



Physiological Advantages for Dominant Dune Species with Climate Warming

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Abstract

Sand dunes are important barriers to the coastal interior and provide habitat for numerous organisms. Species composition influences the shape and size of dunes, yet recent studies have documented changes in range of native species and increased abundance of invasive species. Warming temperatures are attributed to changes in plant species distributions, yet the effects of varying temperature on the physiology of dominant dune grasses in the southeast US are largely unknown. We characterized how the temperature and light environments affected the physiology of dominant species differing in photosynthetic pathways and compared to field values. Species physiological responses were not fully explained by differences in photosynthetic pathways. *Carex kobomugi* (invasive C3) exhibited the highest rates of photosynthesis, stomatal conductance (GSW), and electron transport rate (ETR) at 20 to 40 °C compared to native species. Physiology of *Ammophila breviligulata* (native C3) was negatively impacted at high temperatures, potentially impacting future range distributions, whereas physiological performance was reduced at 25 °C and below in *Panicum amarum* (native C4). In contrast, *Uniola paniculata* (native C4) exhibited similar photosynthetic rates to *A. breviligulata* at most temperatures. These results demonstrate that temperature differentially impacts species physiology and may impact future range distributions with climate warming.

Keywords Dune grass physiology · *Carex kobomugi* · Photosynthetic pathway · Warm season grasses

Introduction

Despite the limited spatial scale of occurrence, dunes are disproportionately valuable as a forefront ecosystem protecting important economic and natural systems (e.g., salt marshes, forests, estuaries) that are vulnerable to rising sea-level, storms, and saltwater intrusion (Barbier et al. 2011; Feagin et al. 2015; Sigren et al. 2018; Innocenti et al. 2021). Coastal sand dunes act as protection for the interior infrastructure (Sigren et al. 2018). Dune formation from sand accretions supports a positive feedback between sediment movement and vegetation (Godfrey and Godfrey 1976; Hesp 1988, 1989); dune formation and erosion relies heavily on the type of vegetation present (Stallins and Parker 2003; Feagin et al. 2015; Maximiliano-Cordova et al. 2019;

Riffe et al. in review). Dune shape and size is determined by the species present and the resulting morphology (Hacker et al. 2019; Jay et al. 2022; Riffe et al. in review) and these species are considered ecosystem engineers.

Warming climate results in range expansion of southern species and contraction of northern species (Channell and Lomolino 2001; Goldstein et al. 2018). There is limited understanding of how dominant dune grasses respond to temperature shifts associated with climate change which will affect future species distributions and dune dynamics along the Virginia coastline. Changes in dune species ranges can impact dune shape and size with ecosystem consequences (Sabo et al. 2024). Non-native species have a greater invasion probability due to climate change and land use change (McKinney and Lockwood 1999; Dukes and Mooney 1999). Invasive species, many of which are ecosystem engineers, have been known to affect the geomorphology of the landscape (Fei et al. 2014). For example, *Carex kobomugi* was accidentally introduced in New Jersey in the early 1900's where it quickly spread south and it was also occasionally used in dune plantings (Small 1954).

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This species is shorter and prostrate than many native dune grasses (Riffe and Zinnert 2024), leading to unique dune morphology. Understanding plant physiological response to abiotic factors allows us to predict species distributions with future climate scenarios (Wang et al. 2015; Heilmeier 2019).

Dominant dune building grasses along the US mid-Atlantic coast include two C4 grasses, *Uniola paniculata* and *Panicum amarum* and a C3 grass, *Ammophila breviligulata* (hereafter referred to by genus). Previous research identified these as the dominant dune species in Virginia (Back Bay National Wildlife Refuge, Riffe and Zinnert 2024) along with the C3 invasive sedge, *Carex kobomugi* (hereafter referred to by genus). *Ammophila* dominates in Virginia and north while *Uniola* is more abundant in North Carolina and south, however *Uniola* has been documented to move further north as the region continues to warm with fewer extreme freezing temperatures (Goldstein et al. 2018; Huang et al. 2018). These species constrain dune shapes and sizes through morphological differences in the rhizome length between clonal individuals, stem density, and plant height (Jay et al. 2022; Riffe et al. in review). *Uniola* initially forms a “hummock” style dune before coalescing (Goldstein et al. 2017), while *Ammophila* quickly builds lateral dune ridges (Woodhouse et al. 1977). *Uniola* is a known competitor with *Ammophila* (Harris et al. 2017; Brown et al. 2018). These native species also compete with the invasive *Carex* in the US mid-Atlantic region (Charbonneau et al. 2020; Riffe and Zinnert 2024). In New Jersey, *Carex* cover doubled in 10 years after invading previously *Ammophila* vegetated habitat following a storm event (Charbonneau et al. 2020). In Virginia, *Carex* and *Uniola* reduce the distribution of *Ammophila* across the dune. As the region continues to warm (Huang et al. 2018), quantifying the physiological responses of dominant dune species to temperature can help predict how variations in climate will impact success and growth of C3 and C4 species.

Literature documenting physiological responses of these species to variations in light and temperature is limited, and *Carex* physiology data exists exclusively for the native range. Studies investigating the effect of salinity flooding concluded that *Ammophila* is the least salt tolerant species of the dominant dune grasses, when compared to *Spartina patens*, *Uniola paniculata*, and *Panicum amarum* var. *amarulum* (Seneca 1969). Temperature studies on germination of *Ammophila*, *Panicum*, and *Uniola* indicated ecotypic variation in germination requirements, where seeds collected from southern sites did not need a cold treatment, while northern seeds required one (Seneca and Cooper 1971; Seneca 1972). Seeds of *Ammophila* from North Carolina could withstand higher temperatures than seeds from Michigan (Seneca and Cooper 1971). *Panicum amarum*

var. *amarum* is sterile from seed (Seneca et al. 1976; Woodhouse et al. 1977), however the varietal *Panicum amarum* var. *amarulum* has viable seeds (Seneca et al. 1972; Palmer 1975; Seneca et al. 1976). Studies of *Carex* in the native coastal habitat of China, Korea, Japan, and Taiwan have documented highest rates of photosynthesis and stomatal conductance at 25 °C than any other temperature and low water use efficiency (Ishikawa et al. 1990; Hwang and Choo 2017). No physiology studies have been conducted on *Carex* in the North American invasive range.

