Response of Leaf Economic Traits of Scirpus validus and Typha to Simulated Warming and Doubled CO2 Concentration Postprint

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Abstract

Climate change represents an environmental issue of global concern, and plant responses to climate change reflect their growth and survival strategies for coping with climate change. Leaf economic traits are directly related to plant resource acquisition, utilization, and storage, and are significantly influenced by temperature conditions and CO2 concentration. This study employed closed-top growth chambers with an artificial environmental control system to examine the responses of leaf economic traits of the widely distributed wetland species Scirpus validus and Typha orientalis to simulated warming (ambient temperature +2 °C) and doubled CO2 concentration (elevated to 850 mol · mol-1). The results demonstrated that: (1) Under the warming treatment, the net photosynthetic rate, nitrogen content, and phosphorus content of Scirpus validus were significantly reduced, while its intercellular CO2 concentration and leaf mass per area were significantly increased; under the doubled CO2 concentration treatment, the intercellular CO2 concentration and net photosynthetic rate of Scirpus validus were both significantly reduced, but leaf mass per area was significantly increased. (2) Under the warming treatment, the leaf mass per area of Typha orientalis was also significantly increased, while nitrogen content and phosphorus content were significantly reduced; the photosynthetic parameters, nitrogen content, and phosphorus content of Typha orientalis were all significantly reduced under the doubled CO2 concentration treatment, while leaf mass per area was significantly increased. (3) Except for carbon content, other economic trait parameters of both Scirpus validus and Typha orientalis, including net photosynthetic rate, stomatal conductance, transpiration rate, intercellular CO2 concentration, nitrogen content, phosphorus content, and leaf mass per area, all played significant roles in responding to warming and elevated CO2 concentration. Overall, these findings reflect the response strategies of Scirpus validus and Typha orientalis in functional traits to warming and elevated

CO2 concentration. The photosynthetic capacity and nutrient content of both plants were significantly suppressed under both treatments, while their stress resistance increased, indicating that warming and elevated CO2 concentration are detrimental to the growth of Scirpus validus and Typha orientalis.

Full Text

Title and Authorship

Responses of Leaf Economic Traits of *Scirpus validus* and *Typha orientalis* to Simulated Warming and Doubled CO_2 Concentration

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Abstract

Climate change represents a pressing environmental challenge of global concern. Plant responses to climate change reflect their adaptive strategies for growth and survival under shifting environmental conditions. Leaf economic traits, which govern resource acquisition, utilization, and storage, are particularly sensitive to temperature and atmospheric CO_2 concentration. This study employed sealed-top growth chambers with artificial environmental control systems to investigate how leaf economic traits of two widespread wetland species—*Scirpus validus* and *Typha orientalis*—respond to simulated warming (ambient temperature +2 °C) and doubled CO_2 concentration (850 $\text{mol} \cdot \text{mol}^{-1}$).

The results revealed distinct response patterns: (1) Under warming, *S. validus* exhibited significantly reduced net photosynthetic rate, nitrogen content, and phosphorus content, but significantly increased intercellular CO_2 concentration and leaf mass per area. Under doubled CO_2, *S. validus* showed significantly reduced intercellular CO_2 concentration and net photosynthetic rate, but significantly increased leaf mass per area. (2) Warming significantly increased leaf mass per area while decreasing nitrogen and phosphorus contents in *T. orientalis*. Under doubled CO_2, all photosynthetic parameters and nutrient contents of *T. orientalis* declined significantly, whereas leaf mass per area increased significantly. (3) Principal component analysis demonstrated that most leaf economic traits—including photosynthetic rate, stomatal conductance, transpiration rate, intercellular CO_2 concentration, nitrogen content, phosphorus content, and leaf mass per area—played important roles in both species' responses to warming and elevated CO_2, with carbon content being the exception.

