Enhancing Estuarine Marsh Ecosystem Models through Biotic Interactions:

Investigating the Role of Root Oxygen Loss and Root Exudation on Carbon Dynamics.

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Dedication

To my dearest parents,

This thesis is dedicated to you, whose unwavering love, sacrifice, and endless support have made this journey possible. From my earliest memories, you have nurtured my curiosity and encouraged my aspirations. Your tireless efforts, boundless patience, and steadfast belief in me have been my greatest sources of strength and inspiration. Without your selfless dedication and the countless sacrifices you've made, I could not have reached this milestone.

You have stood by me through every challenge, offering wisdom when I was lost, comfort when I was weary, and joy in times of success. Your guidance has illuminated my path, and your encouragement has propelled me forward even when obstacles seemed insurmountable. Words cannot express the depth of my gratitude for all that you have done.

Thank you for believing in me, for instilling in me the values of perseverance and integrity, and for being the foundation upon which I build my dreams. This accomplishment is not mine alone but a testament to your love and unwavering support.

1. Abstract

Marsch-Ökosysteme sind wichtige Kohlenstoffsenken, doch die Mechanismen, die ihre Kohlenstoffspeicherung regulieren – insbesondere das Zusammenspiel zwischen Pflanzenmerkmalen und mikrobiellen Prozessen – sind noch nicht vollständig verstanden. Diese Studie untersucht den Einfluss von Wurzel-Sauerstoffverlust (Root Oxygen Loss, ROL) und Wurzelausscheidungen auf die Kohlenstoffdynamik in den Elbe-Marschgebieten und hebt hervor, wie diese biotischen Prozesse durch abiotische Faktoren wie Temperatur und Niederschlag moduliert werden.

Ein prozessbasiertes Modell wurde entwickelt, um die Kohlenstoffflüsse innerhalb des Marschökosystems zu simulieren, wobei detaillierte pflanzenphysiologische Merkmale und mikrobielle Aktivität integriert wurden. Das Modell wurde anhand von Felddaten aus der Hochmarschenzone des Elbe-Ästuars kalibriert und validiert. Sensitivitätsanalysen bewerteten die Auswirkungen unterschiedlicher ROL- und Wurzelausscheidungsniveaus unter verschiedenen Temperatur- und Niederschlagsszenarien.

Die Basissimulation zeigte, dass die Marsch als Nettokohlenstoffsenke fungiert, mit einer Kohlenstoffbilanz von ***210,60*** g C m^{-2} $Jahr^{-1}$. Eine Erhöhung des ROL um 20 % erhöhte die Bodenatmung auf ***1.172,49*** g C m^{-2} $Jahr^{-1}$ und verringerte die Kohlenstoffbilanz auf ***40,99*** g C m^{-2} $Jahr^{-1}$. Wurzelausscheidungen hatten einen moderaten Effekt. Kombinierte Erhöhungen von ROL und Wurzelausscheidungen reduzierten weiter die Kohlenstoffspeicherungskapazität der Marsch.

Abiotische Faktoren modifizierten diese Wechselwirkungen. Erhöhter Niederschlag verringerte die Bodenatmung aufgrund begrenzter Sauerstoffdiffusion in gesättigten Böden, was die Rolle der Marsch als Kohlenstoffsenke stärkte. Im Gegensatz dazu intensivierten steigende Temperaturen die Bodenatmung und verringerten die Kohlenstoffbilanz, wodurch die Marsch bei extremen Erwärmungsszenarien zu einer Nettokohlenstoffquelle werden könnte.

Diese Arbeit unterstreicht die entscheidende Rolle von Pflanze-Mikroben-Interaktionen in der Kohlenstoffdynamik von Marschen und zeigt potenzielle Anfälligkeiten unter zukünftigen Klimaveränderungen auf. Die Ergebnisse legen nahe, dass Änderungen der Pflanzenmerkmale und Umweltbedingungen das Kohlenstoffspeicherpotenzial von Marschen erheblich beeinflussen könnten. Integrierte Managementstrategien, die sowohl biotische als auch abiotische Faktoren berücksichtigen, sind unerlässlich, um die Funktion der Kohlenstoffsenke in Marschökosystemen aufrechtzuerhalten.

English:

Marsh ecosystems are vital carbon sinks, yet the mechanisms regulating their carbon sequestration—particularly the interplay between plant traits and microbial processes—are not fully understood. This study investigates the influence of Root Oxygen Loss (ROL) and root exudation on carbon dynamics in the Elbe Estuarine Marsh, emphasizing how these biotic processes are modulated by abiotic factors like temperature and rainfall.

A process-based model was developed to simulate carbon fluxes within the marsh ecosystem, integrating detailed plant physiological traits and microbial activity. The model was calibrated and validated using field data from the high marsh zone of the Elbe Estuary. Sensitivity analyses assessed the impacts of varying ROL and root exudation levels under different temperature and rainfall scenarios.

The baseline simulation indicated that the marsh functions as a net carbon sink with a carbon balance of ***210.60*** $\mathrm{g\,C\,m^{-2}\,year^{-1}}$. A 20% increase in ROL significantly raised soil respiration to ***1,172.49*** $\mathrm{g\,C\,m^{-2}\,year^{-1}}$, reducing the carbon balance to ***40.99*** $\mathrm{g\,C\,m^{-2}\,year^{-1}}$. Root exudation had a moderate effect. Combined increases in ROL and root exudation further diminished the marsh's carbon sequestration capacity.

Abiotic factors modulated these interactions. Increased rainfall reduced soil respiration due to limited oxygen diffusion in saturated soils, enhancing the marsh's role as a carbon sink. Conversely, rising temperatures intensified soil respiration and decreased the carbon balance, potentially transforming the marsh into a net carbon source under extreme warming scenarios.

This thesis highlights the critical role of plant-microbe interactions in marsh carbon dynamics and underscores potential vulnerabilities under future climate change. The findings suggest that shifts in plant traits and environmental conditions could significantly alter the carbon sequestration potential of marshes. Integrated management strategies that consider both biotic and abiotic factors are essential to sustain the carbon sink function of marsh ecosystems.

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Chapter 1 General Introduction

1. Importance of Marsh Ecosystems

Marsh ecosystems are among the most productive and dynamic environments on Earth. Located at the interface between terrestrial and aquatic systems, they encompass salt marshes, freshwater marshes, and tidal marshes, each characterized by water-saturated soils and a unique assemblage of vegetation adapted to such conditions (Mitsch and Gosselink 2015). These ecosystems are not only crucial for maintaining biodiversity but also play an indispensable role in global biogeochemical cycles, particularly carbon cycling.

A key functions of marsh ecosystems is their ability to act as natural water filters. By trapping sediments and filtering pollutants, marshes enhance water quality and protect downstream aquatic systems from the adverse effects of runoff and pollution (Craft et al. 2009). This filtration process is vital for maintaining the health of adjacent marine environments, including coral reefs and seagrass beds, which are sensitive to changes in water clarity and quality.

In terms of biodiversity, marshes serve as critical habitats for a wide array of plant and animal species. The fluctuating water levels and saline conditions create niches that support specialized flora and fauna (Zedler and Kercher 2005). For migratory birds, marshes provide essential stopover sites for feeding and resting. Fish species utilize these areas as nurseries, benefiting from the abundant food resources and protective cover. Invertebrates, such as crustaceans and molluscs, thrive in the nutrient-rich sediments, contributing to the complexity of food webs within these ecosystems.

Moreover, marshes offer natural protection against coastal hazards. They act as buffers that absorb the energy of storm surges and reduce the impact of flooding on inland areas (Temmerman et al. 2013). This protective function is increasingly important in the context of climate change, where the frequency and intensity of extreme weather events are projected to rise.

Perhaps most significantly, marsh ecosystems are great carbon sinks. Through photosynthesis, marsh vegetation sequesters atmospheric carbon dioxide (CO_2), incorporating it into plant biomass. The anoxic conditions of waterlogged soils slow down the decomposition of organic matter, leading to the accumulation of carbon in the form of peat and other organic materials (Chmura et al. 2003; Moomaw et al. 2018). This process not only mitigates the effects of increasing atmospheric CO_2 levels but also contributes to long-term carbon storage, playing a critical role in regulating global climate.

However, the integrity and functionality of marsh ecosystems are under severe threat from anthropogenic activities. Sea-level rise, driven by climate change, poses a significant risk by potentially submerging low-lying areas and leading to habitat loss (Kirwan and Megonigal 2013). Coastal development and land reclamation disrupt the natural processes and connectivity of these ecosystems. Pollution from agricultural runoff, industrial discharges, and urbanization introduces contaminants that can alter nutrient dynamics and harm sensitive species.

Given the multifaceted importance of marsh ecosystems—from ecological to socio-economic perspectives—there is an urgent need to deepen our understanding of the processes that govern their functioning and resilience. This knowledge is essential not only for conservation and restoration efforts but also for informing policy decisions that balance human needs with environmental sustainability.

2. Plant-Microbe Interactions in Marsh Ecosystems

A key factor in marsh ecosystem functioning is the interactions between plants and microbes. The rhizosphere—the narrow region of soil influenced by root secretions and microbial activity—is a hotspot of biogeochemical processes (Marschner 2011). In this dynamic zone, plants and microbes engage in complex processes involving nutrient exchange, chemical signalling, and mutual modification of the soil environment (Philippot et al. 2013).

Microbial communities, including bacteria, fungi, and archaea, are the primary drivers of organic matter decomposition. They break down complex organic compounds, releasing nutrients such as nitrogen and phosphorus, which are then available for plant uptake. This decomposition process is pivotal for carbon cycling, as it dictates the rate at which carbon stored in biomass and soil organic matter returns to the atmosphere as greenhouse gases like CO_2 and methane (CH_4) (Reddy and DeLaune 2008).

Plants, in turn, influence microbial communities through the release of root exudates—organic compounds that serve as a carbon source for microbes (Bais et al. 2006). These exudates can stimulate microbial activity, leading to enhanced decomposition rates and changes in the composition of microbial communities. Additionally, plants can modify the physical and chemical properties of the soil, such as pH and oxygen availability, which in turn affect microbial processes (Schmidt et al. 2011).

In the anoxic conditions typical of waterlogged marsh soils, oxygen availability becomes a limiting factor for aerobic microbial processes. Some marsh plants have evolved specialized adaptations to cope with hypoxia, such as aerenchyma tissues that facilitate internal oxygen transport from shoots to roots. This adaptation enables a process known as root oxygen loss (ROL), where oxygen diffuses from the roots into the surrounding soil, creating localized aerobic microsites (de la Cruz Jiménez et al. 2021). These microsites are crucial for processes like nitrification and the aerobic decomposition of organic matter, which would otherwise be constrained in anaerobic environments.

The interplay between plants and microbes is not merely a biological curiosity but a fundamental determinant of ecosystem-level functions, including primary productivity, nutrient cycling, and carbon sequestration. However, despite its importance, our understanding of the specific mechanisms driving these interactions in marsh ecosystems remains limited. Factors such as microbial community diversity, functional roles, responses to environmental changes, and plant traits are promising areas that require further research. (Van Der Heijden, Bardgett, and Van Straalen 2008; Mueller et al. 2018).

3. Root Oxygen Loss and Root Exudation in Marsh Ecosystems

Two processes—Root Oxygen Loss (ROL) and root exudation—play crucial roles in shaping microbial communities and driving biogeochemical cycles in marsh ecosystems. ROL, which allows for oxygen diffusion into the surrounding soil, and root exudation, which supplies organic carbon to microbes, are both vital mechanisms influencing microbial activity and nutrient cycling in these environments (Fang et al. 2021; Visser, Bogemann, et al. 2000).

In the unique context of marsh ecosystems, where soils are frequently anoxic, ROL becomes a particularly vital adaptation. These anoxic conditions restrict aerobic microbial decomposition, slowing the breakdown of organic material and potentially trapping carbon in the soil. By introducing oxygen into these environments, plants facilitate microbial activity, enhancing the decomposition of organic matter and contributing to faster carbon cycling. Without ROL, decomposition would largely rely on slower anaerobic processes, which tend to produce methane (CH_4) (Chapman et al. 2019), a potent greenhouse gas, instead of carbon dioxide (CO_2) . Thus, ROL plays a key role in regulating carbon emissions and sequestration in marsh ecosystems, balancing the potential carbon storage benefits of waterlogged conditions with the microbial processes needed to cycle carbon effectively.

ROL varies widely among plant species and even among genotypes within a species, which can lead to significant spatial heterogeneity in soil oxygen levels and associated microbial activity (Hartman and Tringe 2019; Larsen et al. 2015). This variability has important implications for carbon cycling in marsh ecosystems, as areas with higher oxygen availability may experience faster rates of organic matter decomposition and carbon release, while areas with lower oxygen levels may serve as carbon sinks (Chapman et al. 2019).

Root exudation, on the other hand, involves the release of organic compounds such as sugars, amino acids, and organic acids from plant roots into the soil. These exudates provide a source of carbon and energy for soil microbes, stimulating microbial growth and activity. In marsh ecosystems, where organic matter is abundant but often locked up in forms that are not readily accessible to microbes, root exudates can act as priming agents, enhancing the decomposition of more complex organic materials and accelerating carbon cycling (Bais et al. 2006; Dennis, Miller, and Hirsch 2010).

However, the effects of root exudation on microbial processes are complex and can vary depending on the composition of the exudates, the microbial community present, and the environmental conditions (Zhu and Cheng 2011). For example, some exudates may promote the growth of certain microbial groups over others, leading to shifts in microbial community structure and function. Additionally, the increased microbial activity stimulated by root exudation can lead to increased carbon dioxide emissions, counteracting the carbon sequestration benefits provided by plant growth (Ma et al. 2022).

The interplay between ROL, root exudation, and microbial processes is a key area of interest for understanding carbon dynamics in marsh ecosystems. While significant progress has been made in identifying the basic mechanisms involved, much remains to be learned about how these processes vary across different species, environmental conditions, and spatial scales. Moreover, the long-term effects of these interactions on carbon storage and emissions in marsh ecosystems under changing climate conditions are still poorly understood (Bernal, Megonigal, and Mozdzer 2017; Rietl et al. 2021).

Understanding how ROL and root exudation shape carbon cycling in marsh ecosystems is critical for predicting future carbon fluxes under changing environmental conditions. Given the impacts of climate change, including sea-level rise and increased temperatures, further research into plant-microbe interactions will be essential for managing marsh ecosystems and their role in global carbon sequestration.

Microbes also play vital roles in supporting marsh plants. Nitrogen-fixing bacteria improve nutrient availability by converting atmospheric nitrogen into forms accessible for plant uptake—crucial in nutrient-limited marsh soils (Marschner and Rengel 2007). Mycorrhizal fungi, meanwhile, form symbiotic relationships with plants like Phragmites australis, expanding root absorption capabilities, particularly in saline environments. Additionally, certain microbes facilitate iron and sulphur cycling, mitigating sulphide toxicity and supporting root function under anoxic conditions (Smith and Read 2008).

These microbial contributions enhance nutrient availability, stress resilience, and overall ecosystem stability, underscoring the importance of plant-microbe interactions in maintaining marsh function and resilience to climate change. In addition to plants influencing microbes, microbial communities also significantly impact plant health and growth. For example, certain soil microbes help in nutrient acquisition by mobilising nutrients such as nitrogen and phosphorus, which are essential for plant productivity (Fang et al. 2021).

4. Research Gaps and Research Questions

Despite advances in our understanding of plant-microbe interactions, several key research gaps remain, particularly regarding how these interactions scale up from small-scale processes to larger ecosystem-wide carbon dynamics. Most research has focused on localized mechanisms, providing valuable insights into the fine-scale interactions between plants and microbes. However, how these interactions influence carbon cycling at the ecosystem level remains poorly understood, particularly in marsh ecosystems, which are significant global carbon sinks (Singh and Shourie 2021; Tang et al. 2021).

A second area of uncertainty involves how abiotic factors—such as soil moisture and temperature—affect plant-microbe interactions and their influence on carbon fluxes. Environmental conditions strongly influence both plant traits, such as ROL and exudation, and microbial processes, which in turn affect the balance between carbon sequestration and release. For example, elevated soil moisture may limit oxygen diffusion, reducing microbial activity, while temperature changes may accelerate microbial respiration, leading to increased carbon emissions (Butler et al. 2017; Compant, Van Der Heijden, and Sessitsch 2010; De Vries et al. 2012). Understanding how these environmental factors modulate biotic interactions is critical, especially as climate change is expected to alter the environmental conditions of marsh ecosystems (Compant et al. 2010; Sharma et al. 2022).

Moreover, while current models have advanced our understanding of marsh ecosystems, they often simplify plant traits by aggregating them across species. This simplification overlooks the substantial variability in traits like ROL and exudation, which are critical for understanding the nuances of plant-microbe interactions and their effect on carbon cycling at the ecosystem level (Saadaoui et al. n.d.).

Trait variation among marsh plants, such as differences in root oxygen loss (ROL) and root exudation, significantly impacts ecosystem-level processes. Recent studies emphasize that even small differences in these traits can alter microbial activity, nutrient cycling, and carbon flux. For instance, variations in ROL among different plant species can create microenvironments that either promote or restrict aerobic microbial processes, directly influencing the rate of organic matter decomposition and greenhouse gas emissions. Similarly, differences in root exudation patterns can shape microbial community composition and enhance nutrient availability, thereby affecting the carbon balance of marsh ecosystems (Morris et al. 2002; Zhang et al. 2002).

These variations are particularly important in marsh ecosystems, where interactions between plant and microbial traits are strongly influenced by environmental conditions, such as soil moisture and oxygen availability. The unique physiological adaptations of marsh plants to cope with anoxic environments add further complexity, making the aggregation of plant traits a major limitation in accurately modeling marsh ecosystem dynamics.

Addressing this gap by incorporating trait variability in models is crucial for improving predictions of carbon fluxes under different environmental conditions. This more nuanced representation of plant traits will allow researchers to better understand how small-scale plant-microbe interactions scale up to influence ecosystem-wide carbon dynamics, especially under changing climate scenarios.

These gaps lead to the following key research questions:

- *What roles do plant-microbe interactions play in regulating the carbon cycle within the Elbe Estuarine marsh ecosystem?*

This question aims to explore how interactions between plants and microbes influence carbon fluxes, focusing on the processes of ROL and root exudation. Understanding how these interactions drive the decomposition of organic matter and carbon sequestration will provide insights into the broader carbon dynamics within the marsh ecosystem.

- *How do abiotic factors modulate plant-microbe interactions and their influence on the carbon dynamics in this ecosystem?*

This question investigates how environmental factors—such as soil moisture, and temperature—shape the interactions between plants and microbes. Understanding these modulating effects is key to predicting how marsh ecosystems will respond to changing environmental conditions.

5. Addressing the Research Questions through Process-Based Modeling

To address these research questions, a process-based modeling approach was employed. This approach complements empirical and experimental methods by simulating ecosystem dynamics under controlled conditions. While empirical studies provide valuable insights, they are often constrained by spatial and temporal limitations, making it challenging to isolate specific processes or investigate interactions on a larger scale.

Process-based models facilitate the simulation of ecosystems and enable the isolation of key processes, such as ROL and root exudation, by controlling variables that are otherwise difficult to manipulate in field experiments. This approach is indispensable for understanding how biotic interactions regulate carbon fluxes and for exploring various environmental scenarios.

Several existing models simulate the carbon cycle in marsh ecosystems, including the Wetland-DNDC model (Zhang et al. 2002) and models developed by (Morris et al. 2002) and (Kirwan, Walters, et al. 2016) which consider hydrology, soil conditions, and plant productivity. While these models are useful, they often oversimplify plant traits by aggregating species into plant functional types (PFTs), which can mask important trait variability.

In marsh ecosystems, where small differences in plant traits can lead to significant effects on microbial processes and carbon dynamics, accounting for this variability is critical.

The trait-based, functionally diverse modeling approach described in Chapter 2 is designed to explicitly incorporate variability in key plant traits such as root oxygen loss (ROL) and root exudation. By including this trait variability, the model captures the complex and non-linear effects these traits have on nutrient cycling, microbial activity, and overall carbon dynamics. This approach provides a more accurate understanding of how plant-microbe interactions influence carbon cycling under varying environmental conditions, compared to traditional models that oversimplify by aggregating traits across species.

Recognizing these limitations, we propose developing a process-based model that explicitly incorporates trait variability. This model will:

- **Accurately Represent Plant Traits**: Capturing intra- and interspecific differences in traits like ROL and root exudation.
- **Integrate Biotic and Abiotic Factors**: Simulating how environmental variables modulate plant-microbe interactions.
- **Improve Carbon Flux Predictions**: Enhancing the accuracy of ecosystem-level carbon dynamics under different scenarios.

6. Objectives and Thesis Structure

Building on the identified research gaps, the thesis aims to:

- **Clarify the Mechanisms**: Understand how plant traits, particularly ROL and root exudation, influence microbial activity and carbon fluxes in marsh soils.

- **Assess Modulating Factors**: Determine how abiotic factors like soil moisture and temperature modulate plant-microbe interactions and their impact on carbon dynamics.

- **Develop a Novel Model**: Create a process-based model that incorporates trait variability and environmental influences to improve carbon flux predictions.

The thesis is organized as follows:

- **Chapter 2**: The Impact of Trait Variation on Carbon Dynamics—Explores the critical role of trait variation, highlighting limitations of current models and setting the foundation for a new modeling approach.

- **Chapter 3**: Model Development—Presents the development of the new process-based model, integrating trait variability and environmental factors.

- **Chapter 4**: Results and Discussion—Analyses the model simulations, compares them with empirical data, and discusses the implications for carbon dynamics.

- **Chapter 5**: Conclusions and Future Directions—Summarizes findings, discusses their significance for marsh ecosystem management and climate change mitigation, and suggests avenues for future research.

Chapter 2 Trait Variation Effect

1. Introduction

Having established the importance of plant-microbe interactions and the gaps in current modeling approaches, this chapter focuses on the critical role of trait variation in influencing carbon dynamics within estuarine marsh ecosystems.

Process-based modeling approaches have become increasingly valuable for understanding the biotic and abiotic factors that drive the carbon balance of estuarine marshes. These models simulate key ecosystem processes—such as photosynthesis, respiration, and nutrient cycling—to estimate carbon fluxes. However, the representation of plants in these models often relies on plant functional types (PFTs), which aggregate plant traits into averaged values across species or groups of species. While this simplification facilitates modeling efforts, it overlooks the critical role of trait variation in determining ecosystem-level processes, particularly plant-microbe interactions.

For example, widely used models like the Wetland-DNDC Model represent soil microbial processes as primarily driven by plant litter, soil temperature, and hydrology (Zhang et al. 2002). Subsequent iterations of marsh ecosystem models have focused on refining the connections between marsh elevation, vegetation productivity, and carbon sequestration (Morris et al. 2002; Swanson et al. 2014). However, they often omit crucial biotic interactions such as root oxygen loss (ROL) and root exudation, which are pivotal in shaping soil microbial communities and carbon dynamics. Similarly, more complex models that simulate feedback between plant biomass and the geomorphological evolution of marshes (Alizad et al. 2016; Kirwan, Temmerman, et al. 2016) do not explicitly incorporate plant-microbe interactions.

Recent research has begun to recognize the importance of these interactions, particularly in the context of global change. For example, (Rietl et al. 2021) examined how vegetation type and the priming of decomposition by plants influence carbon accumulation in brackish marshes. However, even these more recent models typically aggregate plant functional diversity into a limited number of representative species or functional types. This means that key plant traits affecting soil microbial carbon cycling, such as ROL and root exudation, are often averaged and do not reflect the substantial intra- and interspecific variation observed in natural ecosystems.

