grasses: consequences of differences in stomatal conductance. *Ecology* 74:113–123. <https://doi.org/10.2307/1939506>
- Knapp AK, Medina E (1999) Success of C₄ photosynthesis in the field: lessons from communities dominated by C₄ plants. In: Sage RF, Monson RK (eds) *C₄ plant biology*. Academic Press, San Diego, CA, pp 251–283
- Koch MS, Rawlik PS (1993) Transpiration and stomatal conductance of two wetland macrophytes (*Cladium jamaicense* and *Typha domingensis*) in the subtropical Everglades. *American Journal of Botany* 80:1146–1154. <https://doi.org/10.1002/j.1537-2197.1993.tb15346.x>
- Long SP (1999) Environmental responses. In: Sage RF, Monson RK (eds) *C₄ plant biology*. Academic Press, San Diego, CA, pp 215–249
- Long SP, Drake BG (1992) Photosynthetic CO₂ assimilation and rising atmospheric CO₂ concentrations. In: Baker NR, Thomas H (eds) *Topics in Photosynthesis*, vol 11. Elsevier, Amsterdam
- Long SP, Humphries S, Falkowshi PG (1994) Photoinhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology* 45:633–662. <https://doi.org/10.1146/annurev.pp.45.060194.003221>
- Lu Z, Zeiger E (1994) Selection for higher yields and heat resistance in Pima cotton has caused genetically determined changes in stomatal conductance. *Physiologia Plantarum* 92:273–278. <https://doi.org/10.1111/j.1399-3054.1994.tb05337.x>
- Luo Y, Gerten D, le Marie G et al (2008) Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14:1986–1999. <https://doi.org/10.1111/j.1365-2486.2008.01629.x>
- Mason RE, Craine JM, Lany NK, Jonard M, Ollinger SV, Groffman PM, Fulweiler RW, Angerer J, Read QD, Reich PB, Templer PH, Elmore AJ (2022) Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. *Science* 376: <https://doi.org/10.1126/science.abh3767>
- May JL, Hollister RD, Betway KR, Harris JA, Tweedie CE, Welker JM, Gould WA, Oberbauer SF (2020) NDVI Changes Show Warming Increases the Length of the Green Season at Tundra Communities in Northern Alaska: A Fine-Scale Analysis. *Frontiers in Plant Science* 11:1174. <https://doi.org/10.3389/fpls.2020.01174>
- McDonald EP, Erickson JE, Kruger EL (2002) Research note: can decreased transpiration limit plant nitrogen acquisition in elevated CO₂? *Functional Plant Biology* 29:1115–1120. <https://doi.org/10.1071/FP02007>

- Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, De Angelis P, Forstreuter M, Freeman M, Jackson SB, Kellomäki S, Laitat E, Rey A, Robertz P, Sigurdsson BD, Strassmeyer J, Wang K, Curtis PS, Jarvis PG (2001) Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytologist* 149:247–264. <https://doi.org/10.1046/j.1469-8137.2001.00028.x>
- Melis A (1999) Photosystem II damage and repair cycle in chloroplasts: what modulates the rate of photodamage in vivo? *Trends in Plant Science* 4:130–135. [https://doi.org/10.1016/S1360-1385\(99\)01387-4](https://doi.org/10.1016/S1360-1385(99)01387-4)
- Morison JLL, Lawlor DW (1999) Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell & Environment* 22:659–682. <https://doi.org/10.1046/j.1365-3040.1999.00443.x>
- Murata N, Takahashi S, Nishiyama S, Allakhverdiev SI (2007) Photoinhibition of photosystem II under environmental stress. *Biochimica Et Biophysica Acta* 1767:414–421. <https://doi.org/10.1016/j.bbabi.2006.11.019>
- Nishiyama Y, Murata N (2014) Revised scheme for the mechanism of photoinhibition and its application to enhance the abiotic stress tolerance of the photosynthetic machinery. *Applied Microbiology and Biotechnology* 98:8777–8796. <https://doi.org/10.1007/s00253-014-6020-0>
- Noyce GL, Kirwan ML, Rick RL, Megonigal JP (2019) Asynchronous nitrogen supply and demand produce nonlinear plant allocation responses to warming and elevated CO₂. *PNAS* 116:21623–21628. <https://doi.org/10.1073/pnas.1904990116>