Overall, these findings illuminate the functional trait response strategies of *S. validus* and *T. orientalis* to warming and elevated CO_2. Both species experienced significant inhibition of photosynthetic capacity and nutrient content under experimental treatments, while their stress resistance increased, suggesting that warming and elevated CO_2 may constrain the growth of these wetland plants.

Keywords: climate change, emergent macrophytes, plant functional traits, elemental content, environmental response strategies

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Introduction

Global climate change and its impacts on human and ecological systems have become a worldwide scientific concern. Warming and rising atmospheric CO_2 concentration represent two primary characteristics of global climate change. The IPCC Fifth Assessment Report projects that by the end of the 21st century, global mean surface temperature will increase by 0.3-4.8 °C relative to 1986-2005, while atmospheric CO_2 concentration will reach 540-970 $\text{mol}\cdot\text{mol}^{-1}$, with these trends expected to intensify (IPCC, 2013). Such changes will profoundly affect the structure and characteristics of Earth’ s ecosystems. Wetland ecosystems provide critical services to both ecology and human society, and their sensitivity to climate change makes understanding its impacts on key wetland species essential (Dang et al., 2021).

Leaf economic traits directly relate to plant resource acquisition, utilization, and storage, reflecting a strategic gradient from conservative to acquisitive resource-use strategies. These traits primarily include leaf nitrogen content, leaf phosphorus content, leaf mass per area, and photosynthetic rate (Wright et al., 2004; Reich, 2014). Environmental changes significantly influence the expression of leaf economic traits, making them effective indicators of plant growth and survival strategies under varying conditions (Reich, 2014). Syntheses of 151 studies across 365 wetlands worldwide, along with comparative research on 60 wetland and 85 terrestrial plant species at 38 sites in Shaanxi Province, China, have revealed that wetland plants cluster toward the acquisitive end of the spectrum, characterized by lower leaf mass per area, higher leaf nitrogen and phosphorus, faster photosynthetic rates, and shorter leaf lifespans compared to non-wetland plants (Zhang et al., 2017; Pan et al., 2020). While these studies provide important baseline knowledge, how wetland plant economic traits adapt to climatic and environmental changes remains unclear.

Elevated CO_2 concentration profoundly affects plant economic traits. Photosynthesis represents one of the most sensitive indicators of plant response to high CO_2. Short-term CO_2 enrichment typically enhances photosynthetic capacity (Xu et al., 2016; Jin et al., 2022), whereas long-term exposure may cause photosynthesis to return to or even fall below ambient CO_2 levels—a phenomenon known as "photosynthetic downregulation" (Cheng et al., 2014; Tobita et al., 2021). Some studies have found no significant effect of increased CO_2 on net photosynthetic rate (Zheng et al., 2019). Elevated CO_2 also alters other economic traits by reducing stomatal aperture, decreasing stomatal conductance and transpiration rate per unit leaf area, and improving water use efficiency (Jiang et al., 2006; Jin, 2019). Additionally, high CO_2 increases leaf mass per area while reducing mineral nutrient concentrations such as nitrogen and phosphorus (Jin et al., 2019; Li et al., 2021). These effects vary among species and ecosystems (Jiang et al., 2006; Jin, 2019; Jin et al., 2022).

Temperature constitutes another key factor influencing plant economic traits. Studies on two species in alpine meadows of northwestern Sichuan found that warming increased net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 concentration in the monocot *Deschampsia caespitosa*, but decreased these parameters significantly in the dicot *Thlaspi arvense* (Shi et al., 2009). Xu et al. (2018) reported that short-term warming enhanced photosynthetic rates in *S. validus* but not in *T. orientalis*. Global studies of over 2,500 plant species revealed that higher temperatures and solar radiation correlate with increased leaf mass per area and leaf nitrogen content, but shorter leaf lifespan and weaker photosynthetic capacity (Wright et al., 2005). Conversely, another study across 452 sites and 1,280+ species showed that leaf nitrogen and phosphorus decrease while N:P ratio increases toward the equator with rising temperatures and extended growing seasons (Reich et al., 2004). Low temperatures restrict leaf expansion, resulting in smaller, thicker leaves with higher leaf mass per area (Gentili et al., 2021), though some studies report increased leaf mass per area and decreased leaf nitrogen under warming (Qi et al., 2012). Plant responses to warming have effective ranges; moderate warming can enhance photosynthesis, but temperatures exceeding optimal ranges inhibit photosynthetic activity (Gao et al., 2010). These divergent results across plant groups reflect different adaptive strategies to temperature change.