To understand how these species will respond to a changing climate, we quantified physiological responses (i.e., photosynthesis, stomatal conductance, electron transport rate, water use efficiency, etc.) to light (0–2000 PAR $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and temperature (20–40 °C) for *Ammophila*, *Carex*, *Panicum*, and *Uniola* in growth chamber experiments and through field sampling. Quantifying limitations to photosynthesis under different temperature regimes can help predict future success and growth of these species with climate fluctuations. We expected to observe higher rates of photosynthesis and stomatal conductance with lower water use efficiency for C3 species (*Ammophila* and *Carex*) at lower temperatures than for C4 species (*Panicum* and *Uniola*); however, at 30 °C and above, we expected C4 species to have higher photosynthetic rates with higher water use efficiency than C3 species. Electron transport rate was expected to be higher in C4 species than in C3 species. Previous research found that dark respiration (R_d) is not controlled by photosynthetic pathway (Byrd et al. 1992), and we expected no significant differences.

Methods

Study Species

Ammophila breviligulata, *Uniola paniculata*, *Panicum amarum* var. *amarum*, and *Carex kobomugi* are perennial dune graminoids that were used for this project. These were the top four dominant species at Back Bay National Wildlife Refuge, Virginia Beach, VA according to a recent vegetation survey from 2020 (Riffe and Zinnert 2024) and all native species are dominant along much of the mid-Atlantic coast (Hacker et al. 2019). *Ammophila* and *Uniola* were sourced from local nurseries, Pinelands Nursery & Supply (Columbus, NJ) and Coastal Transplants (Bolivia, NC), respectively in March 2022 as 2-inch plugs. *Panicum* and *Carex* were collected from Back Bay National Wildlife Refuge. *Panicum* was collected and not purchased due to concerns about sourcing the correct sub-species (i.e., co-occurring *Panicum amarum* var. *amarulum*; Palmer 1975). Because *Carex* is an invasive species it is not commercially available for sale

and had to be collected. Mean annual temperature in the region is 15.3 °C, mean maximum temperature is 39.7 °C and mean minimum temperature is − 8.8 °C (Wood et al. 2024). During the growing season (from May to September), maximum temperatures in the region reach ≥ 20 °C and minimum temperatures ≥ 10 °C (Zinnert et al. 2011).

Growth Chamber Environment

Plants of similar sizes were potted with two individuals in a 3.8 L pot for both purchased and field collected species. Pots were filled with a 50:50 mix of sand collected from Hog Island, Virginia with commercially available play sand that was sifted to remove larger grain sizes that were not found in the Hog Island sand. Each pot was placed in plastic watering trays which were filled three times a week throughout the experiment to mimic access to groundwater. Plants were stored in the Virginia Commonwealth University greenhouse until the experiments began. Plants were grown in a Conviron growth chamber (Model E15, Conviron, Winnipeg, Manitoba) under a photosynthetically active radiation (PAR) of approximately $1000 \text{ mmol m}^{-2} \text{ s}^{-1}$, 48% relative humidity, a photoperiod of 12 h. During the day, temperatures were set to the experimental temperature, starting at 20 °C. At night, the temperature was 10 °C lower than the experimental temperature to simulate diurnal temperatures. Experimental temperatures were increased five degrees every two weeks, starting at 20 °C and ending at 40 °C.

Physiological Measurements

After plants had acclimated for 2 weeks at the target temperature, each plant ($n=10$) was measured at that temperature using a Li-6400XT portable gas exchange system (Licor, Lincoln, NE). At each temperature we collected photosynthesis rates (A), stomatal conductance (GSW), and transpiration rates (E), and electron transport rate (ETR). Light and fluorescence curves were measured for each plant at 25 °C and 35 °C. For these curves, the CO_2 was set to 400 ppm, and the flow rate to $1000 \text{ } \mu\text{mol s}^{-1}$. Photosynthetic light curves were completed from a range of 0 to $2000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ($n=10$) using the Li-6400XT (Licor; Lincoln, NE) at two temperatures (25 and 35 °C) for each species. Fluorescence curves were used to collect the quantum yield of photosystem II (ΦPSII also known as $\Delta F/F_m'$). *Panicum* was unable to photosynthesize at 25 °C and was removed from further analysis. Using photosynthetic data WUE (water use efficiency), AQY (apparent quantum yield), LCP (light compensation point), LSP (light saturation point), and R_d (dark respiration) were calculated.

$$\text{WUE} = A_{\text{net}}/E \quad (1)$$

WUE, Water Use Efficiency. A_{net} , Net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). E, Transpiration rate ($\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)

$$\text{AQY} = (y_2 - y_1) / (x_2 - x_1) \quad (2)$$

AQY, Apparent Quantum Yield, the slope of the light limiting portion of the light curve. Here PAR 0–500 was used. x_2 , 500 ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). x_1 , 0 ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)

$$\text{LCP} = -(b/m) \quad (3)$$

LCP, Light Compensation Point, the light level when net photosynthesis is 0. b, y-intercept (dark respiration point). m, slope of the curve where it meets the x-axis ($y=0$)

$$\text{LSP} = (y - b) / m \quad (4)$$

LSP, Light Saturation point, the light intensity that maximizes photosynthesis. y (A_{net}) = 97% of A_{max} . b, y-intercept (dark respiration point). m, slope of the curve where it meets the x-axis ($y=0$).

Field Comparisons

The field comparison measurements were completed at Back Bay National Wildlife Refuge in Virginia Beach, VA. The northernmost mile (1.6 km) of the refuge is not open for public access and was the focus of field data collected in this study. All species were measured on the face of the fore-dune. Measurements were completed on days where cloud cover was low, during full sun, 11 am–2 pm. To capture seasonal differences, measurements were performed in April, June, August, and October 2023.