The practice of averaging traits across plant species or genotypes introduces significant limitations in ecological models. Studies have demonstrated substantial variation in traits like ROL among different genotypes within the same species (Tang et al. 2021), as well as notable interspecific differences (Bernal et al. 2017; Mueller et al. 2020). For example, root oxygen loss can vary widely, with values ranging from 5 to 50 mmol O2 m^{-2} day^{-1} depending on the species (Visser, Colmer, et al. 2000). These variations significantly influence the availability of oxygen in the soil, which in turn affects microbial activity and heterotrophic respiration rates.

The consequence of this trait variation is that microbial communities in marsh soils experience substantial variation in resource availability at small spatial scales. This variation leads to differences in local rates of respiration and complicates efforts to estimate soil carbon emissions at the ecosystem level. Furthermore, the relationship between heterotrophic respiration rates and soil carbon and oxygen levels is non-linear. This non-linearity means that the average respiration rate derived from a range of oxygen levels will differ from the rate calculated using a single averaged oxygen level—a well-known issue in ecological modeling called aggregation error (Rastetter et al. 1992).

To accurately estimate the effects of plant-microbe interactions on the carbon balance of estuarine marshes, it is essential to move beyond models that rely on averaged trait values. Instead, we need models that explicitly represent the spatial and temporal distribution of microbe-related trait values within plant communities. This approach must consider both seasonal variations and long-term changes in plant traits, as well as the associated impacts on microbial processes.

In response to these challenges, process-based numerical vegetation models that explicitly represent functional diversity, or trait ranges of plants, have been increasingly developed over the past few decades (Butler et al. 2017; Pavlick et al. 2012; Scheiter, Langan, and Higgins

2013; Snell et al. 2014). These models are designed to capture the effects of changing climatic conditions on plant community composition and net primary productivity. However, most of these models have focused on terrestrial ecosystems, such as forests and grasslands, rather than on estuarine marshes. The consequences of variation in plant traits for soil microbial functions remain understudied, particularly in the context of coastal wetlands (Piercy et al. 2024).

To address this gap, our study explores the effects of plant-induced variation in oxygen levels on heterotrophic respiration in estuarine marshes. By using the Dual Arrhenius and Michaelis-Menten (DAMM) model) (Davidson et al. 2012), we can estimate the impact of trait variation on soil carbon emissions. Specifically, we compare two model configurations: one that considers a range of soil oxygen levels, reflecting trait variation, and another that uses a single averaged oxygen level. By estimating the aggregation error associated with these different approaches, we highlight the importance of incorporating trait variation into marsh ecosystem models to improve the accuracy of carbon flux predictions.

2. Methodological Approach

We designed a study to directly compare two distinct model configurations to address the need for incorporating trait variation in marsh ecosystem models. The first configuration incorporates trait variation by considering a range of soil oxygen levels, which reflects the variability in plant traits such as root oxygen loss (ROL). The second configuration simplifies the process by using a single averaged oxygen level, similar to traditional models that aggregate plant traits. To quantify the effect of trait variation on microbial respiration, we employed the Dual Arrhenius and Michaelis-Menten (DAMM) model (Davidson et al. 2012), which simulates soil organic matter decomposition by accounting for both temperature dependence (via the Arrhenius equation) and substrate-enzyme dynamics (via the Michaelis-Menten kinetics).

In the first configuration, we simulated respiration rates at a constant temperature for a range of soil organic carbon contents (0.001 to 0.3 g C/cm^3 soil), assuming a constant average oxygen concentration of 0.097 cm^3 O_2/cm^3 air, corresponding to 30% relative soil moisture. This setup represents an average plant type with a fixed ROL value. In the second configuration, we simulated the response of respiration to soil organic carbon content across 70 different soil oxygen concentrations. We varied soil water content from the dry state to full saturation using DAMM model equations to constrain oxygen values (Eq.4 & 5).

By comparing these two configurations, we aimed to estimate the aggregation error associated with averaging traits and demonstrate the importance of incorporating trait variation into marsh ecosystem models for improving the accuracy of carbon flux predictions.

To calculate the heterotrophic respiration rate, Rsx, in the model we used Eq. (1):

$$R_{Sx} = V_{max} \times \frac{[S_x]}{kM_{sx}+[S_x]} \times \frac{[O_2]}{kM_{o2}+[O_2]} \quad \textit{Equation 1}$$

Where V_{max} is the maximum reaction velocity when both substrates are not limiting. $[S_x]$ and $[O_2]$ denote the concentrations of soluble soil organic carbon and soil oxygen, respectively. The constants kM_{Sx} and kM_{O2} are the corresponding half-saturation constants. Vmax is calculated according to the Arrhenius function in Eq. (2):

$$V_{max} = \alpha_{Sx} \times e^{\frac{-Ea_{Sx}}{RT}} \text{, } \textit{Equation 2}$$

Where R is the Universal gas constant, and T is the temperature in Kelvin. α_{Sx} and Ea_{Sx} are a pre-exponential factor and the activation energy of the reaction, respectively.

The concentration of soluble carbon $[S_x]$ is calculated using Eq. (3):

$$[Sx] = C_{org} \times p \times D_{liq} \times \theta^3 \text{, } \textit{Equation 3}$$

where C_{org} is the total amount of the soil organic carbon, p is the soluble fraction, D_{liq} is the diffusion coefficient for the liquid phase, and θ is the volumetric water content of the soil.

To represent root oxygen loss in the model, we use the dependence of soil oxygen concentration on soil moisture that is already implemented in the model according to Eq. (4):

$$[O_2] = D_{gas} \times 0.209 \times a^{\frac{4}{3}}, \qquad \textit{Equation 4}$$

where D_{gas} is the diffusion coefficient for O_2 in air, 0.209 is the volume fraction of O_2 in air, and a is the air-filled porosity of the soil, which is calculated as follows Eq. (5):

$$a = 1 - \frac{BD}{PD} - \theta \text{, } \textit{Equation 5}$$

where BD is the bulk density, PD is the particle density, and θ is the soil volumetric water content. By variation of θ, we modify the diffusion rate of oxygen in the soil and thus mimic root oxygen loss. While this is not a mechanistic representation, the effect of plant aerenchyma on the diffusion of oxygen from the atmosphere into the soil is similar to the effect of increased air-filled pore space during decreasing soil moisture. Since we do not simulate the impacts of soil moisture on plant or microbial physiological processes, our results are not affected by this approximation.

3. Parametrisation

To make our model setup consistent with carbon cycling in estuarine marshes, we adapted the parameters of the original DAMM model, based on a series of incubation experiments carried out with soil samples from the Elbe marshes near Hamburg, Northern Germany (Neiske et al., in prep.). The samples were incubated under aerobic conditions for a period ranging from 316 to 465 days. As a first step, we calibrated the Introductory Carbon Balance Model (ICBM) (André et al. 1997) to the incubation data to be able to estimate respiration rates for a larger range of soil organic carbon contents than were included in the laboratory incubation runs. Methodological details can be found in (Knoblauch et al. 2013) and (Beer et al. 2022). This was done since the saturation effects of the DAMM model are only apparent at relatively high substrate levels. Subsequently, we used the respiration rates simulated after the first 30 days of the incubation from 300 ICBM runs that differed in initial soil organic carbon content **Figure 1**. This period corresponds roughly to average respiration rates under field conditions, where fresh organic matter is continuously provided, preventing a strong decline in respiration rates due to substrate limitation **Figure 1**.

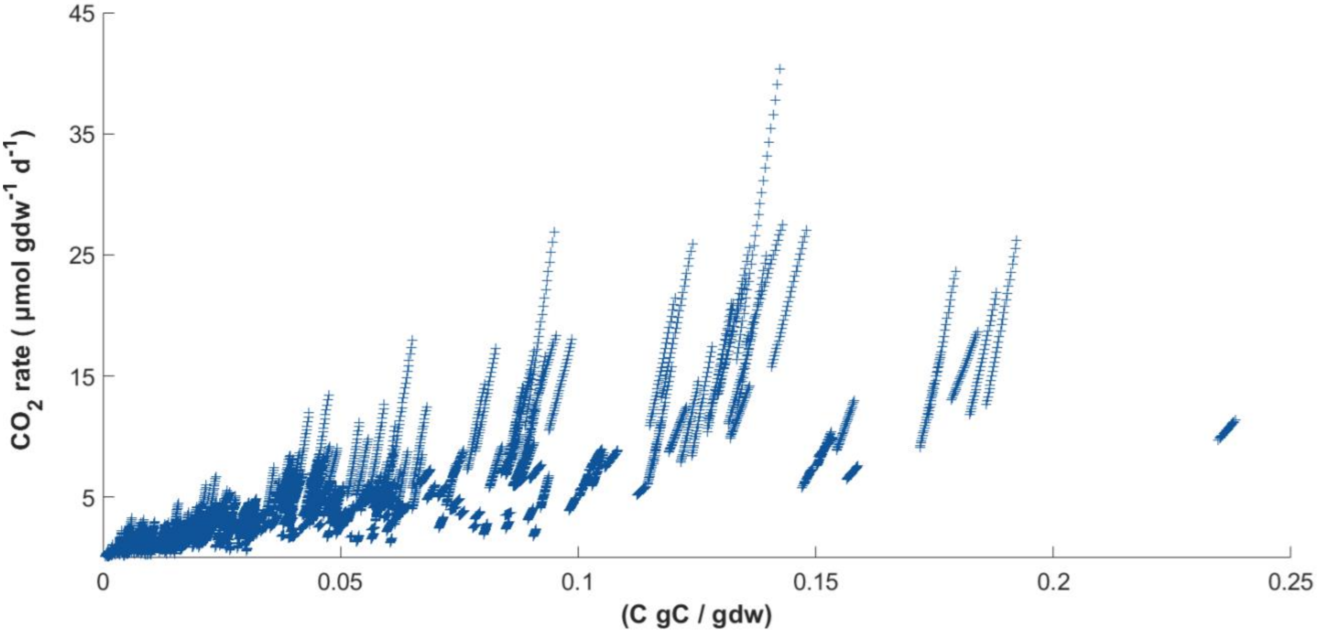


Figure 1*: Respiration rates simulated by the ICBM during the first 30 days of incubation with varying initial soil organic carbon contents (gram carbon per gram dry weight). We assume that this period captures the fluctuations of respiration rates under field conditions where fresh organic matter is continuously provided. Oxygen limitation is not considered here as the incubation was carried out under aerobic conditions.*

Finally, we computed median values of ICBM-simulated respiration for seven bins of the considered soil organic carbon content range and fitted the DAMM model to these data points by visual comparison **Figure 2**. To this end, we varied the parameters α_{Sx}, (Eq. 2) and kM_{Sx} (Eq. 1), thus altering V_{max} and the substrate concentration at which the reaction nears saturation. Other parameters were the same as in the original DAMM model publication (Davidson et al., 2012). See **Table 1** for the model parameters.

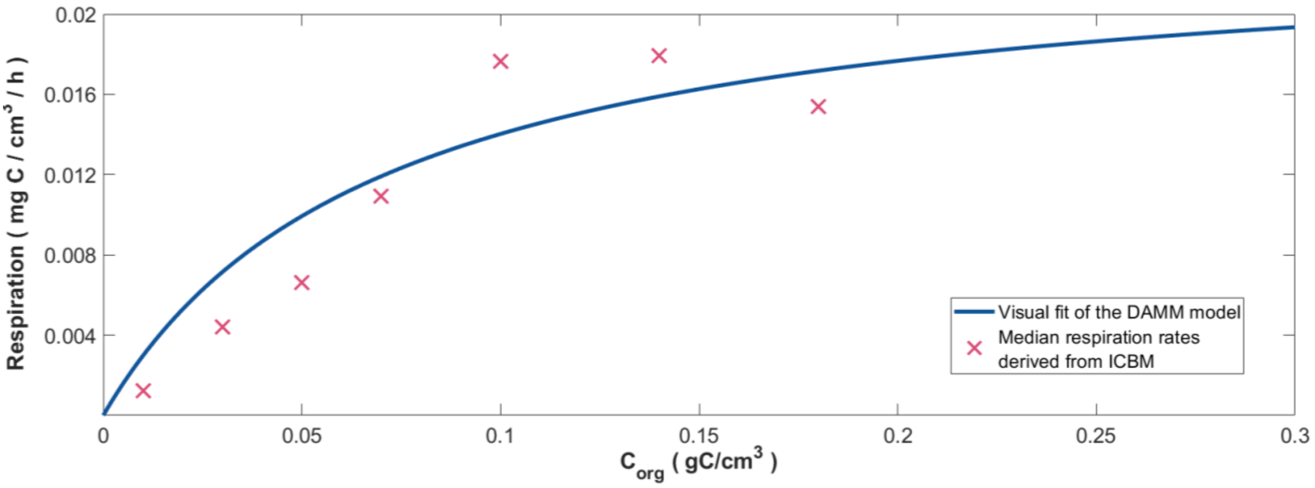


***Figure 2**: Visual fit of the DAMM model (blue line) to median respiration rates (magenta crosses) derived from ICBM simulations across varying soil organic carbon contents.*

Table 1: *Model parameters*

Parameters	**Value**	**Unit**		**Parameters**	**Value**	**Unit**
kM_{Sx}	2.4875E-06	(gC/cm^3)		**θ avg**	0.3	(cm^3 H_2O/ cm^3 soil)
kM_{O2}	0.121	(cm^3 O2/ cm^3 air)		**Range of θ**	[0 - 0.6825]	(cm^3 H_2O/ cm^3 soil)
Ea_{Sx}	72.26E+3	(J mol^{-1})		**D_{liq}**	3.17	-
α_{Sx}	4.0350E+11	(mgC/cm^3/h)		**D_{gas}**	1.67	-
R	8.314	(J mol^{-1} K^{-1})		**BD**	0.8	(g/cm^3)
T	293.15	(K)		**PD**	2.52	(g/cm^3)
p	4.14E-4	-				

4. Results:

By comparing the two model configurations (see **Figure 3**) we find that the variation of the plant trait root oxygen loss leads to a 10% reduced respiration rate, when averaged over all soil oxygen levels, compared to the model configuration driven only by one average soil oxygen concentration, corresponding to a model with one plant functional type. The percentage reduction is averaged over the range of simulated soil carbon content. The first and third quartiles of the distribution of respiration responses comprise a deviation of +33% and -47% from the median curve, respectively.

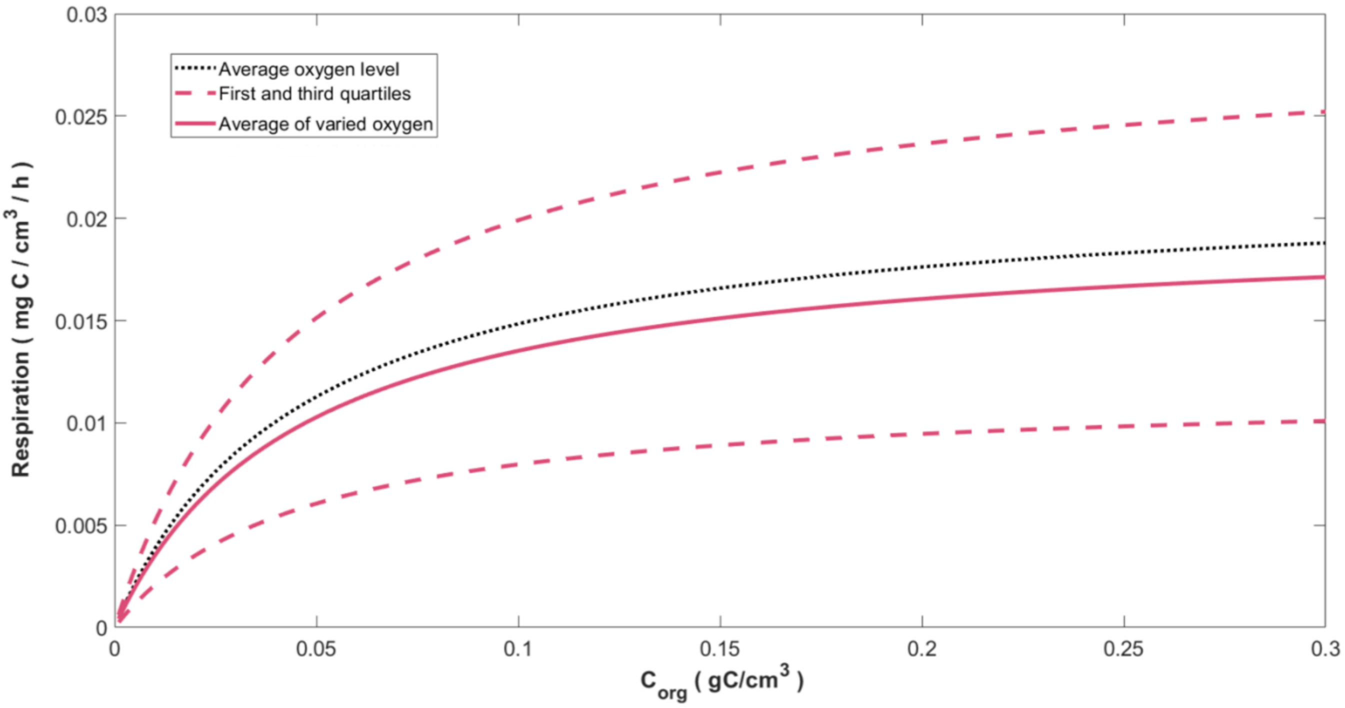


Figure 3: *Comparison of heterotrophic respiration rates assuming an average (black) versus varied (magenta) root oxygen loss. The solid magenta line represents the average heterotrophic respiration response to soil carbon content across the entire range of oxygen levels, while the red dashed lines denote the first and third quartiles of this range. The black dotted line indicates the simulated respiration response assuming an average soil oxygen concentration.*

Our model experiment highlights the significant impact that variation in plant traits, particularly root oxygen loss (ROL) and microbial respiration, can have on the carbon balance of estuarine marshes. By considering a range of soil oxygen levels, we demonstrated how fluctuations in oxygen availability—driven by tidal dynamics, microbial activity, and vegetation composition—can substantially influence carbon cycling in these ecosystems.

However, our current model's assumption of uniform oxygen levels simplifies the complex reality of marsh ecosystems. In natural conditions, oxygen variability is influenced by a multitude of biotic and abiotic factors, including diverse plant species with distinct traits, dynamic vegetation patterns, soil hydrology, and temperature fluctuations. To enhance the accuracy of marsh ecosystem models, it is essential to incorporate these factors.

Developing a more sophisticated modeling approach will not only deepen our understanding of plant-microbe interactions but also enable more realistic predictions of carbon fluxes under changing environmental conditions. Such a model would account for external pressures like warming and sea-level rise, offering more accurate forecasts of future ecosystem responses. For example, based on our simplified model, even a 10% reduction in carbon emissions from marshes could represent nearly 8% of global annual anthropogenic carbon emissions (Intergovernmental Panel on Climate Change (IPCC) 2023), assuming global soil carbon emissions of 31 Tg a^{-1} via heterotrophic respiration from salt marshes (Alongi 2020).

Chapter 3 Model development

1. Introduction

Building upon the insights from our previous findings, it is clear that incorporating trait variability is crucial for accurately simulating carbon dynamics in estuarine marshes. The simplified model underscored how variations in root oxygen loss (ROL) and microbial respiration significantly affect the carbon balance. However, to truly capture the complexity of marsh ecosystems, we need a model that accounts for the diverse factors influencing plant-microbe interactions.

Estuarine marshes are characterized by high biodiversity and intricate interactions among plants, microbes, and the environment. Plants exhibit significant intra- and interspecific trait variability, particularly in traits like ROL and root exudation, which directly impact microbial activity and soil carbon dynamics. These variations lead to non-linear and spatially heterogeneous effects on carbon cycling, highlighting the necessity of including them in ecological models.

In this chapter, we introduce a comprehensive process-based model specifically designed to simulate the effects of biotic interactions—especially plant-microbe interactions—on the carbon cycle in the Elbe Estuarine Marsh. Unlike previous models that aggregate plant traits into averaged functional types, our model explicitly incorporates trait variability. By doing so, it captures the nuanced interactions that influence carbon cycling in marsh ecosystems.

Our model aims not only to reflect the inherent complexity of estuarine marshes but also to provide insights into how these ecosystems may respond to environmental changes, such as shifts in plant community composition, temperature fluctuations, and hydrological variations. By integrating trait variability and environmental dynamics, the model enables a deeper exploration of the processes shaping carbon cycling, ultimately contributing to our understanding of the role of marsh ecosystems in global carbon budgets.

The model comprises four interconnected modules that simulate key processes influencing carbon cycling:

- **Soil Hydrology**: Simulates water movement in the soil, affecting both plant growth and microbial activity by influencing soil oxygen levels through water saturation

- **Soil Temperature**: Models vertical heat flux within the soil, accounting for surface temperature fluctuations, which regulate microbial activity and plant root function.

- **Plant Photosynthesis**: Simulates photosynthetic rates based on environmental factors such as light, temperature, and CO_2 concentration, incorporating trait variability to represent the diverse physiological responses of different plant species and genotypes.

- **Soil Respiration**: Builds on the Dual Arrhenius and Michaelis-Menten (DAMM) model to simulate microbial decomposition and root respiration, integrating the effects of temperature, moisture, substrate availability, and plant traits like ROL and root exudation.

In our model, plants and microbes interact directly through two key processes: root oxygen loss and root exudation. ROL leads to the formation of oxygen-rich microenvironments in the soil, enhancing aerobic microbial activity and accelerating decomposition, which increases CO_2 emissions. Simultaneously, root exudation provides carbon-rich substrates that fuel microbial growth and respiration. By simulating these direct interactions, the model captures the dynamic relationships between plants and microbes that are crucial in determining the overall carbon balance of the marsh ecosystem.

This model represents a significant advancement in modeling estuarine carbon dynamics by integrating the complex interplay between biotic and abiotic factors that shape the carbon cycle. By explicitly accounting for trait variability, the model offers a more detailed and accurate depiction of carbon cycling in marsh ecosystems.

In the following sections, we will provide a detailed description of each module, including the processes they simulate and the equations that govern them. This comprehensive view will illustrate how the modules work together to model carbon cycling in the Elbe Estuarine Marsh.

2. Model Description

To address the gaps identified in our understanding of plant-microbe interactions and their impact on carbon cycling, we developed a new process-based model that captures the key processes driving these dynamics. The model integrates the complex interactions within the marsh ecosystem through four core modules (**Figure 4**).