Temperature and CO_2 concentration interact as key variables affecting plant traits and functions. Since they co-occur and elevated CO_2 affects biomes across all temperature ranges, their interactive effects on carbon balance, photosynthetic growth, and biomass accumulation represent a major focus in global ecology (Gao et al., 2019). Some research suggests warming generally disadvantages wetland plants while elevated CO_2 enhances their photosynthetic rates (Short et al., 2016), whereas other studies indicate synergistic effects (Ma et al., 2020). For example, combined warming and doubled CO_2 increased maximum biomass and normalized photosynthetic rates of Bering Sea phytoplankton by

2.6- and 3.5-fold, respectively, shifting community composition from diatoms to picoplankton (Hare et al., 2007). In contrast, the same treatment significantly reduced photosynthetic carbon assimilation and biomass in the Amazonian aquatic plant *Montrichardia arborescens* (Lopes et al., 2018). Although no consensus has emerged, these studies provide valuable insights.

Building on this background, our study addresses how wetland plants respond to climate change by examining leaf economic trait strategies under warming and elevated CO_2. Using the widespread wetland species *Scirpus validus* and *Typha orientalis*, we conducted controlled experiments in sealed chambers simulating a 2 °C temperature increase and doubled CO_2 concentration (850 $\mathrm{mol} \cdot \mathrm{mol}^{-1}$) based on IPCC projections. By measuring changes in leaf economic traits, we aimed to address: (1) How do leaf economic traits of these wetland plants respond to warming and doubled CO_2? (2) Which traits play stronger roles in these responses? (3) What functional coordination patterns exist among traits? These insights will advance understanding of wetland plant adaptive strategies and inform conservation efforts under climate change.

1.1 Study Site Overview

Experimental materials were transplanted from the Dianchi lakeshore zone near the Dianchi Wetland Ecological Research Station in Jinning District, Kunming, Yunnan Province (102°35 54 -102°40 08 E, 24°39 59 -24°42 17 N) at 1,888 m elevation. Dianchi Lake, located in southwestern Kunming, has a mean elevation of 1,891 m and a perennial water area of 2,960 km^2 (excluding the lower Haikou watershed) with an average depth of 4.5 m. The region features a low-latitude subtropical plateau monsoon climate with distinct wet and dry seasons. Annual temperature variation is small, with a mean annual temperature of 15 °C, annual sunshine of approximately 2,200 h, a frost-free period exceeding 240 days, and $ $10 °C effective accumulated temperature of 4,494.0 °C. Mean annual precipitation is 1,450 mm. The lake never freezes, with a mean annual water temperature of 17.03 °C and maximum monthly mean temperature of 22.40 °C, supporting diverse aquatic plants, birds, and fish. The lakeshore zone hosts abundant emergent vegetation, dominated by the grass *Phragmites australis* and the cattail *Typha orientalis*, along with other common wetland species including *Scirpus validus*, *Zizania latifolia*, *Impatiens aquatillis*, *Nelumbo nucifera*, *Myriophyllum aquaticum*, and planted woody species *Taxodium* cv. Zhongshanshan.