- Öquist G, Chow WS, Anderson JM (1992) Photoinhibition of photosynthesis represents a mechanism for the long-term regulation of photosystem II. *Planta* 186:450–460. <https://doi.org/10.1007/BF00195327>
- Osmond CB, Winter K, Ziegler H (1982) Functional significance of different pathways of CO₂ fixation in photosynthesis. In: Lange OL, Nobel P, Osmond CB, Ziegler H (eds) *Encyclopedia of Plant Physiology*. Springer Verlag, Berlin, pp 479–547
- Owensby CE, Coyne PI, Ham JM, Auen LA, Knapp AK, (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications* 3:644–653. <https://doi.org/10.2307/1942097>
- Perez-Martin A, Flexas J, Ribas-Carbó M, Bota J, Tomás M, Infante JM, Diaz-Espejo A (2009) Interactive effects of soil water deficit and air vapour pressure deficit on mesophyll conductance to CO₂ in *Vitis vinifera* and *Olea europaea*. *Journal of Experimental Botany* 60:2391–2405. <https://doi.org/10.1093/jxb/erp145>
- Piedade MTF, Long SP, Junk WJ (1994) Leaf and canopy photosynthetic CO₂ uptake of a stand of *Echinochloa polystachya* on the Central Amazon floodplain. *Oecologia* 97:193–201. <https://doi.org/10.1007/BF00323149>
- Polley HW, Johnson HB, Tischler CR, Torbert HA (1999) Links between transpiration and plant nitrogen: variation with atmospheric CO₂ concentration and nitrogen availability. *International Journal of Plant Sciences* 160:535–542. <https://doi.org/10.1086/314145>
- Posch S, Bennett LT (2009) Photosynthesis, photochemistry and anti-oxidative defence in response to two drought severities and with re-watering in *Allocasuarina luehmannii*. *Plant Biology* 11:83–93. <https://doi.org/10.1111/j.1438-8677.2009.00245.x>
- Rascher U, Liebig M, Lüttge U (2000) Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. *Plant, Cell and Environment* 23:1397–1405. <https://doi.org/10.1046/j.1365-3040.2000.00650.x>
- Reich PB, Sendall KM, Stefanski A, Rich RL, Hobbie SE, Montgomery RA (2018) Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature* 562:263–267. <https://doi.org/10.1038/s41586-018-0582-4>
- Ripley BS, Gilbert ME, Ibrahim DG, Osborne CP (2007) Drought constraints on C₄ photosynthesis: stomatal and metabolic limitations in C₃ and C₄ subspecies of *Alloteropsis semialata*. *Journal of Experimental Botany* 58:1351–1363. <https://doi.org/10.1093/jxb/erl302>
- Ripley B, Frole K, Gilbert M (2010) Differences in drought sensitivities and photosynthetic limitations between co-occurring C₃ and C₄ Panicoid grasses. *Annals of Botany* 105:493–503. <https://doi.org/10.1093/aob/mcp307>
- Romanowska E, Buczyńska A, Wasilewska W, Krupnik T, Drózak A, Rogowski P et al (2017) Differences in photosynthetic responses of NADPME type C₄ species to high light. *Planta* 245:641–657. <https://doi.org/10.1007/s00425-016-2632-1>
- Sage RF (1994) Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective. *Photosynth Research* 39:351–368. <https://doi.org/10.1007/BF00014591>
- Sage RF, Cowling SA (1999) Implications of stress in low CO₂ atmospheres of the past: are today's plants too conservative for a high CO₂ world? In: Mooney HA (ed) Luo Y. *Carbon Dioxide and Environmental Stress* Academic Press, San Diego, CA pp, pp 289–308
- Sage RF, Li M, Monson R, The taxonomic distribution of C₄ photosynthesis (1999). In: Sage RF, Monson RK (eds) *C₄ plant biology*. Academic Press, San Diego, CA, pp 551–584
- Schreiber U, Bilger W (1993) Progress in chlorophyll fluorescence research: major developments during the past years in retrospect. *Progress in Botany* 54:151–173. https://doi.org/10.1007/978-3-642-78020-2_8