Using a Li-600 (Licor, Lincoln, NE) porometer and fluorometer, measurements were taken at midday on sunny days with minimal to no cloud cover. All four dune species (*Ammophila breviligulata*, *Uniola paniculata*, *Carex kobomugi*, and *Panicum amarum*) were included ($n=15$), replications included one plant from each species, which was repeated 15 times. This method was used to account for time of day on the plant. Individual plants were not repeated on a single day and were chosen at random. This instrument measures stomatal conductance and fluorescence of the leaf, allowing for comparison to the growth chamber.

Statistical Methods

Light curves were analyzed using repeated measures ANOVA with species and light levels (PAR) as factors. *Panicum* was removed from light curve analyses at 25 °C due to the plants respiring at all light levels. Temperature curves

were analyzed using repeated measures ANOVA with species and temperature as factors. Pairwise comparisons using a Bonferonni adjustment were used for post-hoc analyses of repeated measures ANOVA. Light curve metrics (AQY, LCP, RD, LSP, $A_{\max}$) analyzed using one-way ANOVA or Kruskal–Wallis when variances were unequal, with species as the factor. Data were analyzed separately at 25 °C and 35 °C, except for the light curve metrics for *Ammophila*, *Carex*, and *Uniola* which were analyzed with a t-test or Wilcoxon test when variances were unequal. Regressions of A_{net} and GSW included data at 1500 and 2000 PAR, separated by temperature. Field measurements were analyzed using 2-way ANOVA with month and species as factors, and blocked by time of day. Post-hoc analysis for 2-way ANOVA was done with a Tukey test. All analyses and visualizations were completed in R (R studio 4.1.0).

Results

Maximum photosynthesis rates obtained from light curves at 25 °C and 35 °C did not significantly differ among *Carex*, *Ammophila*, and *Uniola* (25 °C, $X^2=2.77$, $p=0.25$; 35 °C, $X^2=5.25$, $p=0.15$; Tables S1–S3). *Ammophila* had significantly higher $A_{\max}$ at 25 °C ($5.05 \pm 0.46 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than 35 °C ($2.83 \pm 0.51 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $p=0.02$; Table 1). *Carex* and *Uniola* had no significant differences in $A_{\max}$ between the two temperatures. Dark respiration rates (R_d) and light saturation points (LSP) did not differ by photosynthetic pathways, but species differences were observed. R_d rates were 69% higher for *Panicum* ($-1.35 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than *Ammophila* ($-1.97 \pm 0.20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 35 °C. Light compensation point (LCP) was lower in *Uniola* than *Ammophila* at 25 °C ($X^2=6.79$, $p=0.03$, Table 1). LSP at 25 °C was 78% lower for *Uniola* ($1350 \pm 89 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) than *Ammophila* ($1738 \pm 97 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Table 1).

Species differences were observed for stomatal conductance (GSW), electron transport rate (ETR), and the quantum yield of photosystem II (Φ_{PSII}). GSW was significantly higher for *Carex* at all light levels relative to all other species at 25 °C (Interaction, $F=2.78$, $p=0.001$; Table S4), except *Ammophila* at 2000 PAR (Table S5). There were no significant differences in GSW for *Ammophila* and *Uniola* at 25 °C. At 35 °C there was no significant interaction for GSW ($F=1.12$, $p=0.32$; Table S6), but the main effect of species was significant ($F=5.91$, $p=0.002$; Table S6) with *Carex* exhibiting higher rates than the other species (Table S6). GSW rates were similar in *Ammophila* to both C4 species (*Uniola* and *Panicum*). *Ammophila* and *Carex* had two times higher ETR at both temperatures (25 °C, Interaction: $F=19.83$, $p<0.0001$; 35 °C, Interaction: $F=12.44$, $p<0.0001$; Tables S7–S10) which is expected of C3 species. No differences occurred between *Ammophila* and *Carex* or *Panicum* and *Uniola*. Φ_{PSII} was also higher for *Carex* and *Ammophila* than *Uniola* at both temperatures and *Panicum* at 35 °C (25 °C, Interaction: $F=5.38$, $p<0.0001$; 35 °C, Interaction: $F=4.03$, $p<0.001$; Fig. 1; Tables S11–S14).

Temperature curves resulted in several species and temperature interactions for A_{net} (Interaction: $F=9.73$; $p<0.0001$; Fig. 2; Tables S15, S16), GSW (Interaction: $F=5.09$; $p<0.0001$; Tables S17, S18), and E (Interaction: $F=10.05$; $p<0.0001$; Tables S19, S20). However, there were no species differences for WUE due to the variation (Table S21). Overall, *Carex* had the highest A_{net} , GSW, and transpiration (E) rates. *Ammophila* (3.39 ± 0.35) had significantly higher photosynthetic rates than *Uniola* ($0.39 \pm 0.22 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 20 °C and *Panicum* at 20 to 25 °C. A_{net} was near 0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Panicum* at all temperatures except 30 °C ($3.29 \pm 0.78 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and 35 °C ($4.49 \pm 3.33 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) indicating a narrow temperature tolerance. GSW and E were significantly higher for *Ammophila* and *Uniola* at temperatures 20 to 35 °C (Fig. 2), *Panicum* GSW rates were near 0 at all temperatures except 30 and 35 °C (Fig. 2; Table S3d). A_{net} and GSW

Table 1 Means and standard errors for physiological metrics for each species at two temperatures, 25 °C and 35 °C, data calculated from light curves

Physiology metrics	Temp (°C)	<i>Ammophila</i>	<i>Carex</i>	<i>Panicum</i>	<i>Uniola</i>
Maximum photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	25	5.05 ± 0.46^B	6.22 ± 0.37	NA	5.33 ± 0.78
	35	2.83 ± 0.51^A	4.73 ± 0.61	4.05 ± 1.06	4.25 ± 0.64
Dark respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	25	−1.57 ± 0.16	−1.87 ± 0.25	NA	−1.25 ± 0.20
	35	−1.97 ± 0.20 ^a	−1.71 ± 0.13 ^{ab}	−1.35 ± 0.09 ^b	−1.78 ± 0.13 ^{ab}
Apparent quantum yield	25	0.009 ± 0.001	0.011 ± 0.0003	NA	0.010 ± 0.001
	35	0.008 ± 0.001	0.008 ± 0.001	0.008 ± 0.001	0.010 ± 0.001
Light compensation point ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	25	83.74 ± 8.94^a	101.10 ± 24.40^{ab}	NA	56.29 ± 5.20^b
	35	138.42 ± 31.72	115.08 ± 22.52	97.45 ± 22.28	97.64 ± 15.13
Light saturation point ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	25	1738 ± 97^b	1594 ± 59^{ab}	NA	1350 ± 89^a
	35	1374 ± 159	1776 ± 63	1344 ± 164	1320 ± 180