1.2 Experimental Design

Based on the latest IPCC projections for temperature and CO_2 increases, we established an artificial environment control system with sealed-top growth chambers at the National Plateau Wetlands Research Center in Kunming, Yunnan [Figure 1: see original paper]. One chamber served as the control (CK) under ambient conditions, while two treatment chambers were established: (1) elevated temperature (ET) at +2 °C above ambient, and (2) elevated CO_2 (EC) at 850 $\mathrm{mol \cdot mol^{-1}}$. All other environmental factors remained consistent across chambers. Each chamber consisted of a lower cylindrical section with 11 glass-sealed facets and an upper spherical cap approximately 1.5 m high, sealed with double-layer PC panels, with a total volume of ~24.5 $\mathrm{m^3}$ [Figure 1: see original paper]. Temperature was controlled via compressors connected to heat exchangers, resistance heaters, and fresh air control valves. Two self-closing pressure-regulating fans and a manual window on the spherical cap maintained pressure balance and prevented overheating during emergencies. The CO_2 control system comprised CO_2 sensors (GMT222), control modules (LT/ACR-2002), solenoid valves, flow meters, pressure reducing valves, and CO_2 cylinders, with each chamber operating independently through an integrated monitoring system.

In April 2015, healthy, uniformly sized *S. validus* and *T. orientalis* plants were transplanted into experimental pots (35 cm diameter × 25 cm height) filled with consistent volumes of soil collected from the Dianchi lakeshore zone. After 15 days of acclimation under natural conditions, plants were randomly placed in three sealed-top chambers (STC), with four pots per chamber. To ensure uniform light conditions and minimize edge effects, plants were arranged in a circular pattern at 0.85 m radius from each chamber' s center (chamber radius = 1.7 m). Throughout the cultivation period, plants were watered twice weekly to maintain consistent flooding depth and environmental conditions. Leaf economic traits were measured during the peak growing season (July–September 2019). After four years of growth, plants had fully acclimated to the treatment conditions, allowing assessment of long-term responses. Post-experiment data extraction confirmed that the warmed chamber averaged 1.995 °C higher than control, while the CO_2 chamber maintained 840.05 $\mathrm{mol \cdot mol^{-1}}$, demonstrating effective environmental control [Figure 2: see original paper].

1.3 Measurement of Leaf Economic Traits

Three plants per species were selected from each treatment group. During the peak growing season (July–September 2019), net photosynthetic rate (Pn, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$), stomatal conductance (Gs, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$), intercellular CO_2 concentration (Ci, $\mathrm{mol \cdot mol^{-1}}$), and transpiration rate (Tr, $\mathrm{mmol \cdot m^{-2} \cdot s^{-1}}$) were measured in situ on clear mornings (9:00-11:30) using a Li-6800XT portable photosynthesis system (LI-COR, Nebraska, USA). Two healthy, fully expanded mature leaves per plant were measured with chamber conditions set to 1,500 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ light intensity, 22–24 °C leaf temperature, 500 $\mathrm{mol \cdot s^{-1}}$ flow rate, and 425 $\mathrm{mol \cdot mol^{-1}}$ reference CO_2 concentration.

After photosynthetic measurements, leaves were harvested, stored in coolers, and transported to a laboratory adjacent to the control chambers. Leaf area was determined by scanning 15 cm mid-leaf sections and analyzing images with ImageJ software (v.1.48). Scanned leaves were oven-dried at 75 °C for at least 48 h to constant mass, then weighed to calculate leaf mass per area (LMA, $\mathrm{g \cdot m^{-2}}$).

For elemental analysis, 3–5 plants per treatment were harvested, washed, and oven-dried at 75 °C. Dried leaves were ground and sieved (0.25 mm mesh). Total carbon content (C, $g \cdot kg^{-1}$) was measured on 3 mg samples using a Vario TOC select analyzer (Elementar, Germany). Total nitrogen (N, $g \cdot kg^{-1}$) and phosphorus (P, $g \cdot kg^{-1}$) contents were determined on 0.2 g samples following H_2SO_4-H_2O_2 digestion and analysis with an AA3 continuous flow analyzer.