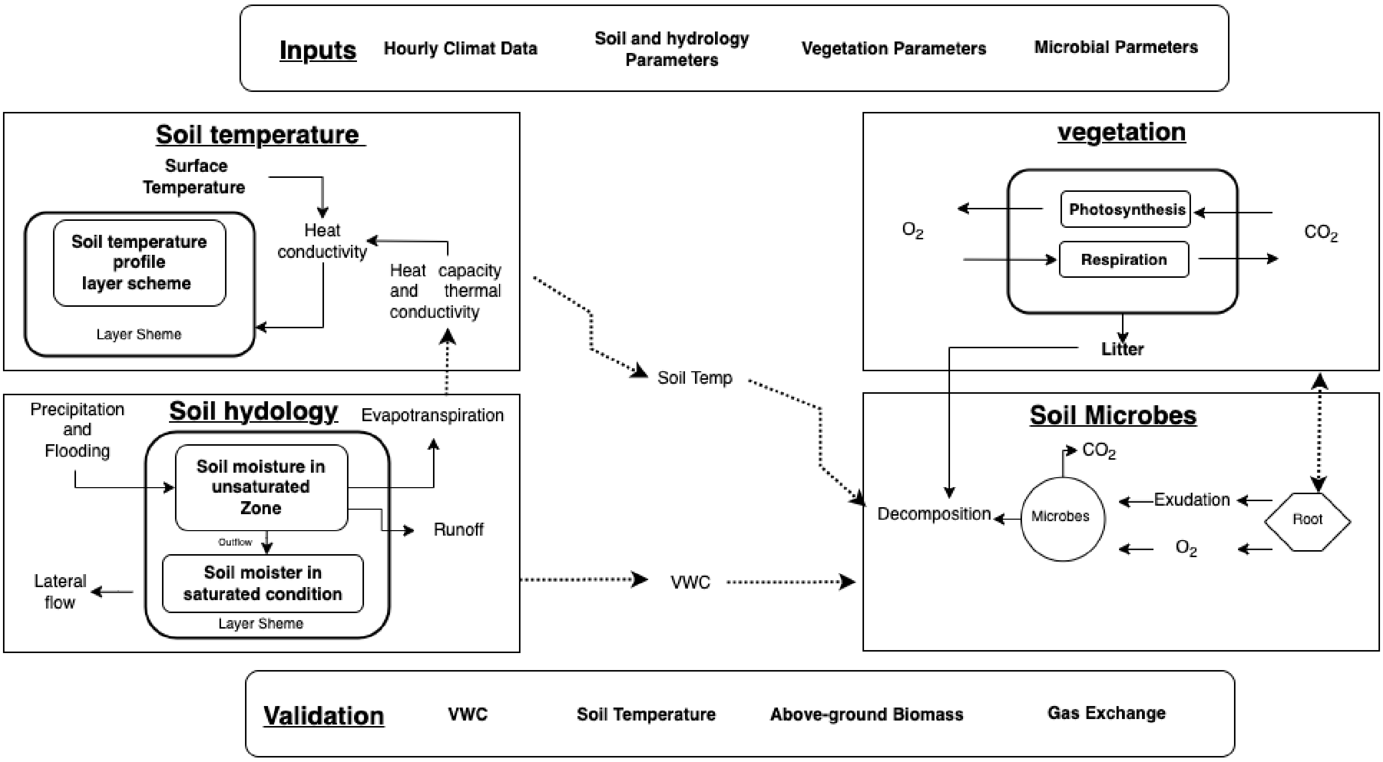


Figure 4: *A graphical representation of the module's structure of the model*

2.1. Surface temperature

Importance of soil surface temperature:

Soil surface temperature is a critical parameter in environmental science and agronomy. It influences various processes such as soil microbial activity, seed germination, plant growth, and evapotranspiration. Accurate estimation of soil surface temperature helps in understanding energy balance, hydrological cycles, and climate modeling. It is also vital for agricultural management, as it affects crop yields and irrigation scheduling (Liu et al. 2007).

In the context of marsh ecosystems, the soil surface temperature plays a pivotal role in maintaining the delicate balance of these habitats. Marshes are characterized by their water-saturated soils, which influence thermal properties differently compared to dry land. Accurate modeling of soil surface temperature in marsh ecosystems is essential for predicting changes in soil moisture, plant growth, and overall ecosystem health. It affects processes such as organic matter decomposition, nutrient cycling, and the habitat suitability for various plant and animal species (Smith et al. 2022)

Approach and Calculation Method:

A detailed simulation model was developed to estimate the wet soil surface temperature, integrating various physical principles and environmental parameters. This comprehensive model ensures that all relevant factors influencing soil temperature are considered, providing robust and reliable predictions.

2.1.1. Components of the Surface Temperature Equation

Radiative Heat Transfer:

This component involves the soil surface's absorption and emission of shortwave and longwave radiation. Shortwave radiation from the sun is absorbed by the soil, while some of it is reflected back due to the soil's albedo. The absorbed energy is then emitted as longwave radiation. This balance between incoming shortwave radiation and outgoing longwave radiation is critical for understanding the soil surface temperature.

Conductive Heat Transfer

This describes the heat flow within the soil, influenced by the soil's thermal properties such as heat conductivity and specific heat capacity. The model simulates vertical heat conduction through the soil layers, which is essential for predicting how heat penetrates the soil over time.

Aerodynamic Resistance

Aerodynamic resistance accounts for the resistance to heat transfer between the soil surface and the overlying air. Factors such as wind speed, surface roughness, and atmospheric stability influence this parameter. Higher wind speeds and surface roughness can enhance heat transfer, while stable atmospheric conditions can reduce it.

Climatic Parameters

The model integrates various climatic data, including air temperature, relative humidity, incoming shortwave and longwave radiation, and other meteorological variables to drive the simulation. These parameters are crucial for accurately simulating the environmental conditions that affect soil temperature.

The following equation was employed to calculate the wet soil surface temperature (xT_s_wet0) at each time step:

$$\begin{aligned}\boldsymbol{xT}_{(\boldsymbol{s\_wet0})} = [&grh0 \cdot (4.0 \cdot peps \cdot c\sigma \cdot Ta3 \cdot (2.0 - XG) + 0.05kSOILdry \cdot XG) + cdg0grh0 \\ &\cdot (srad \cdot fracRADl \cdot (1 - albLsf) + fracRADl \cdot peps \cdot lrad + fracRADl \cdot peps \cdot c\sigma \\ &\cdot Ta4 \cdot (1.0 - XG) + (1.0 - fracRADl) \cdot peps \cdot c\sigma \cdot Ta4 \cdot XG + 3.0 \cdot peps \cdot c\sigma \cdot Ta4 \\ &\cdot (2.0 - XG) + 0.05/kSOILdry \cdot xTg \cdot XG) + tair(k) \cdot cdg0 - cCAIR \\ &\cdot (esatAIR - rhum(k) \cdot esatAIR)]\end{aligned}$$

$$/$$

$$[(grh0 * (4.0 * p\_eps * c\_sigma * Ta3 * (2.0 - XG) + kSOILdry/0.05 * XG) + cdg0)]$$

Equation 6

The variable *grh0* represents the aerodynamic resistance to heat transfer in the air, which is significantly influenced by surface roughness and atmospheric stability. These factors are critical for accurately modeling the resistance encountered by heat as it transfers from the soil surface to the atmosphere (Burakowski et al. 2019).

Incoming shortwave radiation, denoted as *srad*, refers to the solar radiation that reaches the ground. This radiation varies over time and is typically provided by climate data, reflecting the dynamic nature of solar input throughout the day.

The fraction of absorbed long-wave radiation, *fracRADl*, is defined as 1 in the model, indicating that the soil surface absorbs all incoming long-wave radiation. This parameter simplifies the modeling process by assuming maximum absorption efficiency.

The albedo of the bare soil surface, *albLsf*, indicates the reflectivity of the soil surface. Typical values range from 0.1 to 0.2, signifying that a portion of the incoming shortwave radiation is reflected back into the atmosphere (Burakowski et al. 2019).

The emissivity of the land surface, *peps*, describes the efficiency with which the soil surface emits thermal radiation. It is commonly set to around 0.97, reflecting the high emissivity characteristic of natural surfaces like soil (Burakowski et al. 2019).

Incoming longwave radiation, *lrad*, represents the infrared radiation from the atmosphere that reaches the soil surface. This parameter, also provided by climate data, plays a crucial role in the overall energy balance at the surface.

The Stefan-Boltzmann constant, *c_sigma*, is a fundamental physical constant used in the calculation of thermal radiation. This constant is essential for determining the radiative heat flux based on the temperature of the emitting surface (Burakowski et al. 2019).

Air temperature raised to the power of 4, *Ta4*, is derived from the air temperature tair, measured in Kelvin. This term is vital for calculating the longwave radiation emitted by the air, following the Stefan-Boltzmann law.

The variable *XG* is a switch indicating the influence of soil organisms. It is typically set to 1 or 0, depending on whether the biological effects on soil heat transfer are considered in the model.

The dry soil heat conductivity, *kSOILdry*, measures the soil's ability to conduct heat when dry. It is typically around 0.6 W/m·K, reflecting the thermal properties of dry soil materials (Monteith 1981)

Ground temperature at the first soil layer, *xTg*, refers to the initial temperature of the soil surface. This temperature is initialized in the model and serves as a baseline for simulating heat transfer within the soil.

Air temperature at time step k, *tair*, is another crucial climatic parameter provided by climate data. These variable influences both the radiative and convective heat transfer processes at the soil surface.

The combined heat transfer coefficient, *cdg0*, integrates various heat transfer processes and is calculated within the model. This coefficient represents the overall efficiency of heat transfer from the soil surface to the air (Moreira, Colmanetti, and Tibiriçá 2019).

The heat capacity of air, *cCAIR*, is the amount of heat required to raise the temperature of a unit volume of air by one degree Celsius. It has a typical value of ***1297*** J/(m^3·K), reflecting the thermal properties of air.

The saturation vapour pressure of air, *esatAIR*, is the pressure at which air is fully saturated with moisture. This value is calculated using standard meteorological equations and is essential for modeling latent heat fluxes (Monteith 1981).

Finally, relative humidity at time step k, *rhum*, is provided by climate data. This parameter indicates the moisture content of the air relative to its saturation point, affecting both latent and sensible heat fluxes.

***Table 2**: Parameters Utilized in the Calculation of Surface Temperature Dynamics*

Parameter	Description	Value	Unit	Reference
fracRADl	Fraction of absorbed long-wave radiation	1	Dimensionless	-
albLsf	Albedo of the bare soil surface	Typically, 0.1 to 0.2	Dimensionless	(Dickinson 1983)
p_eps	Emissivity of the land surface	Typically, 0.97	Dimensionless	(Jin and Liang 2006)
c_sigma	Stefan-Boltzmann constant	5.67×10^{-8}	W $m^{-2}K^{-4}$	(Crepeau 2009)
Ta4	Air temperature raised to the power of 4	$Tair^4$	K^4	-
XG	Soil organisms influence switch	Typically, 1 or 0	W/m·K	-
kSOILdry	Dry soil heat conductivity	Commonly 0.2	Dimensionless	(Rubio, Josa, and Ferrer 2011)
xT_g	Ground temperature at the first soil layer	Initialized in script	Dimensionless	-
cdg0	Combined heat transfer coefficient	1.976e+05	Dimensionless	(Amer et al. 2014)
c_CAIR	Heat capacity of air	1297	$J/(m^3\cdot K)$	(Mobedi and Gediz Ilis 2023)

2.2. Evaporation- Transpiration

Importance of evapotranspiration:

Accurate estimation of evapotranspiration (ET) is a cornerstone in the fields of hydrology, agriculture, and climate science. ET is the primary process through which water vapor is transferred from land surfaces—including soil, vegetation, and water bodies—back into the atmosphere. It plays a critical role in the water cycle by influencing water availability, irrigation needs, and overall agricultural productivity. The significance of ET in agriculture is particularly profound, as it directly impacts water use efficiency and crop yields, especially in regions where water resources are scarce (Lingling et al. 2013; Past and Wanniarachchi 2022).

In the context of marsh ecosystems, the accurate estimation of ET becomes even more critical. Marshes are unique in their hydrological dynamics, characterized by water-saturated soils that influence the rates of ET differently compared to upland areas. These ecosystems rely on precise ET measurements to maintain the delicate balance between water input and output, which is essential for sustaining plant and animal life. Moreover, marsh ecosystems act as natural buffers against flooding and are crucial for water purification, making the accurate modeling of ET essential for predicting their health and resilience in the face of climate change (Allen et al. 2021; Drexler, Anderson, and Snyder 2008).

As climate change alters precipitation patterns and increases temperatures globally, the need for accurate ET estimation has become more pressing. Higher temperatures and increased atmospheric demand for moisture can lead to enhanced ET rates, exacerbating water stress in plants and making water management more challenging. This is particularly relevant for marsh ecosystems, where changes in ET can disrupt the water balance, leading to altered hydrological conditions that could affect the entire ecosystem's structure and function (Dorau and Mansfeldt 2023).

Understanding ET in marshes is also vital for climate modeling, as these ecosystems play a significant role in carbon sequestration. Any changes in ET rates can influence the carbon balance of these ecosystems, thereby affecting their ability to act as carbon sinks. Thus, accurate ET estimation is not only crucial for local water resource management but also for broader climate change mitigation strategies (Singh et al. 2015).

Approach and Calculation Method

The calculation of evapotranspiration (ET) involves several crucial steps, such as determining net radiation and potential transpiration (ETpot2). This process incorporates key environmental factors such as radiation balance, vapor pressure deficit, and temperature dependencies. The underlying principles stem from energy balance models, where the net available energy (solar radiation minus outgoing radiation and heat flux) is used to drive evapotranspiration processes (Allen, Richard G., PEREIRA, Luis S., RAES, Dirk and SMITH 1998; Brutsaert 1982; Monteith 1981).

Equation:

$$\boldsymbol{ETpot2} = \frac{fRAD_{Hw0} \cdot desatdT + c_{CAIR} \cdot (esatAIR - rhum(k) \cdot esatAIR) \cdot kH2Og0}{(desatdT + \gamma 2)} \times \frac{1}{c_{HH2Olg} \cdot c_{\rho H2Ol}} \qquad \text{Equation 7}$$

The equation for potential transpiration *ETpot2* integrates several environmental factors to estimate water loss through evaporation and transpiration, each playing a crucial role in the overall process.

The term *fRAD_Hw0* represents the net radiation available at the surface after adjusting for soil heat flux and temperature differences.
This term is crucial as net radiation drives the energy available for evapotranspiration, typically calculated by considering the balance between incoming solar radiation and outgoing longwave radiation. Which is calculated as follows:

$$\boldsymbol{fRAD_{Hw0}} = dRAD - 4.0 \times peps \times c\sigma \times Ta3 \times xTs_{wet0} - \frac{kSOILdry \times \left(xTs_{wet0(k)} - xTg(1,1)\right)}{pdz_{SOIL}} \qquad \text{Equation 8}$$

Where:

- **dRAD**: Net shortwave radiation in W/m^2.
- **peps**: Surface emissivity, dimensionless.
- **cσ**: Stefan-Boltzmann constant, W/m2K4.
- **Ta3**: Air temperature raised to the third power in K^3.
- **xTs_wet0**: Surface temperature of the wet soil in Kelvin (K).
- **kSOILdry**: Thermal conductivity of dry soil in W/mK
- **xTg**: Temperature of the ground at the first soil layer in Kelvin (K).
- **pdz_SOIL**: Depth of the soil layer in meters (m).

The slope of the saturation vapor pressure curve, *desatdT*, is essential for determining how vapor pressure changes with temperature, directly influencing the rate of evaporation.

This calculation often involves temperature and empirical constants specific to the air-water system.

The heat capacity of air, *c_CAIR*, measures the amount of energy required to raise the temperature of a unit volume of air by one degree Celsius, influencing the energy available for the ET process, which is calculated as follow:

$$\boldsymbol{desatdT} = e^{\frac{pesatAIR1 \times taC}{pesatAIR1 + taC} \times pesatAIR3 \times \frac{pesatAIR1 \times pesatAIR2}{(pesatAIR2 + taC)^2}} \quad \textit{Equation 9}$$

Where:

- **pesatAIR1**: An empirical constant specific to the air-water system. It is used in the exponent to relate temperature to vapour pressure.
- **pesatAIR2** : Another empirical constant that adjusts the relationship between temperature and vapour pressure when added to the air temperature.
- **pesatAIR3**: A scaling factor that adjusts the overall magnitude of the saturation vapour pressure, typically in units of Pa.
- **taC**: Adjusted air temperature in Celsius (°C).

The terms *esatAIR* and *rhum* denotes the saturation vapour pressure of the air and the relative humidity at the time step, respectively. The difference between these terms reflects the vapour pressure deficit, which drives potential evaporation, with *esatAIR* typically calculated using standard meteorological equations, which are calculated as follows:

$$\boldsymbol{esatAIR} = pesatAIR3 \times e^{\frac{pesatAIR1 \times zTa}{pesatAIR1 + zTa}} \quad \textit{Equation 10}$$

Where:

- **zTa**: Air temperature at time step in degrees Celsius (°C).

- **pesatAIR1**: An empirical constant specific to the air-water system. It is used in the exponent to relate temperature to vapour pressure.
- **pesatAIR2** : Another empirical constant that adjusts the relationship between temperature and vapour pressure when added to the air temperature.
- **pesatAIR3**: A scaling factor that adjusts the overall magnitude of the saturation vapour pressure, typically in units of Pa.

This equation is derived from the Clausius-Clapeyron relation, which describes the phase transition between liquid and vapour states of water and is fundamental in calculating the vapour pressure deficit that drives evapotranspiration (Wallace and Hobbs 2006).

The vapour conductivity coefficient, *kH2Og0*, describes how efficiently water vapour moves through the air, a key factor in the rate of evapotranspiration, which is calculated as follows:

$$\boldsymbol{kH2Og0} = \frac{(Von\ Karman^2 \times max(critD, wind))}{kH2Og}, \quad \textit{Equation 11}$$

Where:

- **Von Karman Constant**: A dimensionless constant that is fundamental in fluid dynamics, particularly in boundary layer theory, representing the turbulence structure near a surface.
- **max (critD, wind)**: The maximum value between a critical wind speed threshold (critD) and the actual wind speed (wind) at the time step, measured in meters per second (m/s). This accounts for the fact that very low wind speeds may have a limited impact on vapour transport.
- **kH2Og**: A parameter representing the aerodynamic resistance or conductance for water vapour transfer, typically determined by environmental conditions and the structure of the plant canopy.

The psychrometric constant, *γ2*, which is modified to account for both aerodynamic resistance and maximum stomatal conductance. It is calculated as:

$$\gamma\mathbf{2}_{=}c_{gamma} \times \left(1.0 + \frac{kH2Og0}{gS\_max\ \_4}\right), \quad \textit{Equation 12}$$

Where:

- **gS_max_4:** represents the maximum stomatal conductance specific to plant traits.

The latent heat of vaporization of water, *c_HH2Olg*, typically around 2.45 MJ/kg, is the energy required to change water from liquid to vapour without a temperature change, crucial for understanding the energy dynamics of ET.

Finally, the density of liquid water, *c_rhoH2Ol*, approximately 1000 kg/m³, is used to convert energy fluxes into volumetric water loss, making the ET estimation applicable to real-world scenarios.

***Table 3**: Parameters Utilized in the Calculation of the Evapo-Transpiration Dynamics*

Parameter	**Description**	**Value**	**Units**	**Reference**
p_eps	Surface emissivity	0.97	Dimensionless	(Monteith 1981)
c_sigma	Stefan-Boltzmann constant	5.67×10−8	$W/m^2 K^4$	(Monteith 1981)
kSOILdry	Thermal conductivity of dry soil	0.6	W/mK	Typical value for dry soils
p_dz_SOIL	Damping depth of the soil for the diurnal cycle	0.15	m	Derived from soil models
c_CAIR	Heat capacity of air	1297	J/(m³·K)	(Monteith 1981)
gamma2_	Psychrometric constant	65.0	Pa/K	(Monteith 1981)
c_HH2Olg	Latent heat of vaporization of water	2.45	MJ/kg	Typical value in physics
c_rhoH2Ol	Density of liquid water	1000	kg/m³	(P 1992)
Von Karman Constant	Turbulence structure near a surface	0.41	Dimensionless	(Bonan 2019)

critD	critical value for any denominator	1.0E-12	Dimensionless	(Bonan 2019)

2.3. Soil hydrology

Importance of soil hydrology:

Soil hydrology is a fundamental aspect of ecosystem management, particularly in marsh environments where water saturation dictates both ecological function and environmental stability. The movement and distribution of water within the soil profoundly affect plant growth, nutrient cycling, and overall ecosystem health. This is especially true in marsh ecosystems, where the proximity of the water table to the surface creates unique hydrological dynamics that are distinct from those in upland areas. The saturated soils in marshes support specialized vegetation types that are well-adapted to these wet conditions. These soils also play a pivotal role in carbon sequestration and nutrient filtering, making it crucial to accurately model soil moisture to predict the resilience of these ecosystems as environmental conditions change. Understanding these dynamics is essential for maintaining the ecological balance and the numerous ecosystem services that marshes provide, including water purification and flood mitigation (Drake et al. 2015; Krauss, Zhu, and Stagg 1963; Moreno-Casasola, Hernández, and Campos 2017) .

Approach:

The developed model employs a layered approach to accurately simulate soil moisture dynamics by dividing the soil into two primary zones: the saturated and unsaturated zones. This stratified structure is vital for precisely capturing the complex behaviour of water as it percolates through the soil profile. Water movement in these zones is predominantly driven by two key forces: matric potential and gravitational potential. In the unsaturated zone, where soil pores are only partially filled with water, matric potential—derived from capillary forces within the soil matrix—plays a crucial role. These potential drives water upward against the gravitational pull, aiding in moisture retention within the soil. Conversely, in the saturated zone, where the soil pores are fully saturated with water, gravitational potential becomes the dominant force, guiding water downward through the soil column as the influence of matric potential diminishes. Understanding the interplay between these forces is essential for predicting soil moisture dynamics, particularly in complex environments like marshes, where these processes are further complicated by specific soil properties and external environmental conditions (Bonan 2019).

Hydraulic conductivity is a pivotal element in this model, as it governs the ease with which water can traverse the soil layers. This conductivity is not a fixed property; it varies according to the soil's water content and type. The Van Genuchten equations are employed to characterize hydraulic conductivity within the model, offering a realistic representation of water movement in both the saturated and unsaturated zones. Saturated hydraulic conductivity (*Ksat*) is particularly critical in the saturated zone, where it determines the rate of water movement downward through the soil. In contrast, within the unsaturated zone, hydraulic conductivity decreases as the soil dries, reflecting the increasing resistance to water flow as matric potential becomes more negative (Bonan 2019).

A critical aspect of the model is its dynamic treatment of thermal conductivity. Unlike simpler models that assign a static value to thermal conductivity, this model recognizes that thermal conductivity is variable and influenced by soil moisture content. In dry conditions, soil exhibits lower thermal conductivity, meaning it is less effective at conducting heat. However, as soil moisture increases, its thermal conductivity also rises, reflecting water's superior heat conduction capability compared to air. This dynamic adjustment is essential for accurately modeling heat and moisture fluxes within the soil, especially under rapidly changing moisture conditions, such as during rainfall events (Bonan 2019).

These components—layered soil moisture representation, dynamic hydraulic conductivity, and variable thermal conductivity—are intricately interconnected. The model continuously adjusts each component based on the prevailing conditions, ensuring that the interactions between water and heat within the soil are accurately represented. The outcome is a robust and detailed simulation capable of capturing the complex dynamics of soil moisture and temperature, offering valuable insights into the functioning of marsh ecosystems under varying environmental conditions. This level of precision is essential for understanding and predicting the behaviour of marsh ecosystems, which are highly sensitive to changes in hydrological and thermal regimes (Bonan 2019).

Soil Moisture Content

The variable O represents the volumetric water content of the soil at each layer and each time step. This parameter is essential for determining the soil's moisture state, which directly influences water availability for plants, the movement of water through the soil, and the soil's thermal properties. Which is calculated as follows:

$$\boldsymbol{O} = min\left(\frac{W}{LD}, Osat\right) \quad \text{Equation 13}$$

- **O**: Volumetric water content of soil (dimensionless).
- **W**: Water content (m).
- **LD**: Thickness of soil layer (m).
- **Osat**: Saturation water content of layer (dimensionless).

This equation ensures that the soil moisture content does not exceed the saturation level, representing the maximum water that the soil can hold.

Effective Saturation

Effective saturation, Se, indicates the degree to which the soil's pore space is filled with water, normalized by the difference between the saturation and residual water contents. It is a crucial parameter in determining the soil's hydraulic properties. Which is calculated as follows:

$$\boldsymbol{Se} = max\left(min\left(\frac{O-Ores}{Osat-Ores}, 1\right), 0\right) \quad \text{Equation 14}$$

- **Se**: Effective saturation of soil k (dimensionless).