Lower case letter codes indicate a significant difference among species at a given temperature resulting from a one-way ANOVA. Uppercase letter codes indicate significant differences between temperatures within a species based on t-tests

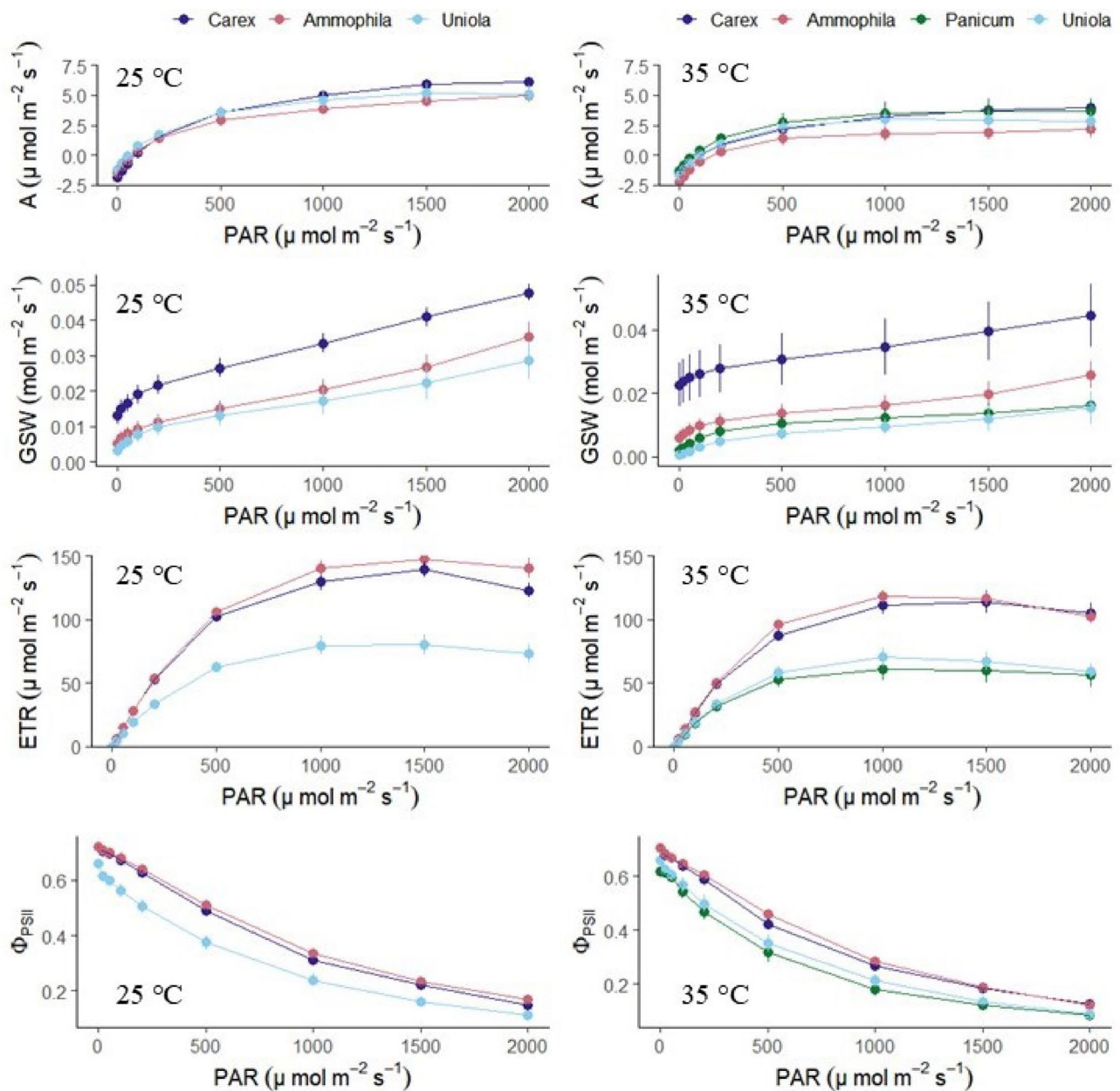


Fig. 1 Light Curves at 25 °C (left side) and 35 °C (right side) with net photosynthesis (A), stomatal conductance (GSW), electron transport rate (ETR), and the quantum yield of photosystem II (Φ_{PSII}) as the response variables from top to bottom. The independent variable is

photosynthetically active radiation (PAR), the light level. Color coded by species, points are means and error bars are standard error. Full repeated measures ANOVA results are in the supplement

were positively linearly related for all species at high light (1500–2000 PAR) at 25 and 35 °C (Fig. 3). The slope for *Panicum* was higher than other species (Fig. 3). A_{net} and ETR were not related in *Carex* at 25 °C, but were positively linearly related for all species at 35 °C (Fig. 4). At 35 °C the relationship was weaker for *Ammophila* ($R^2=0.22$) than at 25 °C ($R^2=0.44$).