1.4 Data Analysis

All statistical analyses were performed using R (v.3.01). One-way ANOVA (using the "vegan" package) tested differences in leaf economic traits among control, warming, and CO_2 treatments at $P<0.05$ significance. Principal component analysis (PCA) identified key traits driving plant responses to warming and elevated CO_2. Figures were generated using SigmaPlot (v.10.0).

2.1 Responses of Leaf Economic Traits to Simulated Warming and Doubled CO_2

Compared to the control, warming (ET) significantly reduced net photosynthetic rate (Pn) but increased intercellular CO_2 concentration (Ci) in *S. validus*; doubled CO_2 (EC) significantly reduced both Ci and Pn. Stomatal conductance (Gs) and transpiration rate (Tr) showed no significant differences among treatments [Figure 3: see original paper]. In contrast, *T. orientalis* exhibited more pronounced responses to EC, with all four photosynthetic parameters declining significantly, while warming alone produced no significant changes in photosynthetic traits [Figure 3: see original paper]. Notably, *S. validus* Pn was significantly lower and Ci significantly higher under ET compared to EC, whereas *T. orientalis* photosynthetic parameters were all significantly higher under ET than EC [Figure 3: see original paper]. These results indicate that *S. validus* photosynthesis is sensitive to both warming and CO_2, while *T. orientalis* is more sensitive to CO_2 than temperature. The Pn decline under warming in both species likely resulted from combined stomatal limitation and reduced mesophyll assimilation capacity.

Both species showed significantly increased leaf mass per area (LMA) under ET and EC, with no significant changes in carbon content [Figure 4: see original paper]. *Scirpus validus* N and P contents decreased significantly under ET but not under EC, whereas *T. orientalis* N and P contents decreased significantly under both treatments [Figure 4: see original paper]. This demonstrates that LMA is highly sensitive to both warming and elevated CO_2 in both species. *Scirpus validus* nutrient contents respond strongly to warming but weakly to CO_2, while *T. orientalis* nutrients respond strongly to both factors.

2.2 Trait Associations Among Leaf Economic Traits

Principal component analysis of *S. validus* revealed that the first two axes explained 75.15% of total variation (49.42% and 25.73%, respectively) [Figure 5A: see original paper]. PC1 correlated positively with N, P, Pn, and Tr, but negatively with Ci; PC2 correlated positively with Gs but negatively with LMA . For *T. orientalis*, the first two axes explained 82.03% of variation (66.12% and 15.91%) [Figure 5B: see original paper]. PC1 correlated positively with Gs, Pn, Tr, N, Ci, and P, but negatively with LMA; PC2 correlated positively with C . These patterns indicate that most leaf economic traits play important roles in both species' responses to warming and elevated CO_2.

3 Discussion and Conclusion

Our findings demonstrate that warming negatively affected photosynthetic production in both species, significantly reducing net photosynthetic rate and nutrient contents while increasing leaf mass per area. Elevated CO_2 also disadvantaged *T. orientalis*, significantly reducing its photosynthetic capacity and N and P contents. The divergent responses reflect species-specific strategies: *S. validus* photosynthetic and nutrient traits were sensitive to warming but less responsive to CO_2, whereas *T. orientalis* exhibited high sensitivity to both factors.

Temperature critically influences plant functional traits, with optimal photosynthetic temperatures determining rate responses. Plant photosynthetic responses to warming can be positive (Ren et al., 2014), negative (Qi et al., 2012), or neutral (Dovis et al., 2021), depending on species and developmental stage (Yamori et al., 2014). Our previous short-term warming study found enhanced photosynthesis in both species (Xu et al., 2018). However, after four years of acclimation, both species showed negative responses, suggesting that a 2 °C increase exceeded their optimal temperatures, reducing photosynthetic enzyme activity and productivity. Thus, long-term warming constitutes a stressor for these plants.