- **O**: Volumetric water content of soil (dimensionless).
- **Ores**: Residual water content (dimensionless).
- **Osat**: Saturation water content (dimensionless).

This equation ensures that Se is bounded between 0 and 1, corresponding to completely dry and fully saturated conditions, respectively.

Matric Potential

Matric potential, Ψ, describes the potential energy of water within the soil due to capillary forces. It is a negative pressure that pulls water into the soil pores, counteracting gravitational forces. Which is calculated as follows:

$$\boldsymbol{\Psi} = -\frac{\left(Se^{-\frac{1}{m}}-1\right)^{\frac{1}{n}}}{Aph+Gp} \quad \textit{Equation 15}$$

- **Ψ**: Matric potential (m).
- **Se**: Effective saturation of soil (dimensionless).
- **m**: Moisture release parameter (Genuchten 1980) (dimensionless).
- **n**: Porosity index (Genuchten 1980) (dimensionless).
- **Aph**: Air-entry pressure (Genuchten 1980) (m−1).
- **Gp**: Gravitational potential (m).

The equation captures the nonlinear relationship between effective saturation and matric potential, which is critical for accurately simulating water retention in the soil. the gravitational potential is prescribed in this model.

Hydraulic Conductivity

Hydraulic conductivity, Hp, measures the soil's ability to transmit water. It depends on both the soil's properties and its moisture content, varying between fully saturated and unsaturated conditions. Which is calculated as follows:

$$\boldsymbol{Hp} = \begin{cases} Ksat,\ if\ \Psi(k,l) > 0 \\ Ksat\ \times Se^{\frac{1}{2}} \times \left(1 - \left(1 - Se^{\frac{1}{m}}\right)^{m}\right)^{2},\ if\ \Psi(k,l) \leq 0 \end{cases} \quad \text{Equation 16}$$

- **Hp**: Hydraulic conductivity (m/s).
- **Ksat**: Saturated hydraulic conductivity (m/s).
- **Se**: Effective saturation of soil (dimensionless).
- **m**: Moisture release parameter (Genuchten 1980) (dimensionless).

This equation provides a dynamic adjustment of hydraulic conductivity based on soil moisture, ensuring realistic water movement simulations.

Base Flow

Base flow, Qb, represents the vertical flow of water between soil layers due to differences in matric potential and gravitational potential. Which is calculated as follows:

$$\boldsymbol{Qb(k,l)} = -Hp \times \left(\frac{\Psi(k,l) - \Psi(k,l+1) + Gp(l+1) - Gp(l)}{LD}\right) \quad \text{Equation 17}$$

- **Qb**: Base flow between layers (m/s).
- **Hp**: Hydraulic conductivity at layer l and time k (m/s).
- **Ψ(k,l)**: Matric potential at layer l and time k (m).
- **Gp(l)**: Gravitational potential at layer l (m).
- **LD**: Thickness of soil layer l (m).

This equation calculates the flow of water through the soil profile, which is essential for understanding water redistribution within the soil.

Lateral Flow

Lateral flow, QbL, accounts for the horizontal movement of water, driven by differences in matric potential across the landscape. Which is calculated as follows:

$$\boldsymbol{QbL}(k,l) = -\left(\frac{Hp}{LW}\right) \times (\Psi(k,l) - \Psi L(k,l)) \times (\frac{W}{Wm}) \quad \textit{Equation 18}$$

- **QbL**: Lateral flow (m/s).
- **Hp**: Hydraulic conductivity (m/s).
- **LW**: Lateral distance to water (m).
- **Ψ(k,l)**: Matric potential at layer l and time k (m).
- **ΨL(k,l)**: Lateral matric potential (m).
- **W**: Water content (m).
- **Wm**: Maximum water holding capacity of the layer (m), Wm = Osat x LD.

This equation models the horizontal redistribution of water, which is particularly important in sloped terrains or areas with varying soil moisture levels.

Water Content

The variable W represents the actual water content of the soil, accounting for inflows, outflows, and internal redistribution. Which is calculated as follows:

$$\boldsymbol{W(k,l)} = \begin{cases} W(k-1,l) + \left(rain(k) + Flood - Et(k,l) - Qb(k,l)\right) \times dt, & If\ (\ l = 1) \\ W(k-1,l) + \left(Qb(k,l-1) - Et(k,l) - Qb(k,l) - QbL(k,l)\right) \times dt, & if\ (1 < l < 8) \\ W(k-1,l) + \left(Qb(k,l-1) - Et(k,l) - QbL(k,l)\right) \times dt, & (if\ \ l = 8) \end{cases} \quad \textit{Equation 19}$$

- **W (k, l)**: Soil water content at layer l and time k (m).
- **W (k−1, l)**: The previous time step water content for layer l (m).
- **rain(k)**: Rainfall at time k (m/s).
- **Flood**: Prescribed flooding input (m/s).
- **Et (k, l)**: Evapotranspiration fraction for layer l at time k (m/s).
- **Qb (k, l)**: Base flow between layers l and l+1 at time k (m/s).
- **QbL (k, l)**: Lateral flow for layer l at time k (m/s).
- **dt**: 3600 (s).
- **Wm**: Maximum water holding capacity of the layer (m), Wm = Osat x LD.

This equation dynamically updates the soil water content, reflecting changes due to precipitation, flooding, evapotranspiration, and internal water redistribution between soil layers. The term dt ensures that the unit conversion of rain(k), Flood, Et(k,l), Qb(k,l) and Qb (k,l-1) from (m/s) to (m).

Soil Thermal Conductivity

The variable Ksoil_wet represents the effective thermal conductivity of the soil at layer l and time step k, considering both the soil and any snow cover.

$$\boldsymbol{Ksoil}_{wet(\boldsymbol{k},\boldsymbol{l})} = lambda_{dry} + \left(lambda_{water} - lambda_{dry}\right) \times \left(\frac{O(k,l)}{Osat(l)}\right)^{n} \quad \textit{Equation 20}$$

- **Ksoil_wet(k,l)**: Effective thermal conductivity of the soil at layer l and time k (W/m-K).
- **lambda_drylambda_dry**: Thermal conductivity of dry soil (W/m-K).
- **lambda_waterlambda_water**: Thermal conductivity of water-saturated soil (W/m-K).
- **LD(l)**: Thickness of soil layer l (m).
- **O(k,l)**: Volumetric water content of the soil at layer l and time k (dimensionless).
- **Osat(l)**: Saturation water content of layer l (dimensionless).

- **n**: Porosity index for layer l (dimensionless).

This equation calculates the thermal conductivity of the soil, considering its current moisture content and the presence of snow. The dynamic nature of this calculation allows the model to account for varying heat fluxes, which are crucial for accurate soil temperature simulations.

***Table 4**: Parameters Utilized in the Calculation of the Soil Hydrology Dynamics*

Parameter	**Description**	**Value/Range**	**Units**	**Reference**
n	Pore-size distribution parameter for each soil layer	[1.19, 1.22]	Dimensionless	(Bonan 2019)
Ksat	Saturated hydraulic conductivity	[0.13, 0.20] × 2.77778e-6	m/s	(Bonan 2019)
Aph	Inverse air-entry value (related to matric potential)	[0.016, 0.020] × 10^2	m^{-1}	(Bonan 2019)
Ores	Residual soil moisture content	[0.007, 0.014]	Dimensionless	(Bonan 2019)
Osat	Saturated soil moisture content	0.68	Dimensionless	(Bonan 2019)
lambda_dry	Thermal conductivity of dry soil	0.2	W/m-K	(Bonan 2019)
lambda_water	Thermal conductivity of water	0.95	W/m-K	(Bonan 2019)
LD	The thickness of soil layers	[0.05,50]	m	(Bonan 2019)
LW	Lateral distance to water	350	m	(Bonan 2019)
PsiL	Lateral matric potential	-100	m	(Bonan 2019)

2.4. Soil temperature

Soil temperature plays a critical role in shaping biotic interactions within marsh ecosystems. The interplay between soil temperature and the biological components of marshes, including plants, microbes, and animals, is complex and integral to the overall functioning and health of these ecosystems (Brzostek et al. 2015a).

Root exudation, the process by which plants release organic compounds into the rhizosphere, is another critical interaction influenced by soil temperature. These exudates include sugars, amino acids, and organic acids, which serve as substrates for soil microbes and play a significant role in nutrient cycling and the stabilization of soil structure (Hinsinger, Plassard, and Jaillard 2006).

Soil temperature directly affects the rate and composition of root exudates. Warmer soils generally increase the metabolic activity of plants, leading to higher rates of exudation. This increased exudation can promote microbial activity in the rhizosphere, enhancing the decomposition of organic matter and the mineralization of nutrients. However, the composition of exudates can also change with temperature, potentially altering the balance of microbial communities and affecting processes such as carbon sequestration and the degradation of pollutants (Brzostek et al. 2015b) (Zhu and Cheng 2011) (Dennis et al. 2010).

In marsh ecosystems, where waterlogged conditions create unique challenges for plant survival, the interactions between soil temperature, ROL, and root exudation are particularly important. Accurate modeling of soil temperature in these environments is essential for predicting how these biotic interactions will respond to environmental changes, including climate change. This understanding is crucial for the conservation and management of marsh ecosystems, which provide essential services such as carbon storage, nutrient cycling, and habitat for wildlife (Kirwan and Megonigal 2013) (Mitsch and Gosselink 2015).

Approach

The model employs a detailed heat transfer model to calculate soil temperature, specifically in a layered soil profile. This approach incorporates both the vertical heat flux within the soil layers and the potential cooling effects of floodwater, allowing for a dynamic and realistic simulation of soil temperature changes over time.

The model divides the soil into multiple layers, each with its temperature and thermal properties. The temperature of each layer is updated based on the heat flux between adjacent layers and the surface. The approach is iterative, starting from the surface layer and progressing downwards, ensuring that temperature updates for each layer are based on the most recent information from the layer above.

Soil Heat Flux Calculation

The primary mechanism for updating soil temperatures in the model is based on calculating the heat flux between soil layers. The heat flux (fQsoil) into a layer from above (fQsoil_ux) and out of the layer downwards (fQsoil_xd) are calculated using Fourier's law of heat conduction:

$$\boldsymbol{fQsoil_{ux}} = \begin{cases} \frac{Ksoil_{wet(k,l)} \cdot (xTu - xTg(k,l))}{LD(l)}, \\ \frac{Ksoil_{wet(k,l+1)} \cdot (xTg(k,l) - xTg(k,l+1))}{LD(l+1)}, \end{cases} \quad \text{Equation 21}$$

Where:

- **Ksoil_wet(k,l)**: is the thermal conductivity of the soil, dynamically adjusted based on soil moisture.
- **xTu**: is the temperature of the upper layer.
- **xTg(k,l)**: is the current temperature of the soil layer l at time step k.
- **LD(l)** and **LD(l+1)**: are the thicknesses of the soil layers l and l+1, respectively.

Temperature Update Mechanism

After calculating the heat fluxes, the temperature of each soil layer is updated using the following equation:

$$\boldsymbol{xTg(k,l)} = xTg(k,l) + \frac{fQsoil_{ux}}{CSOIL(l) \cdot LD(l)} \times dt - \frac{fQsoil_{ux}}{SOIL(l+1) \cdot LD(l+1)} \times dt, \quad \text{Equation 22}$$

Where:

CSOIL(l): is the specific heat capacity of the soil.
dt: is the time step 3600 (s).

This equation ensures that the soil temperature is adjusted based on the net heat flux into and out of each soil layer, considering the thermal properties of the soil.

2.5. Photosynthesis

In marsh ecosystems, photosynthesis serves as the primary energy source for plants, which in turn supports a complex web of interactions among various organisms. The organic carbon produced through photosynthesis is vital for both the plants and the microbial communities in the soil. This process is particularly crucial in marshes because the carbon fixed by plants helps sustain the high levels of productivity characteristic of these ecosystems. Additionally, photosynthetic activity in marsh plants influences the carbon balance of the ecosystem, playing a key role in carbon sequestration—a vital function in the context of climate change mitigation (Ren et al. 2022).

Approach:

In this part of the model, the calculation of photosynthesis is based on the **Farquhar model** (Farquhar, von Caemmerer, and Berry 1980), a widely used biochemical model that describes the photosynthetic response of C3 plants to light, temperature, and CO2 concentration. The model integrates various physiological parameters that govern photosynthesis, including the maximum rate of carboxylation (*Vcmax*), the maximum rate of electron transport (*Jmax*), and parameters related to stomatal conductance and respiration. This approach allows for a detailed and dynamic simulation of photosynthetic processes under varying environmental conditions, which is particularly important for understanding plant function in marsh ecosystems.

The photosynthesis module begins by defining the parameter ranges for the photosynthetic calculations specific to Phragmites australis, a common marsh grass. Key parameters include:

- **Rref4**: Respiration at reference temperature (Tref) [mol/m^2/s].
- **Tref4**: Reference temperature for respiration [K].
- **Vcmax4**: Maximum rate of carboxylation [mol/m^2/s].
- **Kc4**: Michaelis-Menten constant for carboxylation [mol/m^3].
- **Ko4**: Michaelis-Menten constant for oxygenation [mol/m^3].
- **P4**: Light balance point [mol/m^3].
- **sCO2_4** and **sO2_4**: Solubility of CO2 and O2 [mol/ml].
- **Q10_4**: Temperature sensitivity of respiration.
- **gS_4_r(k,h)**: stomata conductivity.

These parameters are crucial as they determine the plant's physiological response to environmental variables like temperature and light. The particularity of this model is that it represents the trait variations of plants.

Random Parameter Selection

For each plant, the model randomly selects parameter values within the defined ranges. This stochastic approach allows the model to capture variability in physiological responses among individual plants, which is important for simulating natural ecosystems where individual plants may vary in their photosynthetic capacity (Saadaoui et al. n.d.).

Equations

Light- and CO2-Limited Photosynthesis

The model calculates two different rates of photosynthesis: one limited by light (*Al2_4*) and the other by CO2 (*Ac2_4*).

Light-Limited Photosynthesis

$$\boldsymbol{a4} = -4.5 \times \frac{gS4r(k,h)}{sCO24 \times 1e6}, \textit{ Equation 23}$$

$$\boldsymbol{b4} = gS4r(k,h) \times \left(\frac{4.5 \times CO2}{1e6} - \frac{10.5 \times P4}{sCO24 \times 1e6}\right) - J4 + 4.5\, R4(k,h), \textit{ Equation 24}$$

$$\boldsymbol{d4} = P4 \times \left(\frac{10.5 \times gS4r(k,h) \times CO2}{1.0e6} + J4 + 10.5 \times R4(k,h)\right), \textit{ Equation 25}$$

$$\boldsymbol{xl4} = \frac{-\,b4 - \sqrt{b4^2 - 4.0 \times a4 \times d4}}{2.0 \times a4}, \textit{ Equation 26}$$

$$\boldsymbol{Al24(k,h)} = \frac{J4 \times (xl4 - P4)}{4.5 \times xl4 + 10.5 \times P4} - R4(k,h), \textit{ Equation 27}$$

This set of equations calculates the light-limited rate of photosynthesis for the plant species Phragmites australis. The Farquhar model integrates the effects of light on photosynthesis by considering how electron transport, influenced by light, supports the carboxylation process, which is critical for CO2 fixation. The equations calculate how the amount of light captured by the plant leaves drives photosynthesis, balanced against the respiration rate.

a4: Coefficient representing the inverse of the solubility of CO2.

gS4r(k,h): Stomatal conductance [mol/m^2/s].

sCO24: Solubility of CO2 in water [mol/ml].

b4: Intermediate variable balancing the effects of CO2 concentration and light-driven electron transport.

CO2: Ambient CO2 concentration [ppm].

P4: Light compensation point [mol/m^3].

J4: Rate of electron transport driven by light [mol/m²/s].

R4(k,h): Respiration rate [mol/m²/s].

xl4: Intermediary variable representing the concentration of CO2 after accounting for light and respiration effects.

Al24(k,h): Light-limited rate of photosynthesis [mol/m²/s].

CO2-Limited Photosynthesis (Ac2_4)

$$\boldsymbol{a4} = -\frac{gS4r(k,h)}{sCO24 \times 1e6}, \text{ Equation 28}$$

$$\boldsymbol{K4} = Kc4 \times \left(1.0 + \frac{O2 \times sO24 \times 1e6}{Ko4 \times 1e6}\right), \text{ Equation 29}$$

$$\boldsymbol{b4} = gS4r(k,h) \times \left(\frac{CO2}{1.0e6} - \frac{K4}{sCO24 \times 1e6}\right) - vcmax4r(h) + R4(k,h), \text{ Equation 30}$$

$$\boldsymbol{d4} = \left(gS4r(k,h) \times \frac{CO2}{1e6}\right) + R4(k,h) \times \boldsymbol{K4} + P4 \times vcmax4r(h), \text{ Equation 31}$$

$$\boldsymbol{xc4} = \frac{-b4 - \sqrt{b4^2 - 4.0 \times a4 \times d4}}{2.0 \times a4}, \text{ Equation 32}$$

$$\boldsymbol{Ac24}(k,h) = \frac{vcmax4r(h) \times (xc4 - P4)}{xc4 + Kc4 \times \left(1.0 + \frac{O2 \times sO2 \times 1e6}{Ko4 \times 1e6}\right)} - R4(k,h), \text{ Equation 33}$$

This set of equations calculates the CO2-limited rate of photosynthesis. Here, the model considers the biochemical constraints of carboxylation, specifically how the concentration of CO2 and the enzyme Rubisco's affinity for CO2 versus O2 determine the rate of carbon fixation. This calculation is crucial when light is not the limiting factor, and CO2 availability becomes the primary driver of photosynthetic efficiency.

Where:

- **K4**: Effective Michaelis-Menten constant for carboxylation, adjusted for the presence of oxygen [mol/m³].
- **Ko4**: Michaelis-Menten constant for oxygenation [mol/m³].
- **vcmax4r(h)**: Maximum rate of carboxylation at the current temperature [mol/m²/s].
- **Ac24(k,h)**: CO2-limited rate of photosynthesis [mol/m²/s].
- **xc4**: Intermediary variable representing the concentration of CO2 accounting for carboxylation efficiency.

Net Primary Productivity (NPP_4)

$$\boldsymbol{NPP4(k,h)} = Ah24(k,h) - R4(k,h), \text{ Equation 34}$$

The net primary productivity (*NPP*) is the difference between the net photosynthesis rate (*Ah24(k,h)*) and the plant's respiration rate (*R4(k,h)*). NPP represents the amount of carbon that is fixed by the plant and available for growth after accounting for the energy lost through respiration. This value is crucial for understanding the overall carbon dynamics within the ecosystem and is particularly important for assessing the productivity of marsh ecosystems

Where:

- **NPP4(k,h):** Net primary productivity [g C/(m²·s)].
- **Ah24(k,h):** Net photosynthesis rate (minimum of light-limited and CO2-limited rates) [g C/(m²·s)].
- **R4(k,h):** Respiration rate [g C/(m²·s)].

***Table 5**: Parameters Utilized in the Calculation of Photosynthesis Dynamics*

Parameter	Description	Value	Units	Reference
Rref4	Respiration rate at reference temperature	[5.60e-07, 0.72e-6]	mol/m²/s	Measured
Tref4	Reference temperature for respiration	298.15	K	Measured
Vcmax4	Maximum rate of carboxylation	[1.12e-05, 0.0010]	mol/m²/s	Measured
Kc4	Michaelis-Menten constant for carboxylation	0.08	mol/m³	(Seibert and Tracy 2021)
Ko4	Michaelis-Menten constant for oxygenation	0.35	mol/m³	(Seibert and Tracy 2021)
P4	Light compensation point	2.5e-3	mol/m³	(Chen et al. 2022)
sCO2_4	Solubility of CO2	4.1e-5	mol/ml	(Khalilzadeh et al. 2022)
sO2_4	Solubility of O2	2.4e-6	mol/ml	(Khalilzadeh et al. 2022)
Q10_4	Temperature sensitivity of respiration	[3.0, 3.6]	Dimensionless	Measured
cpar4	Parameter related to light-use efficiency	2.15e-6	mol/s/W	Measured
LAI_4	Leaf Area Index	5	Dimensionless	(Chen et al. 2022)
gS0	Maximum stomatal conductance	335e-3	mol/m²/s	(Eller et al. 2014)
gS_4	Range of stomatal conductance	[0.10, gS0]	mol/m²/s	(Eller et al. 2014)

2.6. Soil respiration

This section of the model implements a model to simulate soil respiration, incorporating both abiotic factors (like soil temperature and moisture) and biotic factors (such as root oxygen loss and root exudation). The approach taken here builds upon the Dual Arrhenius and Michaelis-Menten (DAMM) (Davidson et al. 2012) model framework, widely recognized for its ability to simulate microbial processes in soil. The model is extended by adding root oxygen loss (ROL) and root exudation, both of which are critical for understanding how they affect the carbon cycle of the Elbe marsh ecosystem.

Modeling Soil Respiration: The DAMM Model

The DAMM model is employed to simulate microbial respiration, which is a function of both the availability of substrates (soluble carbon and oxygen) and the temperature. The DAMM model combines the Arrhenius equation to account for the temperature dependence of microbial activity and the Michaelis-Menten kinetics to model the saturation effect of substrate availability on enzyme activity.

Temperature Dependence (Arrhenius Equation)

$$\boldsymbol{vmax(k,l)} = \alpha s \times \ e^{\frac{-Ea}{(Rgas \cdot xTg(k,l))}}, \ \textit{Equation 35}$$

- **vmax(k,l)**: Maximum microbial activity rate in soil layer l at time step k.
- **αs**: Pre-exponential factor, which sets the baseline activity level.
- **Ea**: Activation energy required for microbial processes.
- **Rgas**: Universal gas constant.
- **xTg(k,l)**: Soil temperature in layer l at time step k.

This equation indicates that as soil temperature increases, microbial activity rises exponentially, leading to increased respiration rates.

Substrate Availability (Michaelis-Menten Kinetics)

The model uses Michaelis-Menten kinetics to describe how the availability of soluble carbon (Sx) and oxygen (O2) as substrates influences microbial respiration:

$$\boldsymbol{Rsx(k,l)} = vmax(k,l) \times \left(\frac{Sx(k,l)}{KMs + Sx(k,l)}\right) \times \left(\frac{O2(k,l)}{KMo + O2(k,l)}\right), \text{ Equation 36}$$

Rsx(k,l): Soil respiration rate in layer l at time step k.
Sx(k,l): Concentration of soluble carbon in soil layer l.
KMs: Michaelis-Menten constant for carbon, representing the substrate concentration at which microbial activity is at half its maximum rate.
O2(k,l): Oxygen concentration in the soil layer l.
KMo: Michaelis-Menten constant for oxygen.
KMs: Michaelis-Menten constant for substrate (carbon)

This equation implies that microbial respiration increases with higher concentrations of soluble carbon and oxygen, but the rate of increase diminishes as these concentrations approach saturation.

Integration of Biotic Interactions: Root Oxygen Loss (ROL) and Root Exudation

Root Oxygen Loss (ROL)

The model incorporates Root Oxygen Loss (ROL), one way how plants like Phragmites australis interact with soil microbes by releasing oxygen into the rhizosphere. This oxygen can then be utilized by soil microbes, affecting the overall respiration rate.

The ROL rate is dynamically generated within the model using a random function bounded by minimum and maximum potential rate **Table 6**:

Root Exudation

Root exudation refers to the release of organic compounds from plant roots into the surrounding soil, providing a direct carbon source for microbes which is another way how plants and microbes interact in this model. This process is modeled similarly to ROL, with the exudation rate dynamically determined:

Litter Decomposition and Carbon Dynamics

In marsh ecosystems, the decomposition of plant litter plays a critical role in soil carbon dynamics and overall ecosystem functioning. Litter decomposition is a key component of carbon cycling, influencing both the release and storage of carbon within soil organic matter pools. The modeled approach in this thesis captures the complexity of litter dynamics by integrating processes such as litter input, distribution, and decomposition.