- Šigut L, Holišová P, Klem K, Šprtová M, Calfapietra C, Marek MV, Špunda V, Urban O (2015) Does long-term cultivation of saplings under elevated CO₂ concentration influence their photosynthetic response to temperature? *Annals of Botany* 116:929–939. <https://doi.org/10.1093/aob/mcv043>
- Slot M, Winter K (2017) In situ temperature relationships of biochemical and stomatal controls of photosynthesis in four lowland tropical tree species. *Plant, Cell, & Environment* 40:3055–3068. <https://doi.org/10.1111/pce.13071>
- Stitt M (1991) Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell & Environment* 14:741–762. <https://doi.org/10.1111/j.1365-3040.1991.tb01440.x>
- Taylor SH, Ripley BS, Woodward FI, Osborne CP (2011) Drought limitation of photosynthesis differs between C₃ and C₄ grass species in a comparative experiment. *Plant, Cell & Environment* 34:65–75. <https://doi.org/10.1111/j.1365-3040.2010.02226.x>
- Taylor SH, Ripley BS, Martin T, De-Wet L, Woodward FI, Osborne CP (2014) Physiological advantages of C₄ grasses in the field: a comparative experiment demonstrating the importance of drought. *Global Change Biology* 20:1992–2003. <https://doi.org/10.1111/gcb.12498>
- Tikkanen M, Mekala NR, Aro EM (2014) Photosystem II photoinhibition-repair cycle protects photosystem I from irreversible damage. *Biochimica et Biophysica Acta* 1837:210–215. <https://doi.org/10.1016/j.bbabi.2013.10.001>
- Vahsen ML, Blum MJ, Megonigal JP, Emrich SJ, Holmquist JR, Stiller B, Todd-Brown KEO, Mclauchlan JS (2023) Rapid plant trait evolution can alter coastal wetland resilience to sea level rise. *Science* 379:393–398. <https://doi.org/10.1126/science.abq0595>

- Volk M, Niklaus PA, Körner C (2000) Soil moisture effects CO₂ responses of grassland species. *Oecologia* 125:380–388. <https://doi.org/10.1007/s004420000454>
- Ward SJE, Midgley GF, Stock WD (2001) Growth responses to elevated CO₂ in NADP-ME, NAD-ME and PCK C₄ grasses and a C₃ grass from South Africa. *Functional Plant Biology* 28:13–25. <https://doi.org/10.1071/PP99104>
- Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta* 218:1–14. <https://doi.org/10.1007/s00425-003-1105-5>
- Ward JK, Strain BR (1999) Elevated CO₂ studies: past, present and future. *Tree Physiology* 19:211–220. <https://doi.org/10.1093/treephys/19.4-5.211>
- Warren JM, Norby RJ, Wullschlegel SD (2011) Elevated CO₂ enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiology* 31:117–130. <https://doi.org/10.1093/treephys/tpr002>
- Wilschut RA, De Long JR, Geisen S, Hannula SE, Quist CW, Snoek B, Steinauer K, Wubs ERJ, Yang Q, Thakur MP (2022) Combined effects of warming and drought on plant biomass depend on plant woodiness and community type: a meta-analysis. *Proceedings of the Royal Society B* 289: <https://doi.org/10.1098/rspb.2022.1178>
- Wong SL, Chen CW, My H, Weng JH (2014) Relationship between photosynthetic CO₂ uptake rate and electron transport rate in two C₄ perennial grasses under different nitrogen fertilization, light and temperature conditions. *Acta Physiologiae Plantarum* 36:849–857. <https://doi.org/10.1007/s11738-013-1463-y>
- Xu Z, Shimizu H, Yagasaki Y, Ito S, Zheng Y, Zhou G (2013) Interactive Effects of Elevated CO₂, Drought, and Warming on Plants. *Journal of Plant Growth Regulation* 32: <https://doi.org/10.1007/s00344-013-9337-5>
- Yang XQ, Zhang QS, Zhang D, Sheng ZT (2017) Light intensity dependent photosynthetic electron transport in eelgrass (*Zostera marina* L.). *Plant Physiological Biochemistry* 113:168–176. <https://doi.org/10.1016/j.plaphy.2017.02.011>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.