Results from the field experiment indicated several species differences in physiology. *Carex* had significantly higher

ETR (Species effect: $F=8.67$; $p<0.0001$; Fig. 4; Tables S22, S23) and Φ_{PSII} (Species effect: $F=5.68$; $p=0.001$; Tables S24, S25) than *Ammophila* and *Panicum*, but not different from *Uniola*. There was a significant interaction GSW (Interaction: $F=2.03$, $p=0.04$; Table S26). *Carex* GSW was significantly higher than *Panicum* in all months, and higher than *Ammophila* and *Uniola* during October (Species effect: $F=29.66$; $p<0.0001$; Table S27). E rates were 1.5 to 2 times higher in *Carex* and differed significantly among species

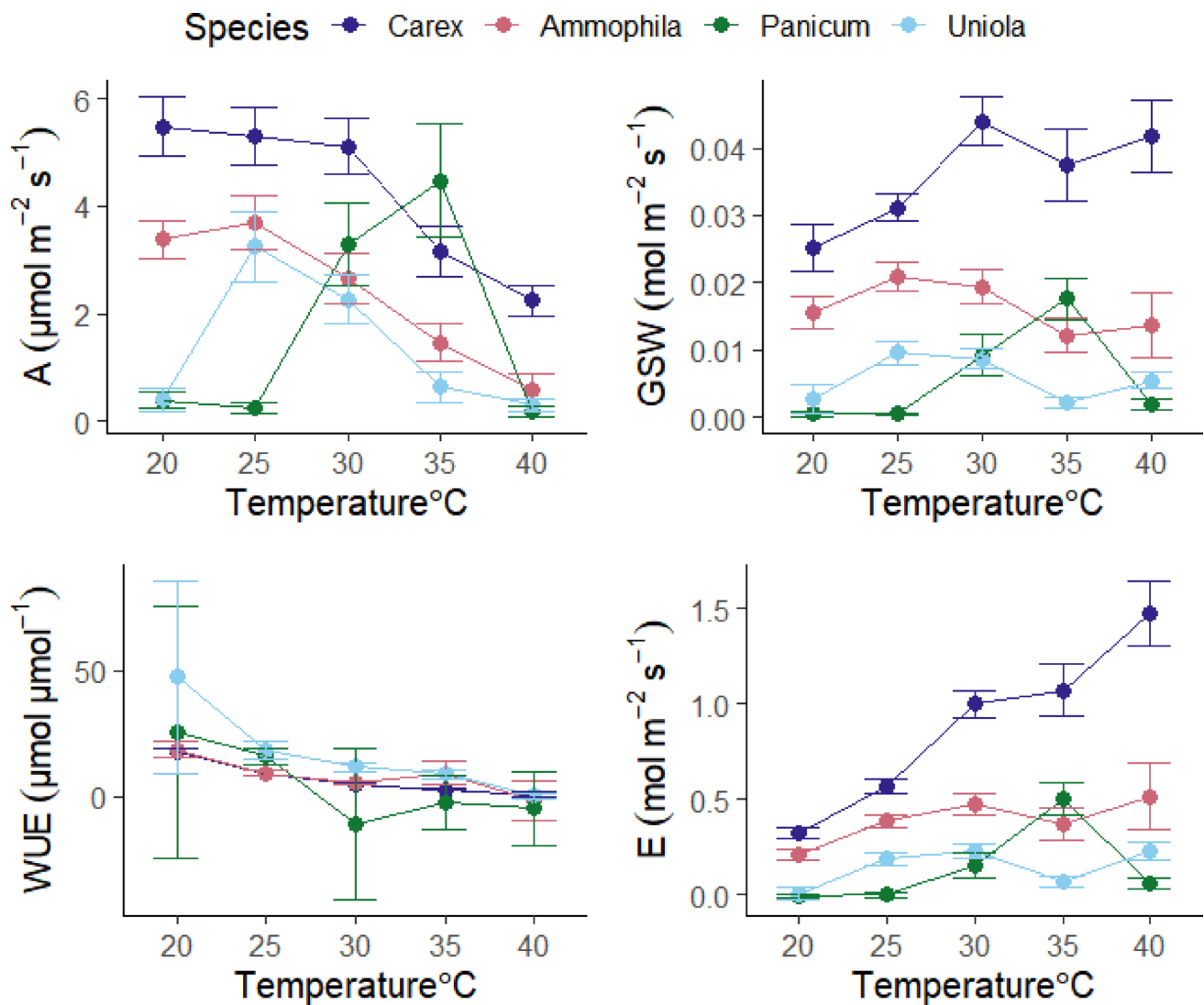


Fig. 2 Temperature curves with net photosynthesis (A), stomatal conductance (GSW), water use efficiency (WUE), and electron transport rate (ETR). Color coded by species, points are means and error bars are standard error. ANOVA tables can be found in the supplement

(Species effect: $F=32.22$; $p<0.0001$; Table S28), except for *Ammophila* and *Uniola* which had similar transpiration rates (Table S29). E was lowest in *Panicum*.

Discussion

Species differences occurred in several physiological responses, most notable across temperatures, and were not always separated based on photosynthetic pathways. *Carex* (invasive C3) exhibited the highest rates of A_{net} , GSW, and E across temperatures from both lab and field measurements. Interestingly, high GSW and E rates did not result in lower WUE for *Carex*. There were no significant differences among species in WUE at any temperatures. *Panicum* (native C4) had consistently low rates of A_{net} , GSW, and E

at all temperatures except 30 and 35 °C, indicating a narrow thermal optimum window. Surprisingly, *Ammophila* (native C3) and *Uniola* (native C4) exhibited many physiological similarities at most temperatures, although LCP and LSP were lower in *Uniola* and ETR was higher in *Ammophila*. A_{max} obtained from light curves did not differ among species, however *Ammophila* had lower A_{max} at 35 °C compared to 25 °C which may result in growth limitations at high temperatures.