The model assumes that a fixed fraction of the Net Primary Production (NPP) is allocated to litter, with 5% of the total NPP becoming soil organic matter. This fraction is applied to each species at every time step, ensuring a consistent input of organic material into the soil system. The litter is then evenly distributed across eight soil layers, which simplifies the natural complexity of litter decomposition. Although this uniform distribution is a simplification, it is essential for capturing the impact of litter inputs on soil organic carbon dynamics without introducing additional complexity related to spatial heterogeneity.

Once incorporated into the soil, the litter undergoes decomposition at a rate determined by the litter decay constant ($decay\_constant\_base = 0.2\ yr^{-1}$), a value selected based on typical decay rates observed in marsh ecosystems. Research indicates that decay constants for litter decomposition in various ecosystems, including forests and marshlands, generally fall within the range of 0.1 to 0.3 yr^{-1}, depending on litter quality, soil properties, and climatic conditions (Cornwell et al. 2008; Cusack et al. 2009). Although the model uses a single decay constant for simplicity, it acknowledges that actual decomposition rates are influenced by several environmental factors such as soil moisture, temperature, and oxygen availability. These factors regulate microbial activity and organic matter breakdown, which are critical determinants of litter decomposition rates.

The soil organic carbon content (*Corg*) is continuously updated throughout the simulation based on litter inputs and the specified decomposition rate. This iterative process provides valuable insights into the temporal dynamics of carbon cycling and storage within marsh ecosystems. By simulating these interactions, the model helps to elucidate the complex relationships between plant litter inputs and microbial processes, highlighting the critical role of marsh ecosystems in global carbon cycling and their potential as long-term carbon sinks. The simplified approach used in the model serves as a basis for understanding carbon fluxes in marsh environments and can be refined further by integrating spatial variability and species-specific decomposition rates.

Table 6: *Parameters Utilized in the Calculation of Soil Respiration Dynamics*

Parameter	Description	Value	Units	Reference
Rgas	Universal gas constant	8.314	J/mol/K	(Davidson et al. 2012)
BD	Bulk density of soil	1.4	g/cm³	Neiske not published
PD	Particle density of soil	2.70	g/cm³	Neiske not published
alpha_s	Pre-exponential factor for microbial activity	4.035×10^{11}	mgC/cm³/h	Modeled
Ea	Activation energy for microbial activity	72.26×10^{3}	J/mol	(Davidson et al. 2012)
KMs	Michaelis-Menten constant for substrate (carbon)	2.4875×10^{-6}	g C/cm³ soil	(Davidson et al. 2012)

KMo	Michaelis-Menten constant for oxygen	0.121	cm^3 O2/cm^3 air	(Davidson et al. 2012)
p	Conversion factor of soil organic matter to soluble carbon	4.14×10^{-4}	Dimensionless	(Davidson et al. 2012)
Dliq	Diffusivity of soluble carbon in soil	3.17	Dimensionless	(Davidson et al. 2012)
Dgas	Diffusivity of oxygen in soil	1.67	Dimensionless	(Davidson et al. 2012)

3. Input Data and Model Validation

Developing a robust and reliable model to simulate carbon cycling in marsh ecosystems requires not only a solid theoretical framework but also high-quality input data and rigorous validation against empirical observations. This section details the data sources supporting our model, including comprehensive meteorological measurements and plant physiological data. Additionally, the methods and datasets used for model validation are outlined, ensuring that the simulations accurately capture the complex dynamics of the marsh environment.

3.1. Weather Data

The Crucial Role of Weather Data

The model primarily addresses biotic interactions, specifically between plants and microbes, which are significantly affected by surrounding environmental conditions.

Meteorological data play a crucial role in influencing soil temperature, moisture, and energy inputs, thereby shaping these interactions. Accurate weather data are essential for contextualizing the physical environment and ensuring that model simulations reflect real-world conditions.

Establishing a Comprehensive Monitoring Network

A network of three weather stations was established across the Elbe estuary to capture the spatial variability of environmental conditions. The stations were located at:

- Freshwater Site
- Brackish Water Site
- Saltwater Site

These locations represent the salinity and tidal gradient typical of the estuary. Monitoring these distinct environments allows for a comprehensive assessment of how weather patterns influence biotic processes across various marsh types.

***Figure 5**: Weather station at the Fresh water Site*

***Figure 6**: Location of the Weather station and the Freshwater site*

***Figure** 7: Location of the Weather station and the Brakishwater site*

Figure 8: *Location of the Weather station and the Saltwater site*

Table 7: *Location and coordinates of the weather stations*

Locations:	
Freshwater site Hohenhorst	**Latitude** : 53°40'10.54"N **Longitude** : 9°33'19.82"E
Brackish water site Hollerwettern	**Latitude** : 53°49'32.70"N **Longitude** : 9°23'44.96"E
Saltwater site Kaiser Wilhelm Koog	**Latitude** : 53°54'56.74"N **Longitude** : 8°56'47.98"E

High-Resolution Data Collection

The weather stations are equipped with advanced sensors that record meteorological variables at five-minute intervals. This high temporal resolution enables the capture of short-term fluctuations, such as sudden rainfall events or temperature spikes, as well as long-term climatic trends. Capturing these short-term events is essential because they can lead to rapid changes in soil conditions, such as soil oxygen levels, moisture availability, or temperature, which in turn directly affect microbial activity and plant physiological responses. Daily or monthly data would fail to capture these transient events and the subsequent rapid shifts in plant-microbe interactions that play a crucial role in nutrient cycling and carbon dynamics in marsh ecosystems. The continuous data stream, therefore, provides a detailed understanding of how these fine-scale variations influence ecosystem processes, which is vital for accurately modeling and managing marsh environments.

Key Meteorological Variables Monitored

Air Temperature

Air temperature is a crucial factor that influences plant growth, microbial activity, and plant-microbe interactions in marsh ecosystems. For plants, temperature regulates physiological processes such as photosynthesis, transpiration, and root oxygen loss (ROL). Warmer temperatures generally enhance photosynthesis and root exudation rates, increasing the availability of carbon substrates for microbial communities.

For microbes, air temperature affects soil temperature, which in turn drives microbial metabolic rates, including processes such as organic matter decomposition and nutrient mineralization. Higher temperatures often stimulate microbial respiration, accelerating the breakdown of organic material and releasing carbon dioxide, although extreme temperatures can inhibit microbial activity and reduce efficiency.

Air temperature also shapes plant-microbe interactions by modulating the availability of oxygen and nutrients in the rhizosphere. For instance, increased root exudation at higher temperatures can provide more substrates to microbes, potentially enhancing microbial growth and activity, which in turn influences nutrient cycling. However, elevated temperatures can also lead to rapid depletion of oxygen in the root zone, affecting both root function and microbial processes, thereby altering the balance between carbon sequestration and emission.

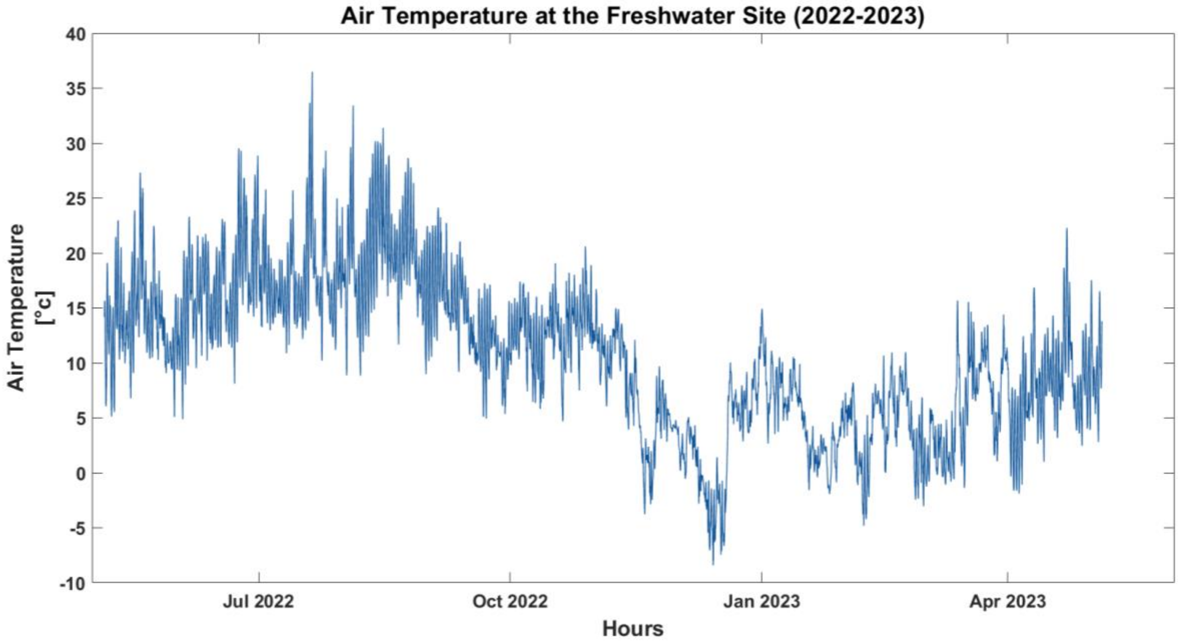


Figure 9: *Air temperature in [°c] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution*

Wind Speed and Direction

Wind speed and direction influence marsh ecosystem dynamics by affecting evaporation rates and soil moisture levels. Higher wind speeds can increase evaporation from the soil surface, potentially reducing soil moisture and influencing plant root functions, such as root oxygen loss (ROL), in response to changes in water availability. Variations in soil moisture caused by wind also affect microbial activity by modifying the availability of water and oxygen, which are important for microbial respiration and organic matter decomposition. These changes can impact both plant and microbial processes, reflecting the interconnected nature of biotic and abiotic factors in marsh ecosystems.

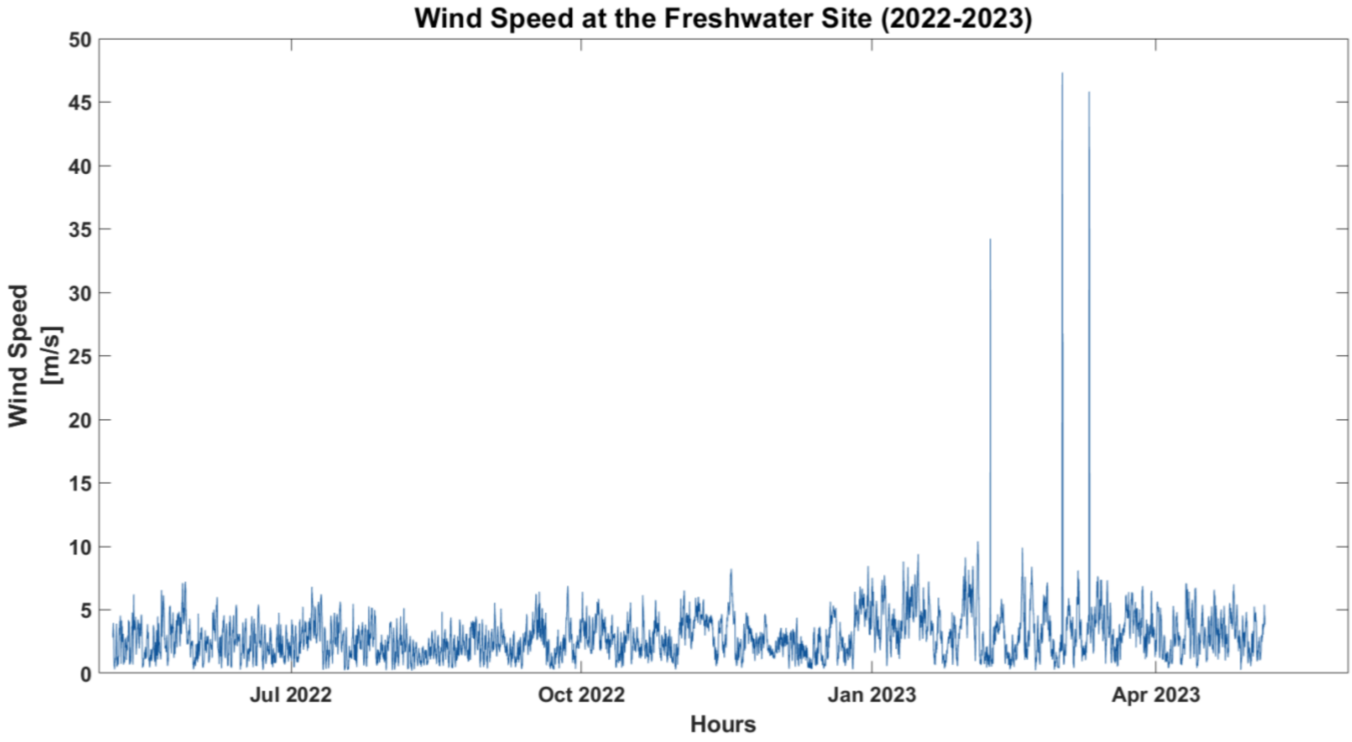


Figure 10: Wind Speed in [m/s] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution

The figure illustrates wind speed measurements at the Freshwater site from May 2022 to May 2023 with an hourly resolution. The y-axis is limited to a maximum of 50 m/s, representing the typical range for wind speeds. Data points exceeding this threshold have been excluded from the plot, as they represent extreme values that are physically implausible and likely result from measurement errors or anomalies in the dataset.

Solar Radiation (Short-wave and Long-wave)

Solar radiation, including both shortwave and longwave components, plays a role in driving energy input into the marsh ecosystem. Shortwave radiation influences photosynthesis by providing the necessary energy for plants, while longwave radiation contributes to heat retention in the system, affecting soil temperature. These factors, in turn, impact both plant growth and microbial activity, influencing carbon cycling processes mediated by plants and microbes.

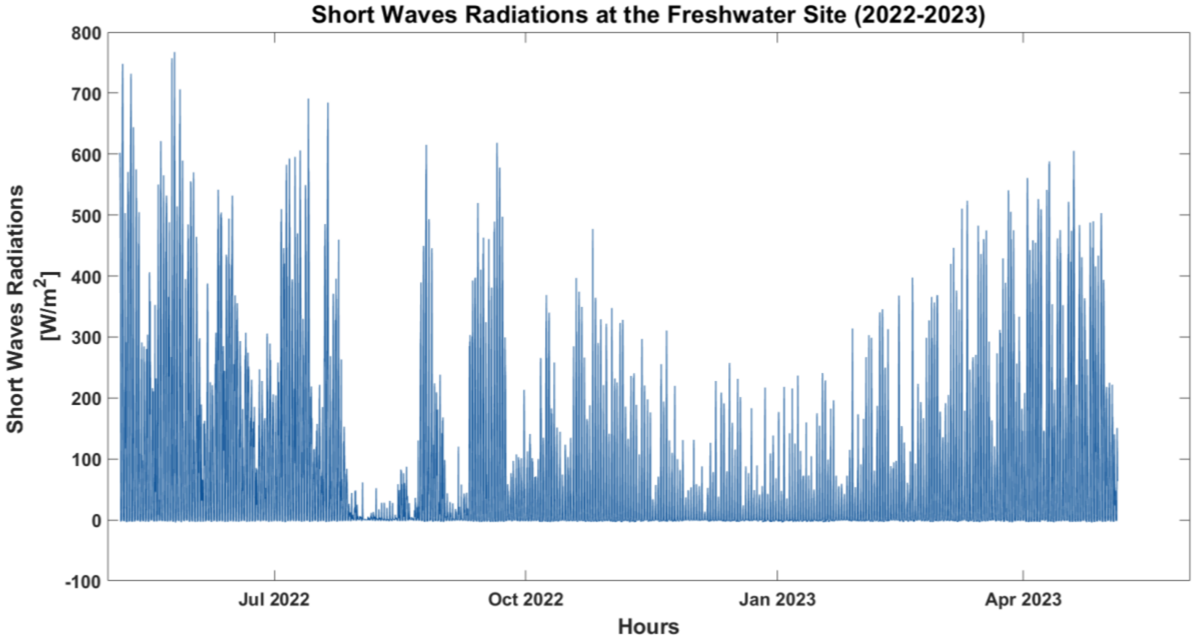


Figure 11: *Short-wave Radiation in [W/m^2] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution*

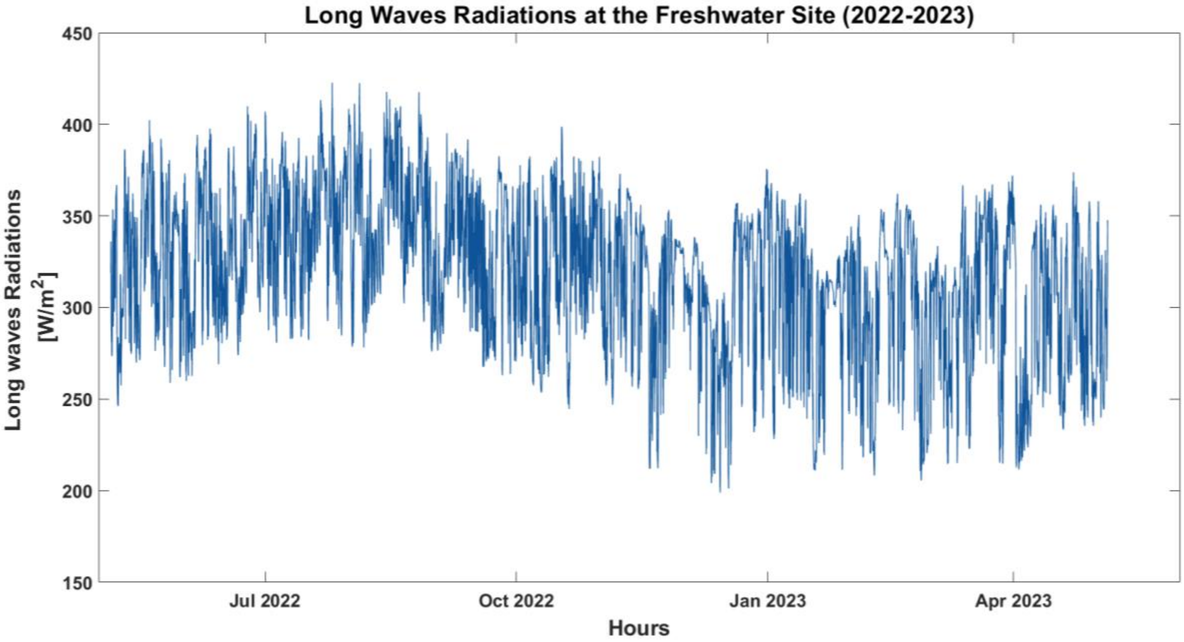


Figure 12: *Long-wave Radiation in [W/m^2] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution*

Precipitation

Precipitation plays a critical role in marsh ecosystems by directly influencing soil moisture levels. For plants, sufficient soil moisture is crucial for supporting physiological processes, such as root oxygen loss (ROL) and root exudation, which contribute to nutrient uptake. For microbes, precipitation impacts their activity by providing necessary moisture, which influences microbial respiration and the decomposition of organic matter. Changes in soil moisture due to precipitation also affect the interactions between plants and microbes, as moisture availability can enhance or limit root exudation, which in turn regulates microbial growth and nutrient cycling. Consequently, variations in precipitation can alter both plant and microbial activities, ultimately impacting carbon fluxes within the marsh ecosystem.

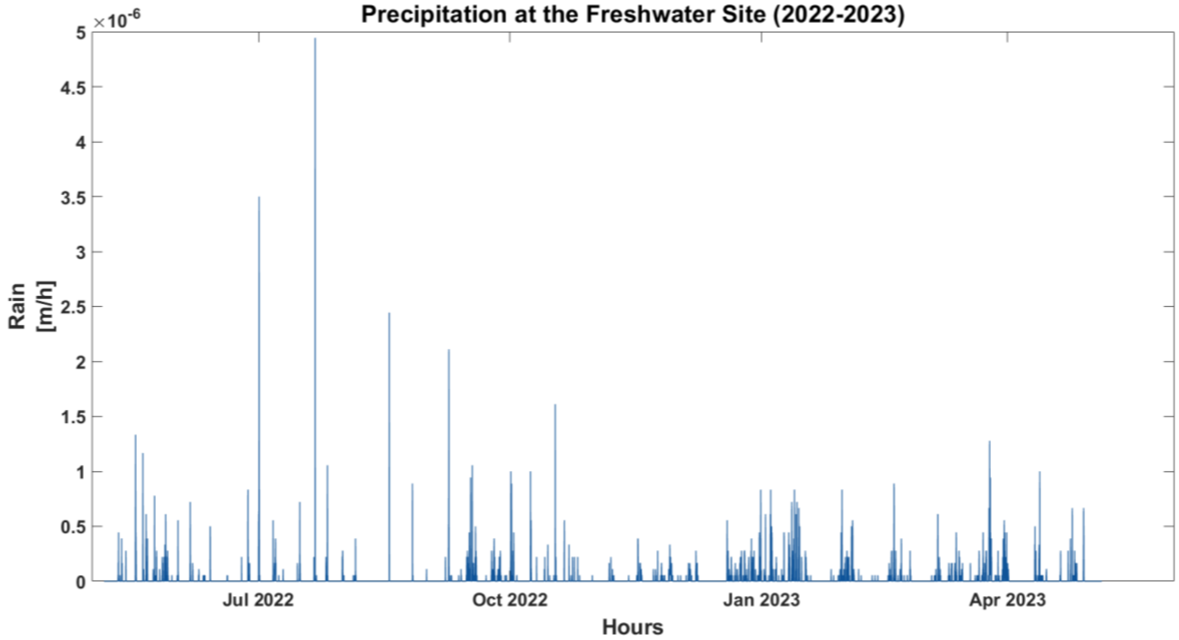


***Figure 13**: Precipitation in [m/h] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution*

Relative Humidity

Relative humidity plays a key role in marsh ecosystems by influencing both plants and microbial processes. It affects evapotranspiration rates, which in turn impact soil moisture availability and plant water status. Lower relative humidity can lead to increased transpiration, potentially causing water stress in plants and reducing root exudation. For microbes, soil moisture influenced by relative humidity affects microbial respiration and decomposition rates. The interaction between plants and microbes is also affected, as changes in root exudation impact the availability of carbon substrates for microbial communities, thereby influencing nutrient cycling and carbon dynamics.