The negative photosynthetic effects likely involve both stomatal and non-stomatal limitations. Warming marginally reduced Gs in both species, potentially limiting CO_2 supply. However, concurrent Ci increases in both species opposite to Pn trends suggest reduced mesophyll assimilation capacity rather than stomatal limitation (Chikov et al., 2016). The slight Gs and Tr reductions in *S. validus* under warming may represent an adaptive strategy to prevent excessive water loss and improve water use efficiency under high-temperature stress, though this trade-off reduces photosynthesis.

Plants also adjust economic strategies under stress. Warming reduced N and P supply, consequently lowering Pn—a pattern consistent with previous research (Reich et al., 2014; Sun et al., 2017). Increased LMA in both species likely represents a structural adaptation to prevent water loss, as greater leaf density and thickness extend water retention time and transport distance (Zwieniecki et al., 2007; Sack et al., 2012).

As the substrate for photosynthesis, elevated CO_2 directly alters plant carbon assimilation. Short-term experiments consistently show enhanced photosynthesis, particularly in C_3 plants (Ma et al., 2022; Guo et al., 2022), and our previous short-term study on *S. validus* found similar results (Xu et al., 2016). However, after four years of doubled CO_2, *S. validus* showed no significant photosynthetic differences from control, while *T. orientalis* exhibited significant reductions in Pn, Gs, Ci, and Tr—demonstrating photosynthetic downregulation. Long-term high CO_2 reduces Rubisco content and activity (Wang et al., 2012), and increased Ci necessitates Gs reduction to maintain CO_2 gradients, limiting CO_2 entry and reducing Pn. The concurrent Gs decline also increases resistance to water diffusion, explaining the significant Tr reduction in *T. orientalis.*

Elevated CO_2 alters carbon assimilation and allocation, affecting C, N, and P stoichiometry (Hong et al., 2013). Studies report reduced mineral nutrients (K, Mg, P, S, Zn) in rice under high CO_2 (Tong et al., 2020), consistent with our findings of significantly reduced N and P in *T. orientalis* and similar results for *Betula albosinensis* seedlings (Qiao et al., 2007). The mechanisms remain unclear but may involve dilution effects from accelerated growth and starch accumulation (Reich et al., 2014), reduced mineral uptake due to lower Gs (Hong et al., 2013), or decreased N investment in photosynthetic enzymes (Zhang et al., 2021). The non-significant change in C content and marginal N and P increases in *S. validus* under elevated CO_2 suggest stronger adaptive capacity compared to *T. orientalis.*

Plant functional traits exhibit plasticity and coordinate through trait combinations to form adaptive syndromes (Rodríguez-Rodríguez et al., 2018). Except for carbon content, all studied traits were important for both species' adaptation to warming and elevated CO_2, forming an "economic spectrum" trait set. The significant negative correlation between LMA and N, P, and Pn across both species aligns with global patterns and case studies (Chaturvedi et al., 2011; Pérez-Harguindeguy et al., 2013), confirming that these wetland species conform to fundamental leaf economics relationships.

In summary, warming significantly reduced photosynthetic rate and nutrient contents while increasing LMA in both species. Elevated CO_2 significantly reduced photosynthetic capacity and nutrient contents in *T. orientalis* but had minimal effects on *S. validus* nutrients. Photosynthetic traits, LMA, and nutrient contents were all important for adaptation, whereas carbon content played a minor role. The significant functional associations among traits reflect adaptive strategies consistent with established leaf economics principles. These results provide valuable case studies for wetland plant responses to climate change. However, limitations include single chambers for each treatment and lack of warming × CO_2 interaction treatments, which may introduce error. Based on individual treatment effects, interactive effects would likely further reduce photosynthetic capacity and nutrient contents, particularly for *T. orientalis.* Future research should expand taxonomic breadth and include replicated interactive treatments to enhance precision.

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Note: Figure translations are in progress. See original paper for figures.