Photosynthetic Pathway

Although many physiological responses were not explained by photosynthetic pathways, a few measurements were consistent with C3 vs. C4 expectations. For example, ETR and Φ_{PSII} were significantly higher in C3 than C4 species

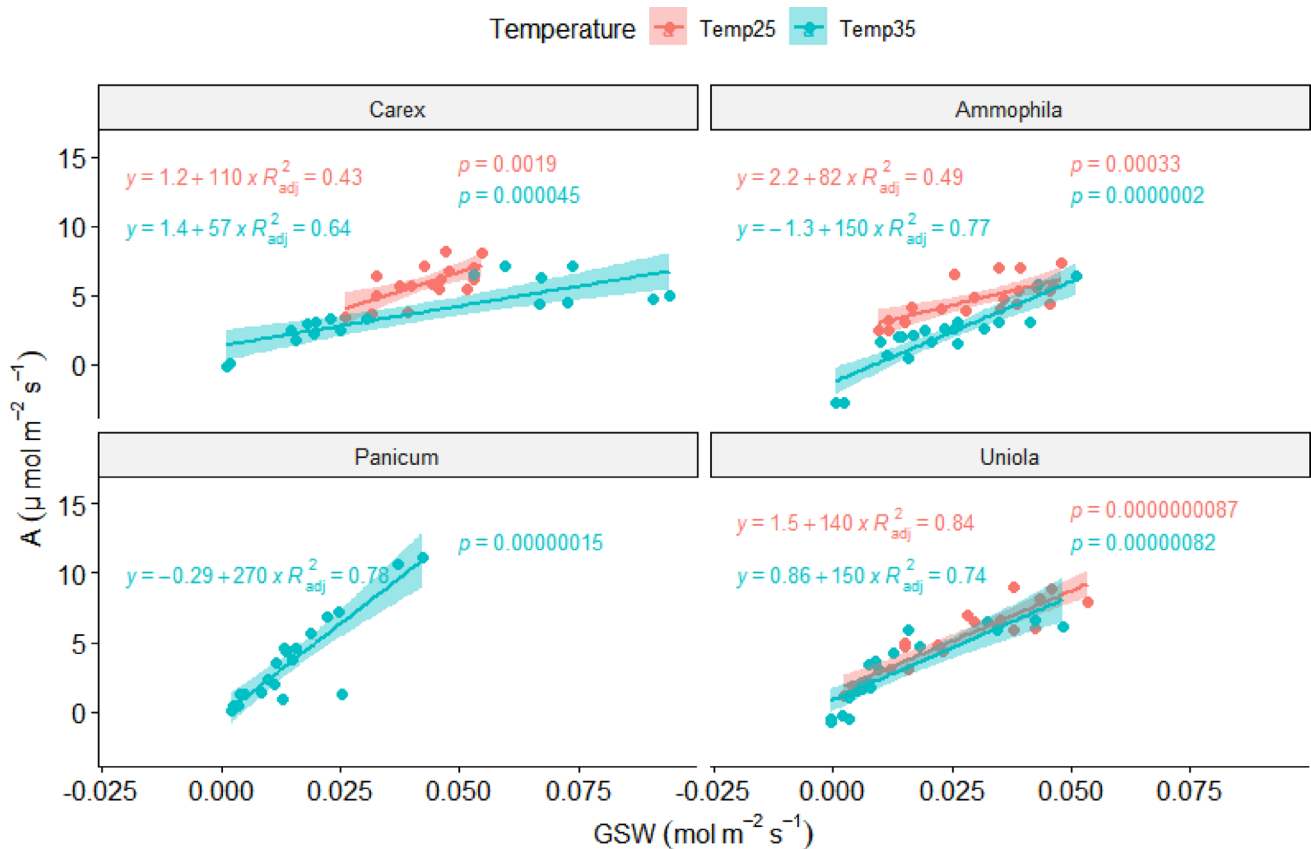


Fig. 3 Regressions of photosynthesis (A) and stomatal conductance (GSW) at high light (1500–2000 PAR), color coded by growing temperature

at multiple light levels. ETR was not a limiting factor for photosynthesis in C3 or C4 species. Although C3 species are less photosynthetically efficient than C4 species due to increased photorespiration, high rates of ETR in *Ammophila* and *Carex* likely contributed to the high rates of A_{net} observed in these C3 species. GSW rates were lower in C4 species because they are more photosynthetically efficient (Wang et al. 2015). WUE was not lower in C3 species as expected, and there was high variation among all species. C4 species are known to be physiologically prepared for hot and dry climate conditions but can also thrive in a variety of conditions (Watcharamonkol et al. 2018). Here we found that *Panicum* and *Uniola* were physiologically active at different temperatures. *Panicum* A_{net} was near 0 μmol CO₂ m⁻² s⁻¹ below 30 °C and peaked at 35 °C, while *Uniola* A_{net} peaked at 25 °C, similar to *Ammophila*. These species will likely respond differently to a warming climate. Phylogeny plays an important role in understanding the physiological responses of C4 species (Taylor et al. 2010) and may explain differences observed in this study.

Species Specific Physiology

These results indicate varying levels of plasticity among species. Correlations between A_{net} and GSW indicate stomatal conductance regulates photosynthesis for all species regardless of photosynthetic pathway. We observed higher A_{max} in *Ammophila* at 25 °C compared to 35 °C, which has implications for restoration projects, distributions across the dune, and habitat range along the southeast US with warming climate. Previous studies at Back Bay National Wildlife Refuge have noted declines in abundance and performance of *Ammophila* (Woods et al. 2023; Riffe and Zinnert 2024). *Ammophila* is widely planted in Virginia and North Carolina, but survival and growth may be limited if temperatures continue to warm in the region as has been historically noted (Huang et al. 2018). Although ETR was higher for *Ammophila* relative to C4 plants in our experimental study, these results were not observed in the field where plants are exposed to multiple abiotic and biotic stressors. In our environmental chamber study, plants were regularly watered, whereas in the field, dune faces tend to have low soil moisture during the summer (Fischman et al. 2019; Zinnert, unpublished data). High variation in WUE resulted in no significant differences among species and temperatures,