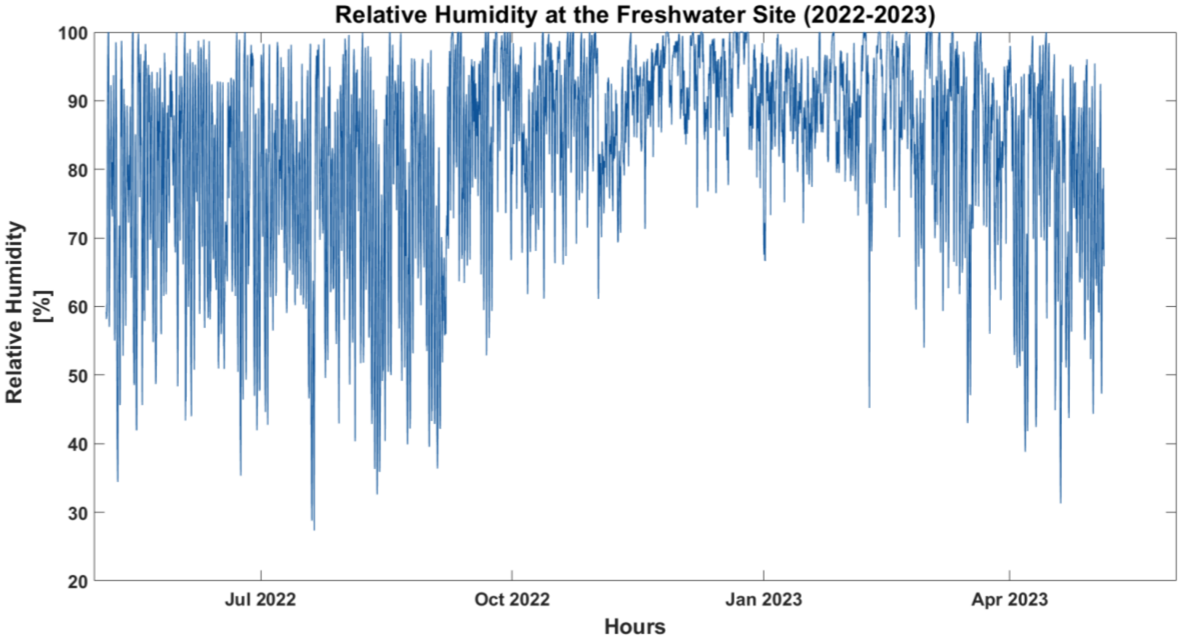


Figure 14: *Relative Humidity in [%] at the Freshwater site from Mai 2022 to Mai 2023 hourly resolution*

Incorporating this detailed meteorological data enables the model to accurately simulate the environmental conditions experienced by plants and microbes. Differentiating between freshwater, brackish, and saltwater sites allows us to capture the varying effects of weather across the salinity gradient of the estuary. This comprehensive environmental context is essential for understanding and predicting the biotic interactions that drive carbon cycling.

3.2. Plant Physiological data

Plants serve as the foundation of marsh ecosystems, functioning as primary producers and playing a pivotal role in carbon cycling, nutrient exchange, and interactions with microbial communities. Accurately modeling these complex dynamics requires capturing plant physiological responses under varying environmental conditions.

Focus on Photosynthetic Responses

The analysis concentrated on measuring the photosynthetic responses of dominant plant species across freshwater, brackish, and saltwater marshes. Understanding how these plants convert light energy into chemical energy under diverse conditions is crucial for quantifying their role in carbon sequestration and overall ecosystem productivity.

Measurement of Light Response Curves

Light response curves illustrate how the rate of photosynthesis varies with light intensity. Generating these curves for each species allows for the following:

- **Quantify Photosynthetic Capacity**: Determine the maximum rate at which plants can fix carbon under optimal light conditions.
- **Assess Environmental Impact**: Understand how factors like salinity, temperature, and stress affect photosynthetic efficiency.
- **Parameterize the Model**: Use empirical data to calibrate the photosynthesis module, enhancing simulation accuracy.

Methodology

- **Instrumentation**: Utilized the GFS 3000 Portable Photosynthesis System for precise, in-field measurements.
- **Replicates**: Collected data from a minimum of three individual plants per species to account for genetic and phenotypic variability.
- **Environmental Conditions:**
    - **Stressed**: Measurements taken during periods of drought or high salinity.
    - **Non-Stressed**: Measurements taken under optimal growing conditions.

- **Seasonality**: Conducted studies during both summer and winter to capture seasonal variations in photosynthetic activity.

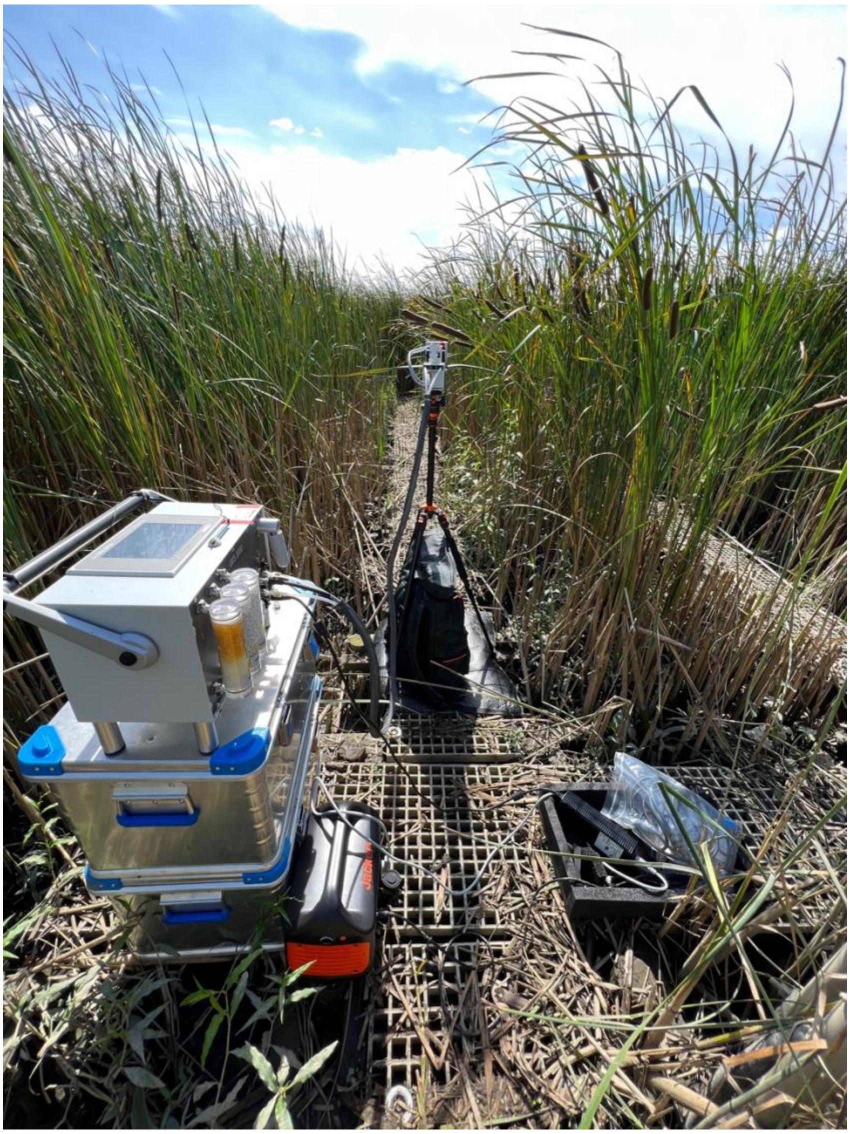


Figure 15: *Light response curve measurements conducted in the pioneer zone of the freshwater site using the GFS 3000 system.*

Capturing Variability for Enhanced Modeling

By measuring plants under different stress levels and across seasons, we ensure our model accounts for:

- **Physiological Plasticity**: Reflects how plants adjust their physiology in response to environmental changes.
- **Species-Specific Traits**: Incorporates differences in photosynthetic responses among species prevalent in different marsh types.
- **Dynamic Ecosystem Interactions**: Simulates the real-world complexity of marsh ecosystems, where conditions are far from static.

Parameterization and Model Integration

The light response data were instrumental in calibrating key parameters within the plant module, including:

- Maximum Photosynthetic Rate
- Light Saturation Point
- Dark Respiration Rate
- Temperature coefficient Q10
-

By fitting the model to empirical observations, we enhance its predictive capabilities, allowing for more accurate simulations of carbon fixation under varying environmental conditions.

3.3. Soil Temperature and Moisture

Data Acquisition

We sourced soil temperature and volumetric water content (VWC) data from the "Volumetric Water Content and Temperature in Soil of RTG2530 Marsh Research Stations" dataset (Neiske et al. Not published). This resource provided high-frequency measurements at depths of 5 cm, 10 cm, 30 cm, and 60 cm below the soil surface.

Soil Temperature

- **Measurements**: Automated sensors recorded temperatures every 10 minutes.
- **Significance**:
  - Captures diurnal fluctuations and seasonal trends.
  - Provides insight into heat transfer within the soil profile.
- **Validation Use**:
  - Assesses the accuracy of the soil temperature module.
  - Helps refine thermal conductivity parameters and heat flux calculations.

Volumetric Water Content

- **Measurements**: Soil moisture sensors collected data at the same intervals and depths as temperature sensors.
- **Significance**:

  - Reflects soil's ability to retain and transmit water.
  - Influences root function, microbial activity, and nutrient cycling.

- **Validation Use**:
  - Validates the soil hydrology module.
  - Enhances understanding of water movement and storage in the soil profile.

3.4. Plant Photosynthesis

Above-Ground Biomass Collection

To validate the photosynthesis module, we collected data on above-ground biomass—the tangible product of photosynthetic activity (Neiske et al. 2024).

Sampling Strategy

- **Locations: Multiple sites along the estuary, covering**
  - Salt Marsh
  - Brackish Marsh
  - Freshwater Marsh

- **Zones**
  - High Marsh (HM)
  - Low Marsh (LM)
  - Pioneer Zone (PZ)

- **Methodology**

    - **Plot Design**: Established five replicate plots (2 x 2 m) per zone.
    - **Harvesting**: Collected biomass from two 20 x 20 cm quadrants within each plot.
    - **Processing**: Dried samples at 60°C to constant weight for dry biomass determination.

Table 8: *Biomass data (Neiske et al. 2024)*

Marsh Type	**Elevation**	**Biomass** (g DW m^2)	**Estimated Carbon** (g C m^2 year)
Salt Marsh	High Marsh	1427.5 ± 174	713.8 ± 87
	Low Marsh	860.4 ± 42	430.2 ± 21
	Pioneer Zone	960.2 ± 55	480.1 ± 27.5
Brackish Marsh	High Marsh	2421.0 ± 365	1210.5 ± 182.5
	Low Marsh	2213.6 ± 314	1106.8 ± 157
	Pioneer Zone	1367.9 ± 140	683.95 ± 70
Freshwater Marsh	High Marsh	1999.0 ± 421	999.5 ± 210.5
	Low Marsh	3404.4 ± 234	1702.2 ± 117
	Pioneer Zone	2504.3 ± 235	1252.15 ± 117.5

- **Conversion**: Estimated carbon content calculated as 50% of dry biomass.
- **Significance**: Provides empirical evidence of plant productivity across environmental gradients.
- **Validation Use**:

    - Compares model-predicted carbon fixation with observed values.
    - Assesses the accuracy of the photosynthesis module under varying conditions.

3.5. Soil Respiration

Gas Exchange Measurements

To validate the soil respiration module, we conducted field measurements of CO_2 fluxes using closed chamber methods (Lexmond et al, not published).

Methodology

- **Equipment**: Chambers equipped with infrared gas analysers (IRGA).
- **Procedure:**
  - Chambers placed over soil plots to enclose a known area.
  - CO_2 concentration monitored over time to calculate flux.
- **Temporal Coverage**: Measurements taken multiple times to capture diurnal and seasonal variations.

Table 9: *Gas Exchange Data (Lexmond et al, not published)*

Date	**Start Time**	**CO_2 Flux** (μg CO_2 m^{-2} s^{-1})	**CO_2 Flux** (g C m^{-2} h^{-1})
17/05/2022	11:10	-95.237610	-0.0935
17/05/2022	12:10	-295.13525	-0.2899
17/05/2022	13:10	-186.66906	-0.1832

- **Conversion Factor**: Used 9.818×10^{-4} to convert μg CO_2 m^{-2} s^{-1} to g C m^{-2} h^{-1}.
- **Interpretation**: Negative values indicate net CO_2 uptake—photosynthesis exceeds respiration.

Validation Process

- **Model Simulation**
  - **Inputs**: Aligned environmental parameters in the model with field conditions (soil temperature, moisture, vegetation cover).
  - **Execution**: Ran simulations to generate predicted CO_2 flux values.
- **Comparison**

  - **Analysis**: Directly compared simulated CO_2 fluxes with measured values.
  - **Assessment**: Evaluated the degree of alignment to determine model accuracy.

- **Calibration**

  - **Adjustment**: Tweaked parameters related to microbial activity, substrate availability, and temperature sensitivity.
  - **Iteration**: Re-ran simulations post-adjustment to refine outputs.

- **Final Validation**

  - **Confirmation**: Ensured that the adjusted model consistently matched empirical data.
  - **Readiness**: Established confidence in the model for broader application.

Implications for Model Reliability

By rigorously validating the soil respiration module, we enhance the model's credibility in simulating carbon emissions. This is vital for understanding the ecosystem's role in global carbon budgets and for predicting responses to environmental changes.

Chapter 4 Results

1. Overview

This chapter presents the outcomes of the *Trait Variation and Biotic Interaction in the Marsh Ecosystem Model* (**TRIBE-M)** developed to investigate how plant traits, particularly root oxygen loss (ROL) and root exudation, influence carbon dynamics in the Elbe Estuarine Marsh ecosystem. The model incorporates a range of plant trait variations to capture the complexity of plant-microbe interactions that are central to soil carbon processes and overall ecosystem functioning.

The results are organized into four main sections corresponding to the core modules of the model: soil hydrology, soil temperature, plant photosynthesis, and soil respiration. Each section compares model outputs with field measurements and discusses the findings in the context of marsh environmental and biological processes. Additionally, the impact of specific plant traits on carbon cycling is examined, providing insights into how trait variability affects the carbon balance within the marsh ecosystem.

2. Soil Hydrology Module

The model effectively simulated the hydrological dynamics of the Elbe Estuarine Marsh, achieving a minimal water balance error of -0.0012329 (m). It accurately represented the intricate water movements, including tidal influences, precipitation, and evapotranspiration. At a soil depth of 5 cm, the volumetric water content (VWC) closely aligned with field measurements, demonstrating the model's reliability in capturing soil moisture variations (**Figure 16**).

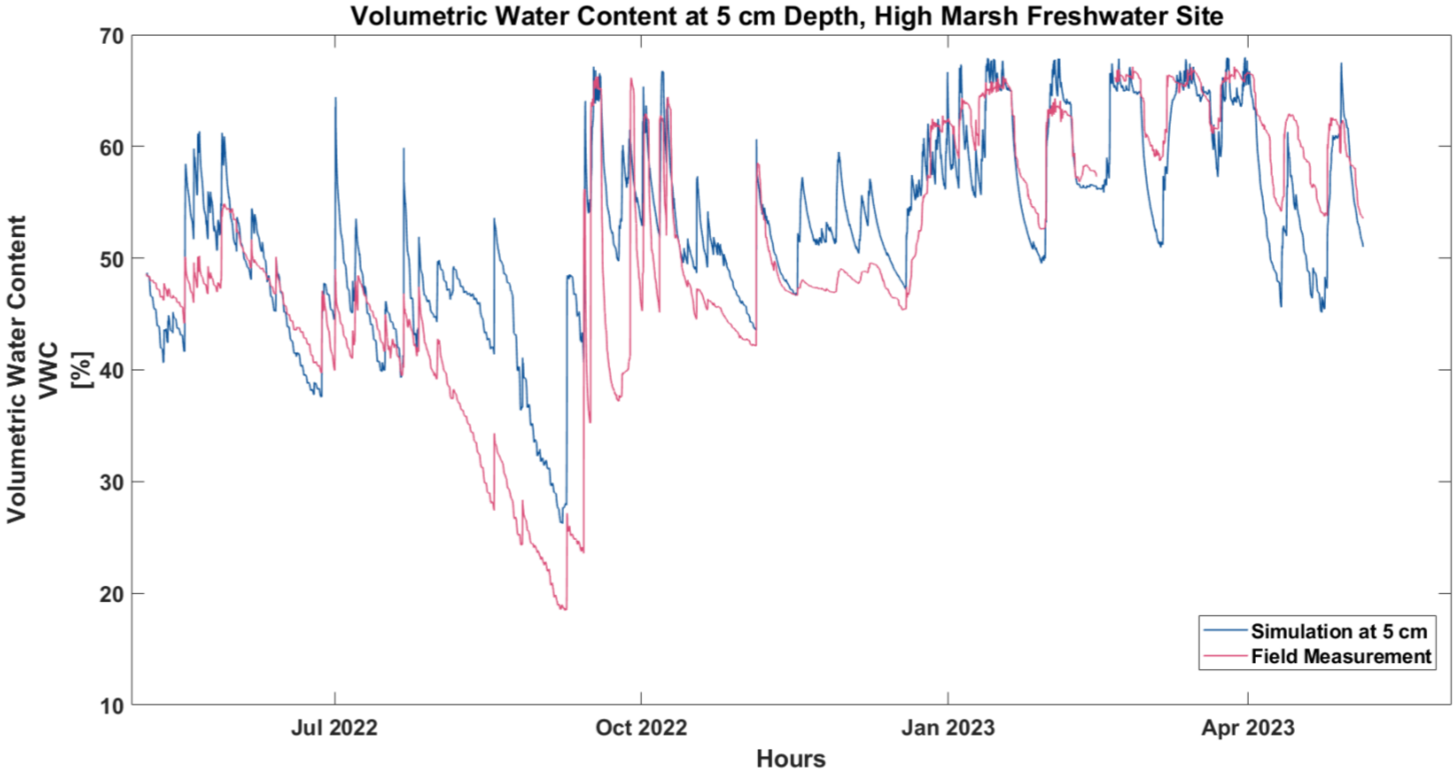


Figure 16*: Simulated vs. Measured Volumetric Water Content at 5 cm Depth*

The successful simulation of soil moisture is critical, as it influences soil temperature, plant physiological processes, and microbial activity. The model maintained an overall water balance throughout the simulation period, with inputs from rainfall and tidal flooding effectively balanced against losses from evapotranspiration and subsurface flow. This accurate hydrological representation ensures the robustness of subsequent model components related to carbon cycling.

3. Soil Temperature Module

Soil temperature significantly affects microbial respiration and plant productivity by influencing the rates of carbon cycling processes. The model accurately simulated soil temperatures at a depth of 5 cm, closely matching the diurnal and seasonal patterns observed in field measurements (**Figure 17**).

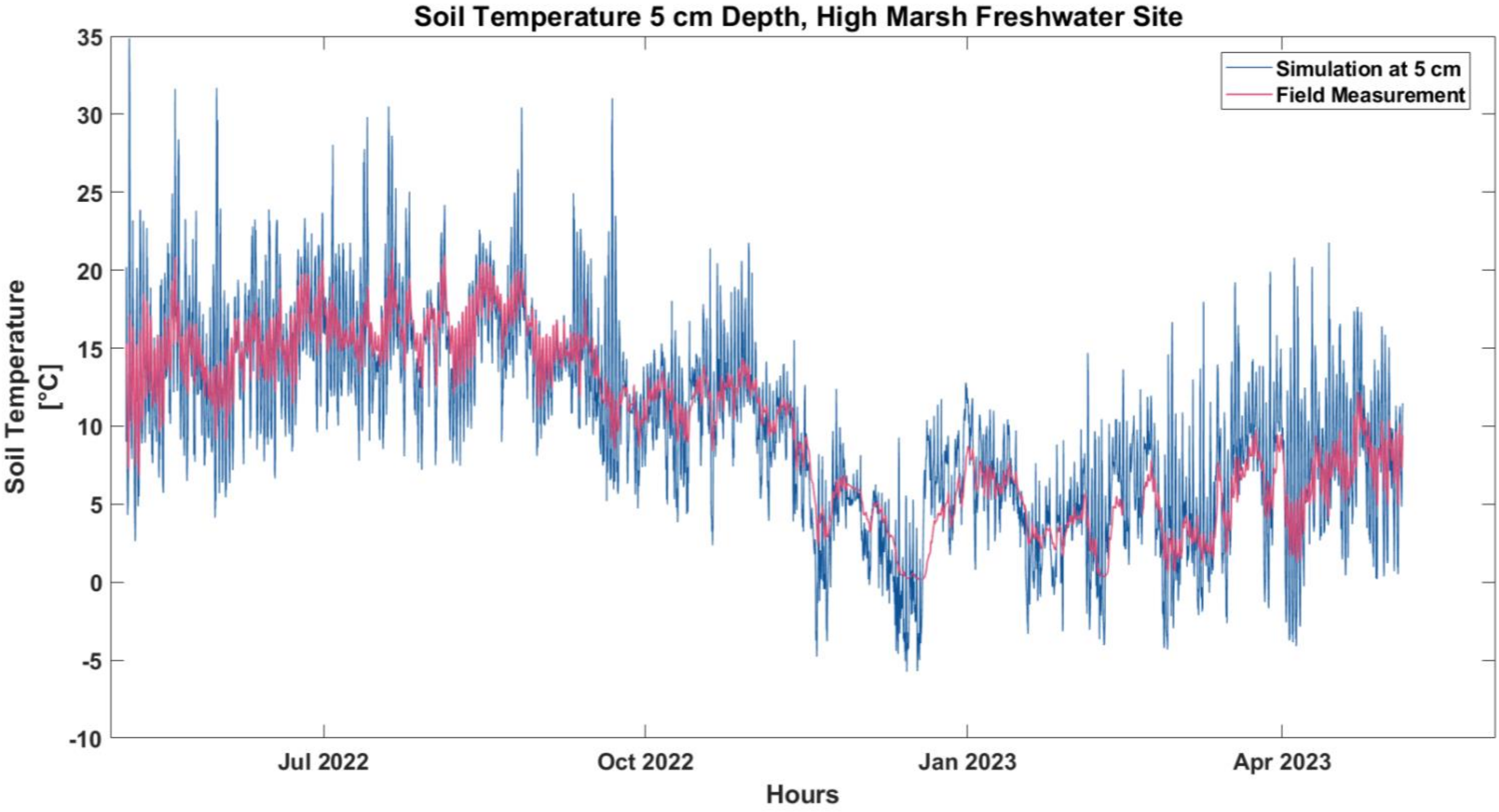


***Figure 17**: Simulated vs. Measured Soil Temperature at 5 cm Depth*

This alignment confirms the model's capability to capture temperature dynamics driven by external climatic factors and internal soil properties. Accurate soil temperature simulations are essential for understanding temperature-sensitive processes such as microbial activity and plant respiration, thereby enhancing the reliability of the overall ecosystem simulations.

4. Plant Photosynthesis Module

The model estimated the total annual photosynthesis for Phragmites australis at *1720.45* g C/m²/year and total plant respiration at *506.97* g C/m²/year, resulting in a net primary production (NPP) of ***1213.47*** g C/m²/year. While *Phragmites australis* demonstrates high productivity, its role in carbon sequestration also depends on the balance between productivity and soil respiration. High productivity alone does not necessarily lead to high carbon sequestration.

Comparison with Field Measurements

When comparing the model’s predicted NPP to empirical measurements from the freshwater marsh's high marsh zone, which recorded an estimated carbon content of 999.5 ± 210.5 g C/m²/year (Neiske et al. 2024), the model’s value of 1213.47 g C/m²/year is slightly higher. This difference is well within a reasonable range, considering the variability in environmental conditions and assumptions made during the modeling process. Factors such as root biomass contributions, local environmental gradients, or seasonal fluctuations in plant growth may contribute to these differences.

The alignment between the model's predictions and field measurements validates the model's accuracy in simulating plant productivity. The measured biomass data serve as a valuable benchmark, reinforcing confidence in the model’s ability to represent carbon dynamics in marsh ecosystems. While the model might slightly overestimate productivity, this is expected given the variability in plant growth and the complexity of marsh ecosystems.

Comparison with Global NPP Ranges

In a broader context, high marsh ecosystems with dominant species like Spartina and Juncus typically exhibit NPP values ranging from 500 to 1500 g C/m²/year, depending on factors such as nutrient availability and hydrological conditions. Studies such as the global synthesis of carbon balance in salt marshes and mangroves and more specific ecosystem research (Alongi 2020; Bautista, Gassmann, and Pérez 2023) provide this typical range of NPP values

The model's NPP estimate of 1213.47 g C/m²/year fits comfortably within this established range, suggesting that the freshwater marsh ecosystem being modeled is relatively productive. Given that nutrient levels and hydrological conditions in the Elbe Estuarine Marsh are favourable, this productivity level is expected, further supporting the model’s reliability. The higher end of the range can be associated with moderate to high nutrient levels, which is consistent with the high productivity observed in the field.