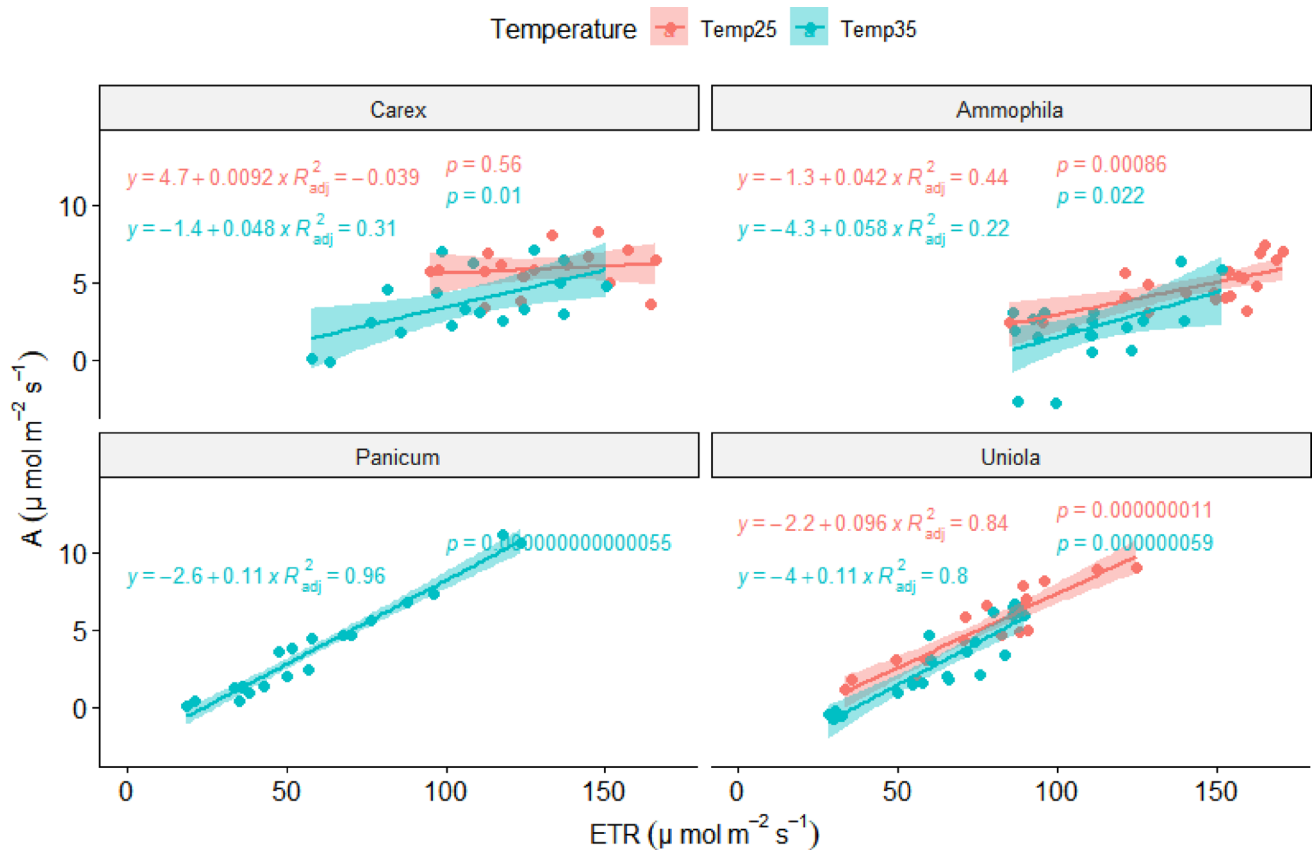


Fig. 4 Regressions of photosynthesis (A) and electron transport rate (ETR) at high light (1500–2000 PAR), color coded by growing temperature

making it difficult to assess the contribution of how these species will respond to concurrent increases or decreases in precipitation and water availability. Further studies investigating drought and flooding impacts to the physiology of these dominant dune grasses will enhance robust projections of future climate scenarios.

Panicum has a narrow temperature optimum window and cannot grow at low temperatures. It tends to be the last species to green up on the dunes (Riffe, personal observation). This study found that *Panicum* is unable to photosynthesize at temperatures 25 °C and below, indicating that it has likely adapted to a shorter growing season (Seneca et al. 1976). In the US mid-Atlantic region, *Panicum* exhibits a shorter growth form relative to other co-occurring species (Walker and Zinnert 2022; Riffe and Zinnert 2024) and relative to *Panicum* that grows further south (Fischman et al. 2024). Cooler temperatures in the US mid-Atlantic region compared to the southeastern US may limit *Panicum* growth due to photosynthetic temperature limitation observed in this study. However, at 35 °C *Panicum* had high rates of photosynthesis. As climate warms, *Panicum* may increase dominance at higher latitudes as observed at sites in Virginia (Sabo et al. 2024). *Panicum* has been found to increase growth when co-planted with *Uniola* (Sciolino 2024), and

vice versa (Fischman et al. 2024). Along the Florida coast, *Panicum* has been described as a pioneer species, increasing species richness when planted (Fischman et al. 2024).

Compared to *Panicum*, *Uniola* was capable of photosynthesizing at lower temperatures and exhibited similar rates across most temperatures as *Ammophila*. *Uniola* is slowly expanding northward attributed to warming temperatures (Goldstein et al. 2018), but the low photosynthetic rates observed at 35 and 40 °C could indicate growth limitations in warmer climates. Higher rates at cooler temperatures (20 to 25 °C) may contribute to northern range expansion. Growth of *Uniola* is not affected by the presence of *Ammophila* (Brown et al. 2018), or other dominant species (Sciolino 2024), but *Uniola* tends to outcompete *Ammophila* (Harris et al. 2017). *Uniola* also builds dunes that differ from those built by *Ammophila* (Jay et al. 2022, Riffe et al. in review). Although *Uniola* and *Ammophila* exhibited several similar physiological responses to temperature, *Uniola* has a competitive advantage that may further contribute to observed declines in *Ammophila* (Brown et al. 2018; Woods et al. 2023; Riffe and Zinnert 2024).

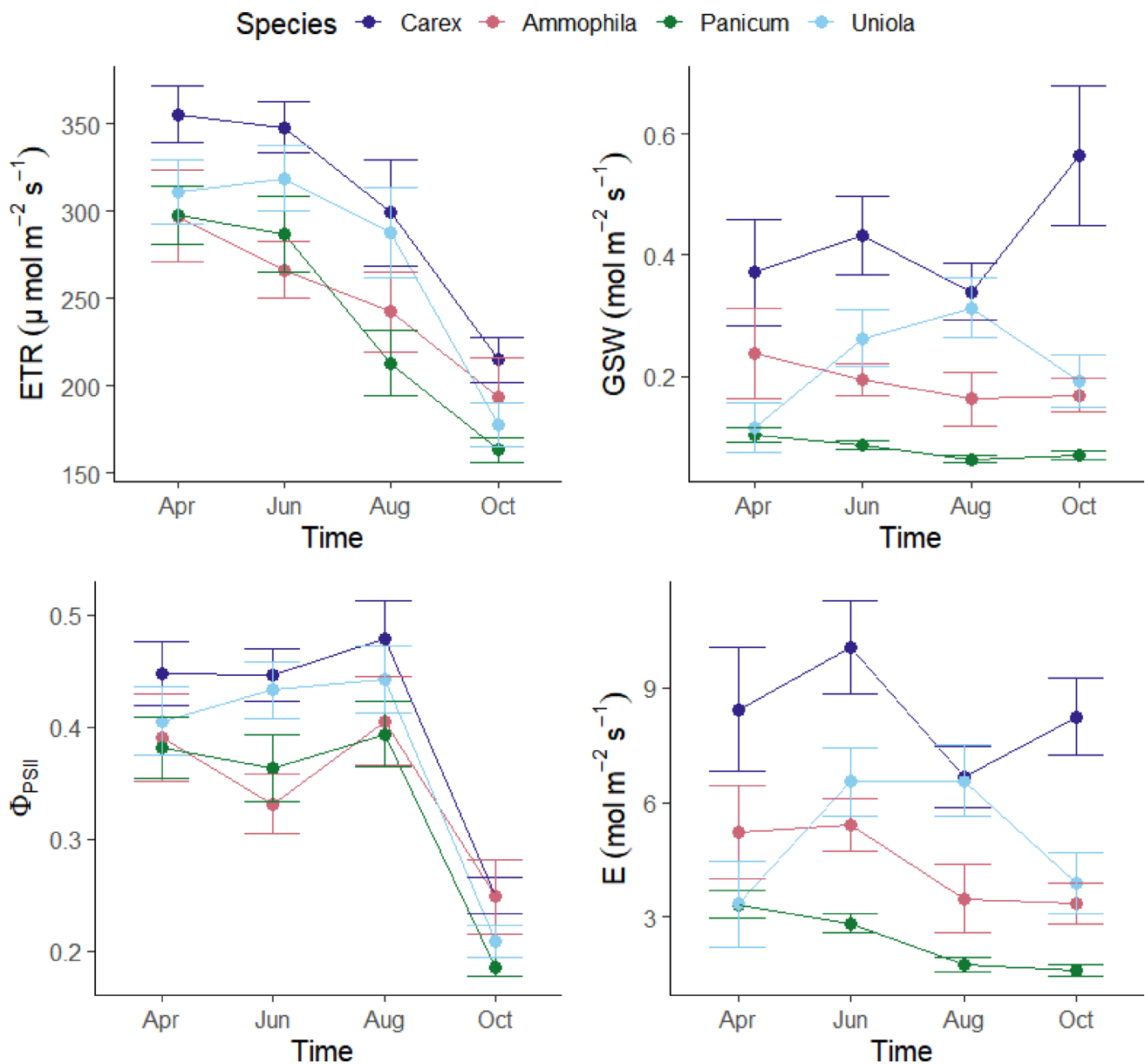


Fig. 5 Field results of physiology metrics through time, color coded by species. Collected throughout 2023, each species had an $n=15$ and data were controlled for time through a blocking variable. ETR (electron transport rate), GSW (stomatal conductance), Φ_{PSII} (quan-

tum yield of photosystem II), E (transpiration). Points are means and error bars are standard error. Full ANOVA results are presented in the supplementary material

Invasive Species

Carex exhibited physiological responses typical of invasive species, with a wider thermal range of tolerance than the dominant native species. *Carex* had consistently high rates of stomatal conductance and transpiration in both the growth chamber experiments and field measurements. Previous physiology on *Carex* in its native habitat, found that photosynthetic capacity was controlled by stomatal conductance, with a decreased stomatal opening in the middle of the day when temperatures were highest (Hwang and Choo

2017). Although stomatal conductance was linearly related to photosynthesis, stomatal conductance of *Carex* was high at midday across multiple months and rates remained consistent from 30 to 40 °C. Transpiration in *Carex* increased with temperature as well, indicating high water use at high temperatures. High transpiration rates along with traits that maximize resource capture (Riffe and Zinnert 2024) may further explain the mechanism of *Carex* invasion. As climate warms, *Carex* has a physiological and functional trait advantage (Riffe and Zinnert 2024) that will likely enhance growth of this species relative to native dune species.

Conclusions and Implications

Here we demonstrate that photosynthetic pathway is not a reliable indicator of physiological performance to changes in temperature. The invasive sedge, *Carex* outperformed native species with consistently higher photosynthetic rates at all temperatures except 35 °C. This along with high rates of stomatal conductance and transpiration across temperatures contribute to the success of this invasive species in the dune system (Riffe and Zinnert 2024). Without active management *Carex* will continue to expand and dominate dune systems along the US East Coast. Reduced physiological performance at high temperatures will likely limit growth of *Ammophila* with climate warming and restrict the distribution to cooler climates. Conversely, *Panicum* distribution and growth is limited by low temperatures as it was unable to photosynthesize at 20 or 25 °C, but higher rates at 30 °C may indicate future northern expansion if the climate continues to warm. Surprisingly, several physiological responses of *Uniola* were similar to C3 species (i.e., comparable photosynthetic rates at 25 °C). Warming in cooler months may contribute to a northern range expansion of *Uniola*. These results demonstrate that species-specific physiological responses must be considered when making future predictions. Species growth is impacted by temperature and will likely influence future distributions, which have landscape-level implications due to species influence on dune shape and size (Jay et al. 2022; Riffe and Zinnert 2024; Sabo et al. 2024).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12374-026-09503-0>.

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Data Availability Data will be available on Zenodo once accepted. A draft of the data upload can be sent upon request from the corresponding author.

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