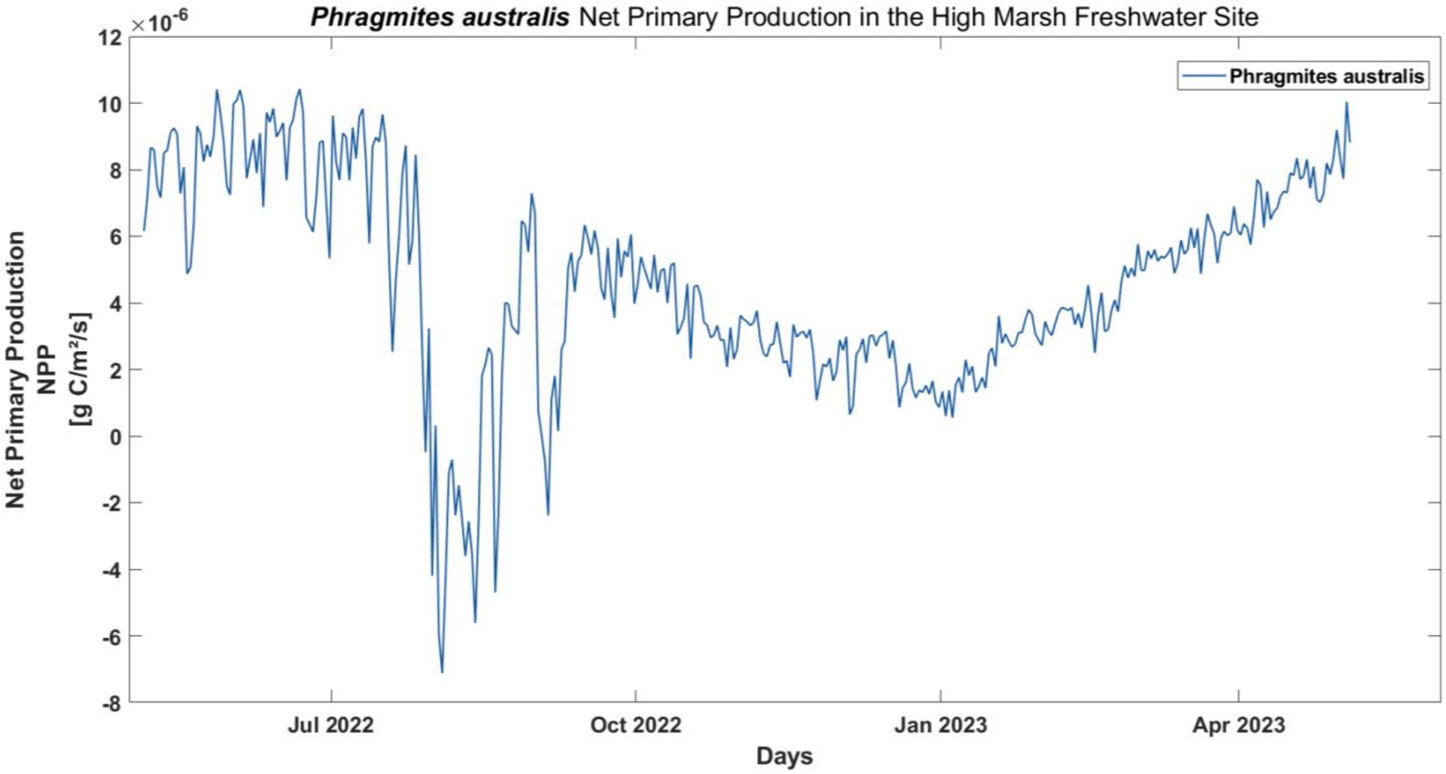


Figure 18*: Simulated Net Primary Production of Phragmites australis in the High Marsh of the Elbe Estuary*

The NPP pattern in **Figure 18** shows a decline in winter due to low temperatures, as expected. Interestingly, there is also a decline in NPP during the summer, where it even becomes negative. This could be attributed to environmental stress factors such as extreme temperatures or increased plant respiration exceeding photosynthetic rates during peak summer months.

Overall, the close alignment between the model's NPP predictions, field measurements, and global benchmarks strengthens the case for the model's accuracy in simulating plant processes. This comparison suggests that the freshwater marsh ecosystem modeled here is functioning as a highly productive system, likely contributing significantly to carbon sequestration in the region. The small differences between predicted and measured values are understandable and reinforce the model's robustness in capturing complex ecological processes.

5. Soil Respiration Module

Soil respiration is a major contributor to carbon fluxes in marsh ecosystems, driven primarily by microbial decomposition of organic matter and plant root activity. In the model, soil respiration is calculated as the sum of microbial respiration and root respiration, which are estimated independently. In this study, the model simulated a baseline soil respiration rate of **1002.88** g C/m^2/year, which represents the combined flux of microbial and root respiration and is within the expected range for marsh ecosystems.

To validate the model's performance, empirical gas exchange data were collected on May 17, 2022, at three different time points. The measured CO_2 fluxes closely matched the model's predictions, providing support for the model's accuracy:

***Table 10**: Comparison of Simulated vs. Measured CO_2 Flux Values*

Time	**Measured Flux (g C/m^2/h)**	**Simulated Flux (g C/m^2/h)**
11:10	0.0935	0.2283
12:10	0.2898	0.2676
13:10	0.1833	0.1955

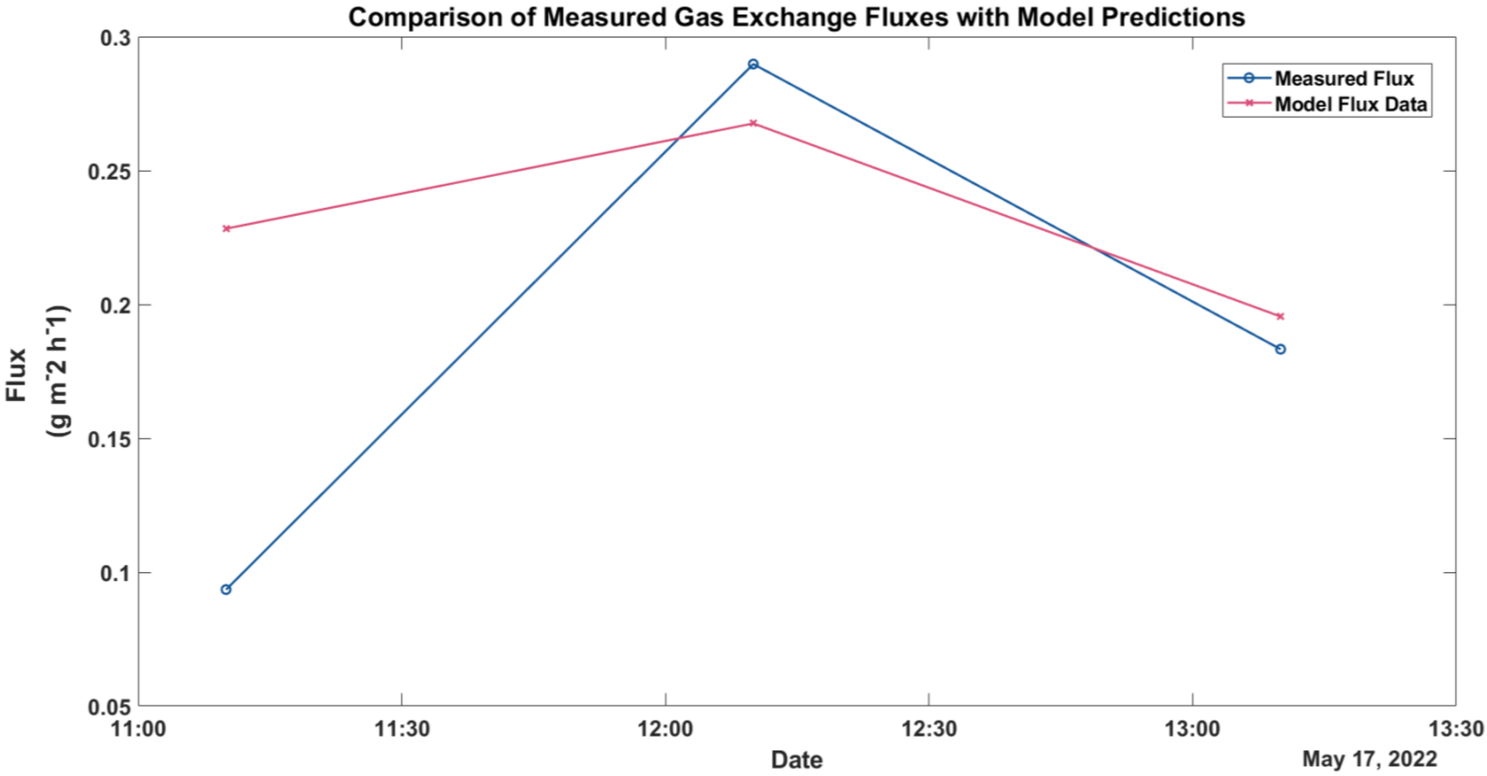


Figure 19: *Comparison of Measured Gas Exchange Fluxes with Model Predictions at the Freshwater High Marsh Site*

Although only three flux measurements were available, the close agreement between these observed values and the model's predictions indicates that the model can capture the general range of soil respiration dynamics in the ecosystem, suggesting consistency with field measurements and that predictions are in the correct range.

Moreover, when comparing this baseline soil respiration value to other global studies, it aligns well with established research. For example, in the study "Carbon Balance in Salt Marsh and Mangrove Ecosystems: A Global Synthesis" by (Alongi 2020), soil respiration in salt marshes was reported to range from 300 to 1500 g C/m^2/year. The model’s predicted value of 1004.75 g C/m^2/year falls comfortably within this range, further supporting the validity of the model’s results. This comparison highlights that the model's simulation of soil respiration is consistent with observed global patterns, reaffirming its reliability in predicting carbon fluxes in marsh ecosystems.

The seasonal pattern of soil respiration depicted in **Figure 20** shows considerable variability throughout the year. In winter, the respiration rates are lower, reflecting decreased microbial and root activity due to cooler soil temperatures. During summer, respiration rates increase significantly, driven by higher temperatures that boost microbial decomposition and root metabolic processes. Interestingly, there are periods in late summer where respiration declines slightly, potentially due to soil moisture limitations or high temperature-induced stress, which can limit microbial activity.

The increased evapotranspiration during summer months leads to reduced soil moisture, which, in turn, enhances oxygen availability in the soil pores. This increased oxygen level can stimulate aerobic microbial activity, thereby affecting soil respiration rates. Additionally, plant water uptake during the summer further influences soil moisture levels, creating fluctuations in both oxygen availability and microbial activity, particularly in the rhizosphere.

Additionally, **Figure 20** illustrates the differences in respiration rates across soil layers. The uppermost layers show higher respiration rates compared to deeper layers, which is attributed to greater root density and more active microbial populations in the topsoil, where organic matter and oxygen availability are highest. As depth increases, reduced oxygen availability and organic carbon lead to diminished microbial activity and therefore lower respiration rates. This vertical differentiation emphasizes the complex interplay between soil depth, oxygen diffusion, root presence, soil moisture, and microbial dynamics in regulating soil respiration.

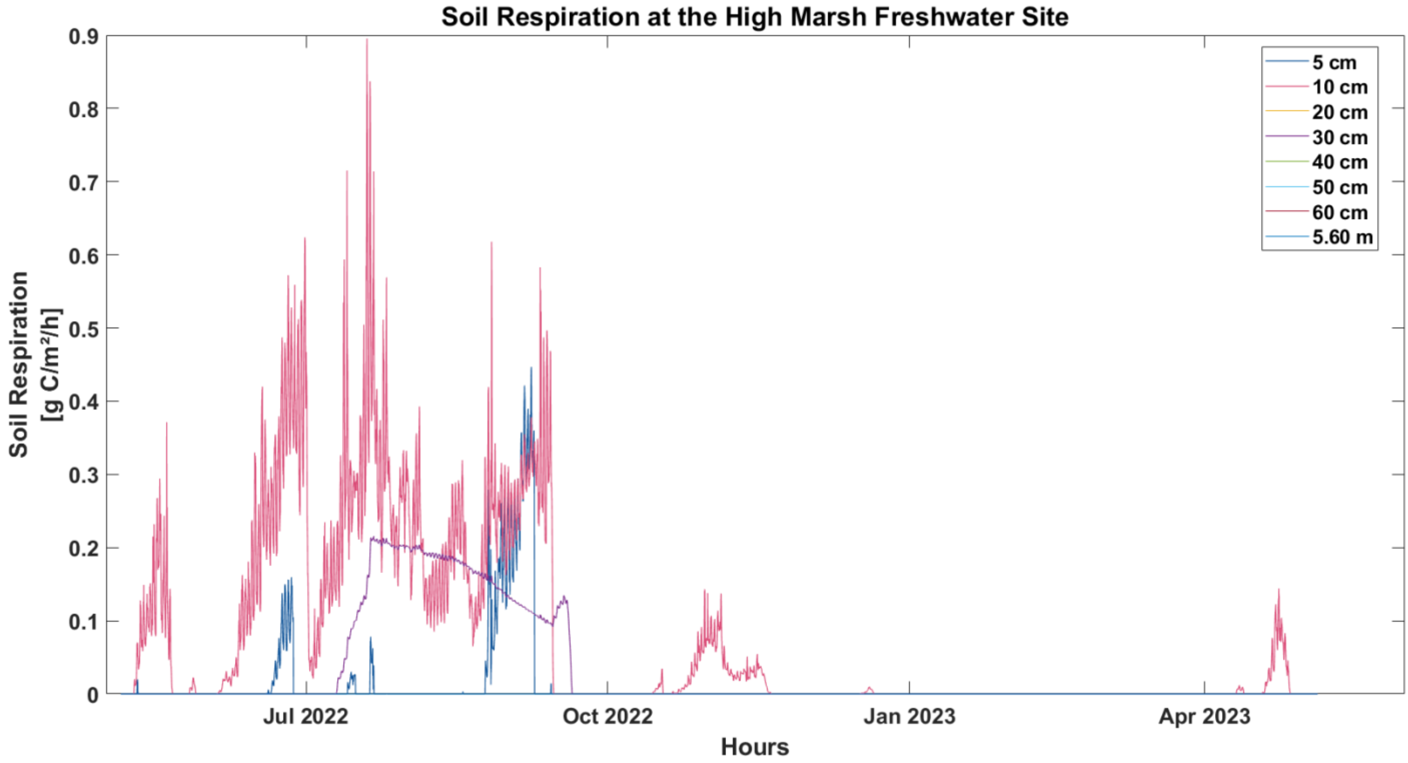


Figure 20*: Simulated Soil Respiration Rates in the High Marsh of the Elbe Estuary*

This validation is crucial because soil respiration plays a key role in carbon cycling, directly influencing whether a marsh acts as a net carbon sink or source. The model's accurate replication of observed respiration rates enhances our confidence in its application for broader ecosystem assessments and climate change studies.

6. Carbon balance

Baseline Carbon Balance

Under baseline conditions, where no interaction from root oxygen loss (ROL) or root exudation is considered, the carbon balance was calculated to be 210.60 g C/m²/year. This carbon balance is determined by the difference between carbon inputs from photosynthesis and carbon outputs through plant and soil respiration. The positive balance suggests that the marsh functions as a net carbon sink, sequestering more carbon than it releases to the atmosphere.

This baseline scenario reflects the carbon dynamics of the marsh ecosystem, where carbon inputs via photosynthesis exceed losses through respiration. The ability of the marsh to act as a net carbon sink indicates its current contribution to atmospheric carbon regulation. However, both carbon sequestration and carbon release are part of the natural carbon cycle, which must be balanced over the long term for ecosystem sustainability. Marsh ecosystems play an important role in moderating atmospheric CO_2 levels, providing a valuable ecosystem service (Shiono and Nakazono 2024).

The baseline simulation provides a crucial reference point for further analysis. It assumes no significant contributions from ROL or root exudation, both of which are processes known to influence soil respiration but remain poorly understood in their full complexity. Root exudation and ROL are highly variable, influenced by plant species, environmental conditions, and microbial interactions (Canarini et al. 2019; Vives-Peris et al. 2020). Since the exact quantities of ROL and exudates released by plant roots are challenging to quantify in dynamic field conditions, this baseline scenario offers a foundation for sensitivity analyses where these processes are introduced.

Sensitivity Analysis of ROL and Exudation on Carbon Balance

Given the uncertainties surrounding ROL and root exudation—both in terms of their drivers and the extent of their release (Canarini et al. 2019; Vives-Peris et al. 2020)—a sensitivity analysis was conducted to explore their potential impact on soil respiration and overall carbon balance. This analysis allowed us to examine how changes in ROL and exudation might affect the carbon sequestration potential of the marsh ecosystem.

Impact of Root Oxygen Loss (ROL)

Increased ROL had a significant impact on soil respiration:

- A 5% increase in ROL raised soil respiration to 1,046.07 g C/m^2/year.

- A 20% increase led to 1,172.49 g C/m²/year.

These elevated levels of soil respiration caused the carbon balance to decline sharply:

- With a 20% increase in ROL, the carbon balance dropped to 40.99 g C/m²/year.

This substantial reduction indicates that increasing ROL significantly diminishes the ecosystem's carbon sink capacity by accelerating soil respiration. The enhanced oxygen availability due to ROL likely fuels microbial activity, leading to higher rates of organic matter decomposition and increased CO_2 emissions from the soil(Vives-Peris et al. 2020).

Impact of Root Exudation

In contrast to ROL, increasing root exudation had a smaller effect on soil respiration and carbon balance:

- A **5% increase** in exudation led to a slight rise in soil respiration to **1,006.06** g C/m²/year.
- A **20% increase** resulted in soil respiration of **1,014.13** g C/m²/year.
- The carbon balance declined modestly to **199.34** g C/m²/year with a 20% increase in exudation.

These results indicate that root exudation alone does not drastically alter the carbon dynamics of the marsh. While exudates provide additional substrates for microbial decomposition, their overall contribution to soil respiration appears to be moderate compared to the effects of ROL. This is likely because the marsh soil already has a high soil organic carbon (SOC) content, meaning that adding more substrates from exudation has a relatively smaller impact on microbial activity. In high SOC soils, the microbial community may already have abundant organic matter to decompose, which limits the effect of additional exudates on respiration rates. Furthermore, the model currently does not consider the quality of organic matter—specifically, the fact that root exudates are more readily decomposed by microbes compared to older organic matter in the soil. This priming effect could potentially enhance microbial activity but is not yet represented in the model, which may partly explain the moderate impact observed.

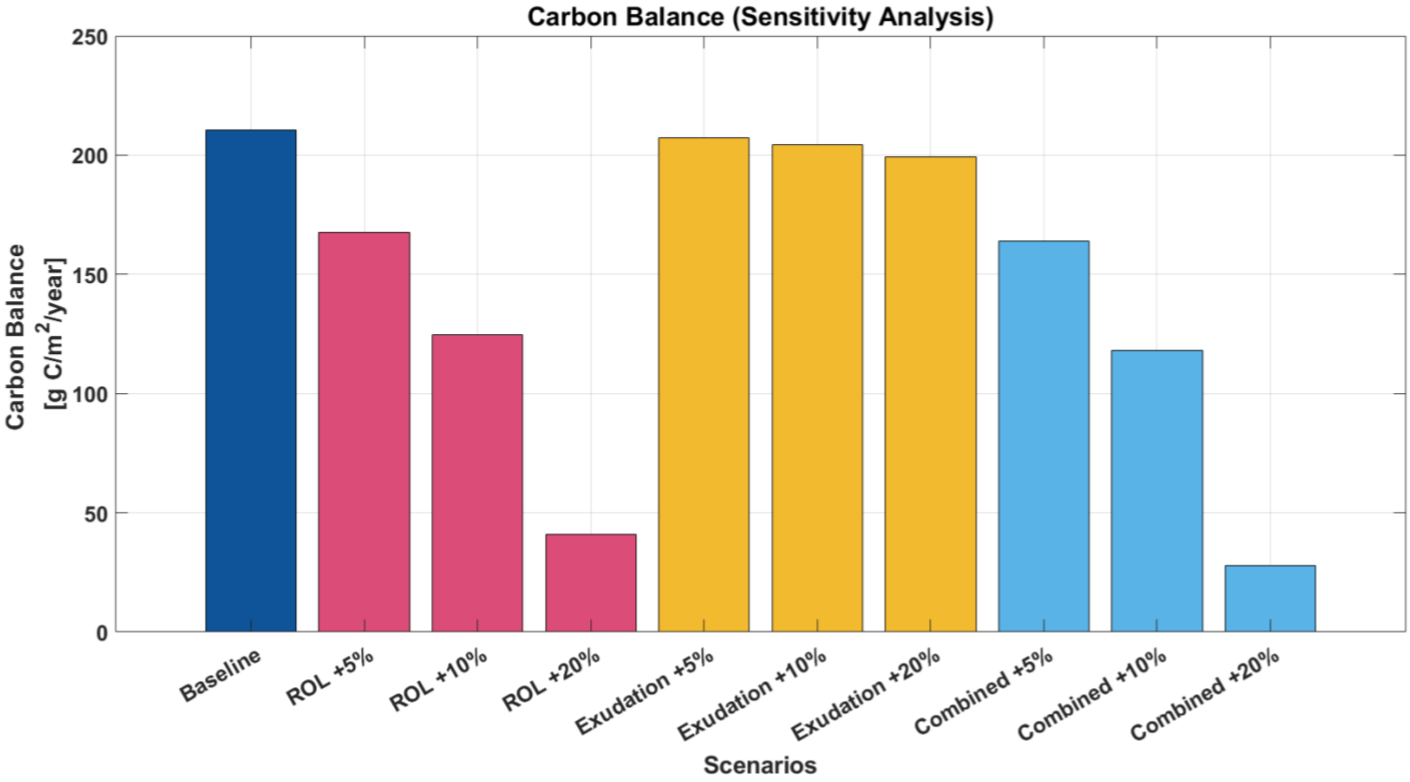


Figure 21*: Sensitivity Analysis of Carbon Balance Across Different Abiotic Conditions*

Combined Effect of ROL and Exudation

The combination of increased ROL and root exudation had a more pronounced impact on the ecosystem's carbon balance:

- When both processes were increased by **20%**, soil respiration reached **1,185.58** g C/m²/year.
- The carbon balance decreased to **27.90** g C/m²/year.

While the carbon balance remained positive, the significant decline from the baseline indicates that the marsh's carbon sequestration potential is greatly reduced under these conditions. The marsh continues to function as a net carbon sink, but its capacity to sequester carbon is substantially diminished.

This combined effect demonstrates that when both ROL and exudation are elevated, their interactive effects can significantly reduce the carbon sequestration potential of the marsh. The high respiration rates suggest that microbial decomposition is greatly enhanced under these conditions, leading to substantial CO_2 emissions.

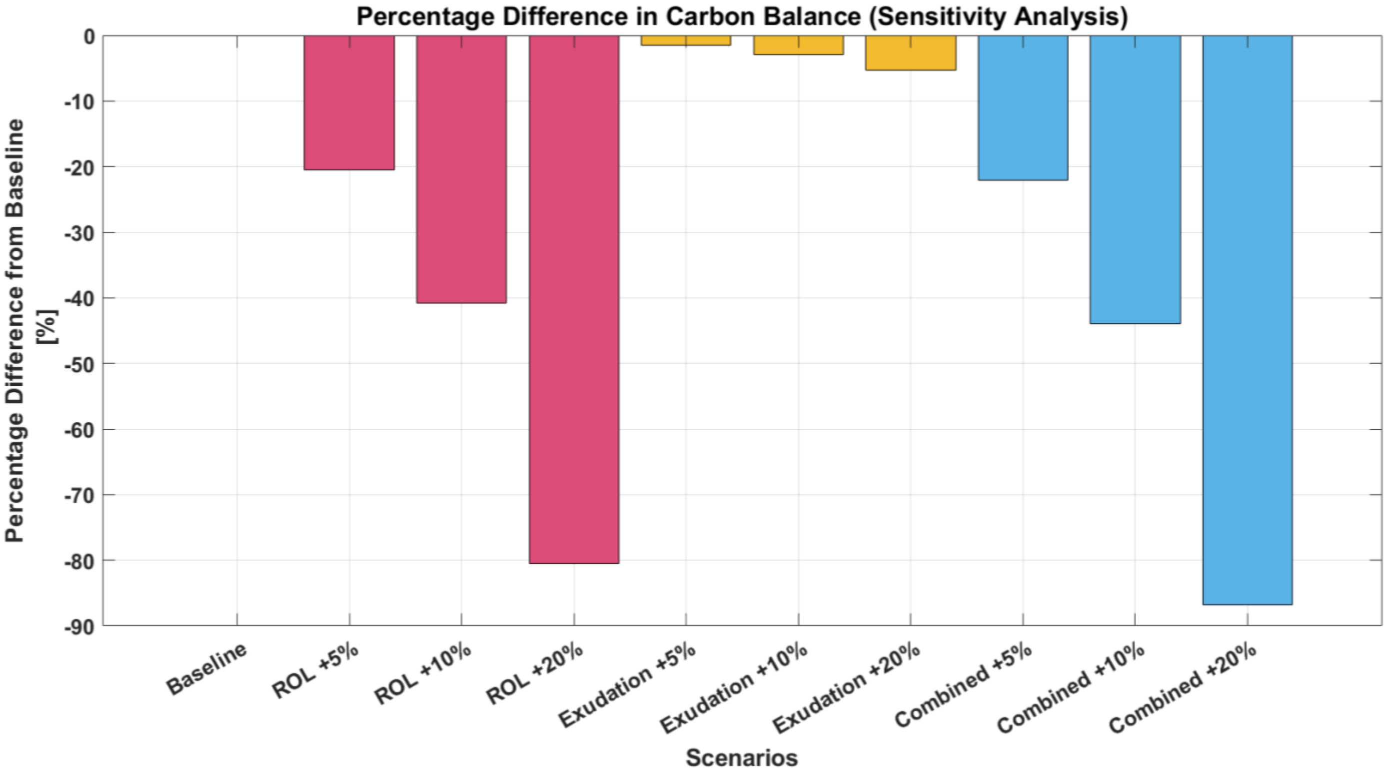


Figure 22 *Percentage Difference in Carbon Balance from Sensitivity Analysis*

This analysis underscores the sensitivity of the Elbe Estuarine Marsh's carbon balance to plant traits such as ROL and root exudation. Under baseline conditions, the marsh acts as a significant carbon sink. However, increasing ROL and exudation—particularly in combination—can drastically reduce this sequestration potential. Although the marsh does not become a net carbon source under the combined increase, the drastic reduction in carbon balance highlights the ecosystem's vulnerability.(Canarini et al. 2019; Vives-Peris et al. 2020).

Understanding the dynamics of these processes is essential for predicting how marsh ecosystems will respond to environmental changes, such as rising temperatures, increased nutrient inputs, or shifts in plant species composition. Given the potential for marshes to have significantly reduced carbon sequestration under certain conditions, this research reinforces the need for continued study into the factors that regulate plant-soil interactions and their influence on carbon cycling in coastal wetlands.

7. Sensitivity Analysis of Root Oxygen Loss and Exudation on Carbon Balance under varying abiotic factors

The sensitivity analysis examined how Root Oxygen Loss (ROL) and root exudation influence the carbon balance of the marsh ecosystem under different abiotic conditions, specifically changes in air temperature and precipitation. The results reveal how these plant-mediated processes impact soil respiration and overall carbon balance, significantly depending on the environmental context. This section discusses the effects of these abiotic factors on plant respiration and photosynthesis, soil respiration, and carbon balance, incorporating figures to illustrate key findings.

Adjusting Relative Humidity with Temperature Increases

In the context of climate change, it is anticipated that air temperatures will rise while solar radiation inputs remain relatively constant. However, increased temperatures affect relative humidity due to the relationship between air temperature and the saturation vapor pressure of water. As temperature rises, the air's capacity to hold moisture increases, which can lead to a decrease in relative humidity if the actual moisture content stays the same. This decrease in relative humidity can significantly impact plant physiological processes, including photosynthesis and respiration.

To accurately simulate this effect in the model, an empirical analysis was conducted to quantify how relative humidity decreases with rising temperatures:

- A correlation matrix was computed to identify relationships between air temperature and other meteorological variables. The analysis confirmed a strong inverse relationship between air temperature and relative humidity, indicating that as air temperature increases, relative humidity decreases.

- Regression Modeling:

  To model the relationship between air temperature and relative humidity, a quadratic regression model was fitted to the data. The quadratic form was chosen because it effectively captures the non-linear nature of the relationship. The regression equation is as follows:

$$Relative\ Humidity = a + b\ Air\ Temperature + c\ \times\ (Ait\ Temperature)^2 \quad \textit{Equation 37}$$

  where a, b, and c are coefficients determined by the regression analysis.

  The regression analysis provided a reliable equation to predict relative humidity based on temperature increases.

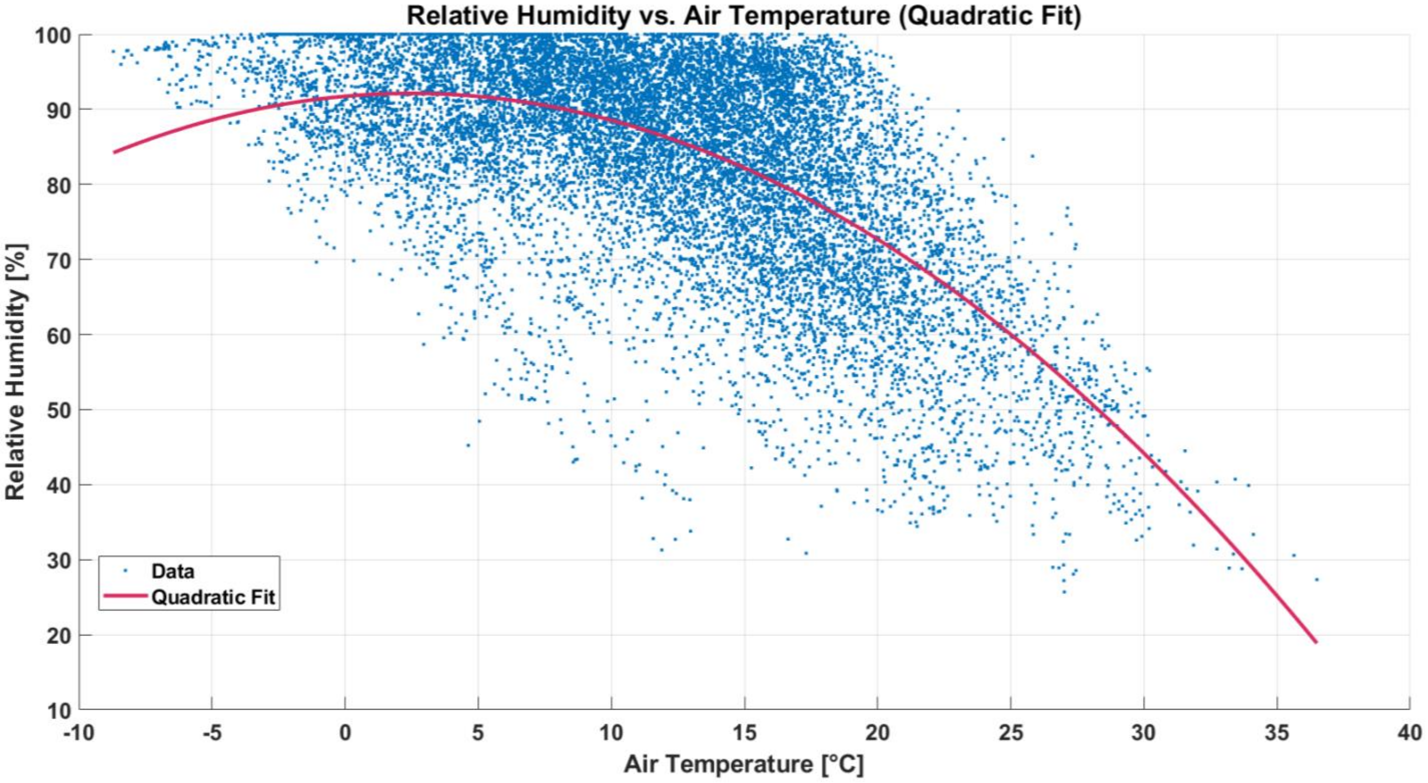


Figure 23: Quadratic Fit Between Relative Humidity and Air Temperature

- Calculation of Relative Humidity Decrease:

  Using the validated regression model, relative humidity values were predicted for scenarios where air temperature was increased by +1°C, +2°C, and +3°C. The average decreases in relative humidity were calculated by comparing these predicted values to the baseline (current temperature) values:

  - **-1.250%** for a **+1°C** increase.
  - **-2.626%** for a **+2°C** increase.
  - **-4.129%** for a **+3°C** increase.

These calculated decreases in relative humidity were incorporated into the model to simulate the physiological responses of plants and microbes under warmer and drier conditions.

Table 11*: Sensitivity Analysis of the Impact of Abiotic Factors on Biotic Responses (all values are in [g C/m²/year])*

All the values are in [g C/m²/year]	***Control***	**+5% rain**	**+10% rain**	**+20% rain**	**+ 1c Air temp / -1.250% relative humidity**	**+ 2c Air temp / -2.626 % relative humidity**	**+ 3c Air temp / -4.129 % relative humidity**
Plant Respiration	*506.9785*	507.1413	507.0309	506.9698	533.5466	561.2509	590.441
Plant Photosynthesis	*1720.4557*	1722.1376	1720.3021	1719.9959	1709.173	1693.4251	1675.5378
Plant NPP	***1213.4772***	***1214.9963***	***1213.2712***	***1213.0261***	***1175.6264***	***1132.1741***	***1085.0967***
Soil respiration (Baseline)	***1002.88***	**823.38**	**696.72**	**580.33**	**1052.41**	**1108.07**	**1175.00**
Soil respiration (ROL +5%)	*1046.07*	858.68	726.40	605.07	1097.83	1155.96	1225.80
Soil respiration (ROL +10%)	*1088.73*	893.52	755.67	629.47	1142.70	1203.26	1275.99
Soil respiration (ROL +20%)	*1172.49*	961.89	813.08	677.31	1230.80	1296.16	1374.56
Soil respiration (Exudation +5%)	*1006.06*	826.07	699.05	582.26	1055.72	1111.51	1178.61
Soil respiration (Exudation +10%)	*1008.98*	828.54	701.19	584.03	1058.74	1114.66	1181.93
Soil respiration (Exudation +20%)	*1014.13*	832.89	704.97	587.15	1064.08	1120.22	1187.77
Soil respiration (Combined +5%)	*1049.39*	861.48	728.83	607.08	1101.27	1159.54	1229.57
Soil respiration (Combined +10%)	*1095.34*	899.10	760.52	633.48	1149.54	1210.40	1283.50
Soil respiration (Combined +20%)	*1185.58*	972.95	822.67	685.26	1244.36	1310.31	1389.44
Carbon Balance (Baseline)	***210.60***	**391.62**	**516.55**	**632.70**	**123.21**	**24.10**	**-89.90**
Carbon Balance (ROL +5%)	*167.40* *(-20.51%)*	356.32 *(-9.01%)*	486.88 *(-5.75%)*	607.96 *(-3.91%)*	77.79 *(-36.86%)*	-23.78 *(-198.68%)*	-140.71 *(56.52%)*
Carbon Balance (ROL +10%)	*124.74* *(-40.77%)*	321.48 (-17.91%)	457.60 (-11.41%)	583.55 (-7.77%)	32.93 (-73.27%)	-71.09 (-394.94%)	-190.89 (112.34%)
Carbon Balance (ROL +20%)	*40.99* *(-80.54%)*	253.10 (-35.37%)	400.19 (-22.53%)	535.71 (-15.33%)	-55.17 (-144.78%)	-163.99 (-780.39%)	-289.47 (221.99%)

Carbon Balance (Exudation +5%)	*207.41* *(-1.51%)*	388.92 (-0.69%)	514.22 (-0.45%)	630.77 (-0.31%)	119.91 (-2.68%)	20.66 (-14.28%)	-93.52 (4.03%)
Carbon Balance (Exudation +10%)	*204.50* *(-2.90%)*	386.46 (-1.32%)	512.08 (-0.87%)	629.00 (-0.59%)	116.89 (-5.13%)	17.51 (-27.35%)	-96.83 (7.71%)
Carbon Balance (Exudation +20%)	*199.34* *(-5.34%)*	382.10 (-2.43%)	508.31 (-1.60%)	625.87 (-1.08%)	111.55 (-9.47%)	11.95 (-50.42%)	-102.68 (14.21%)
Carbon Balance (Combined +5%)	*164.08* *(-22.09%)*	353.52 (-9.73%)	484.44 (-6.89%)	605.94 (-4.23%)	74.35 (-39.66%)	-27.37 (-213.56%)	-144.48 (60.71%)
Carbon Balance (Combined +10%)	*118.14* *(-43.90%)*	315.89 (-19.34%)	452.75 (-12.35%)	579.54 (-8.40%)	26.08 (-78.83%)	-78.22 (-424.55%)	-198.40 (120.69%)
Carbon Balance (Combined +20%)	*27.90* *(-86.75%)*	242.05 (-38.19%)	390.61 (-24.38%)	527.76 (-16.59%)	-68.74 (-155.79%)	-178.13 (-839.07%)	-304.34 (238.54%)

Effect of Abiotic Factors on Photosynthesis and Plant Respiration

The first notable observation is how rainfall and temperature changes influence plant respiration and photosynthesis. As shown in **Figure 24**, the percentage difference in both plant respiration and photosynthesis from control conditions highlights that:

- **Rainfall increases** of +5%, +10%, and +20% show minimal impact on plant respiration and photosynthesis. For example, plant respiration under +5% rainfall is *507.14* g C/m²/year compared to the control of *506.98* g C/m²/year, and photosynthesis is *1722.14* g C/m²/year compared to the control of *1720.46* g C/m²/year. This stability suggests that marsh plants are relatively resilient to small variations in moisture availability.
- **Temperature increases** have a more pronounced effect on plant metabolism. Plant respiration rises sharply with temperature increases, reflecting heightened metabolic activity under warmer conditions. A +1°C increase results in a rise in plant respiration to *533.55* g C/m²/year, and a further +3°C increase elevates it to *590.44*, showcasing strong sensitivity to warming.
- Photosynthesis shows a slight decrease with rising temperatures. For instance, with a +1°C increase, photosynthesis drops slightly from the control value of *1720.46* g

C/m²/year to *1709.17* g C/m²/year, representing a decrease of 0.66%. Similarly, at +3°C, photosynthesis drops further to *1675.54* g C/m²/year, representing a total decrease of 2.61% from the control. This indicates that photosynthesis becomes less efficient as temperatures rise, leading to lower carbon fixation under warmer conditions.

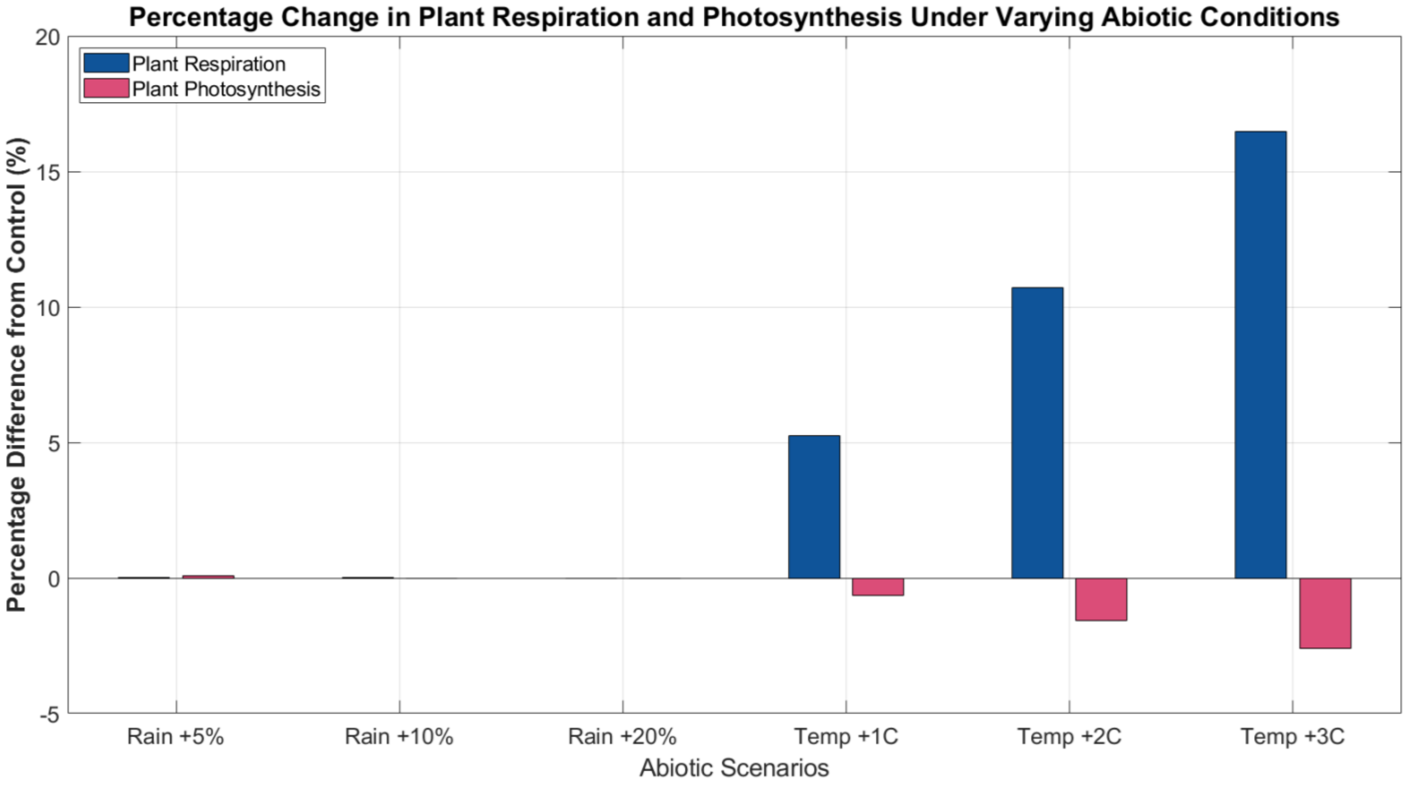


Figure 24: *Percentage change in plant respiration and photosynthesis under varying abiotic conditions*

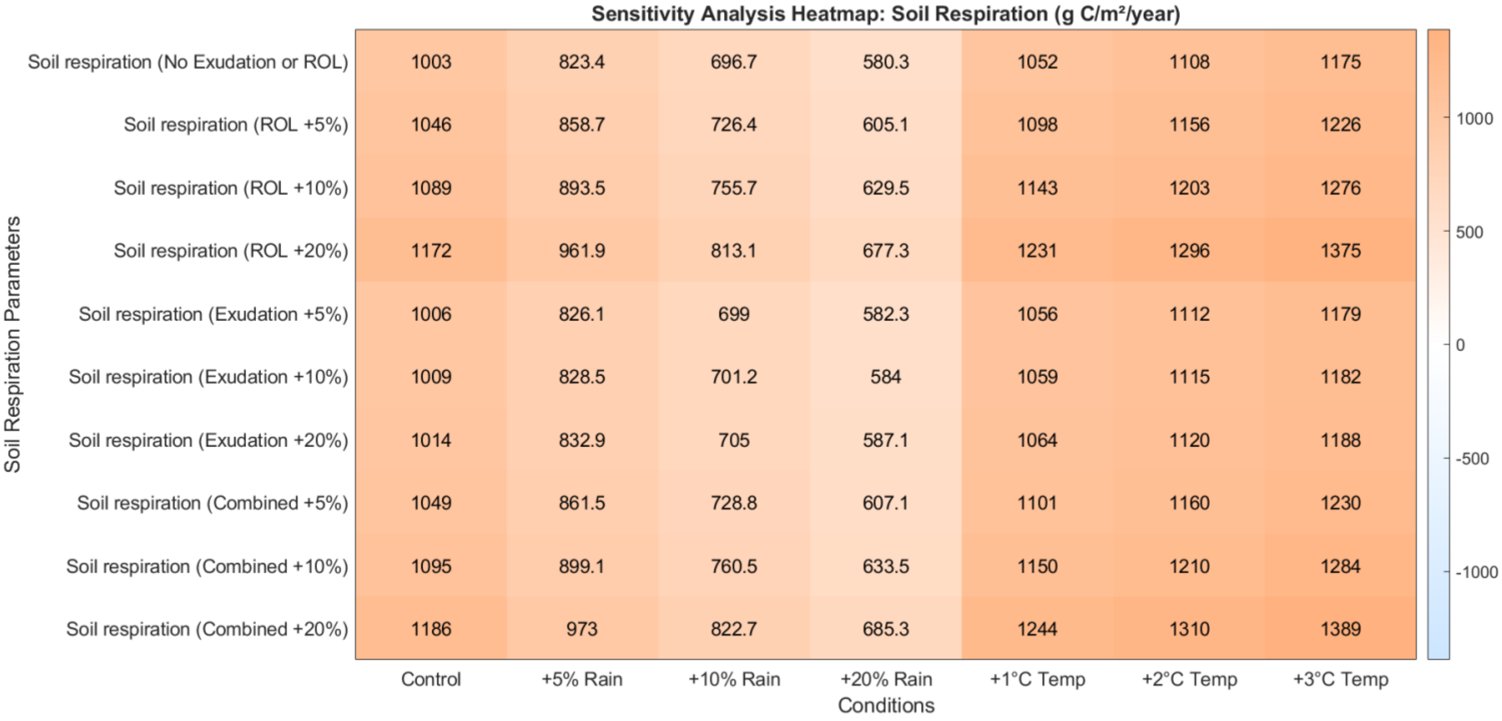
The disparity between the rate of change in photosynthesis and respiration suggests that under warming scenarios, plants may become less effective at sequestering carbon. As temperatures increase, plant respiration rates rise significantly (up to 16.46% at +3°C), while photosynthesis decreases moderately (by 2.61% at +3°C). This imbalance means that there is a risk of increased carbon loss through increased respiration compared to carbon gain through photosynthesis, potentially affecting the net carbon dynamics of the ecosystem. However, it is important to note that the **Figure 24** does not provide conclusive evidence that plants will shift to being net carbon sources, and this shift would also depend on other factors, such as soil microbial respiration and the resilience of the plant community. Under extreme conditions where plants become significant carbon sources, their survival may be compromised, which would further impact the ecosystem's carbon balance.

Effect of Abiotic Factors on Soil Respiration

The impact of abiotic factors on soil respiration was analysed in three scenarios: ROL changes, exudation changes, and combined ROL-exudation changes. **Figure 25** and **Figure 26** visualizes the response of soil respiration under varying rainfall and temperature scenarios:

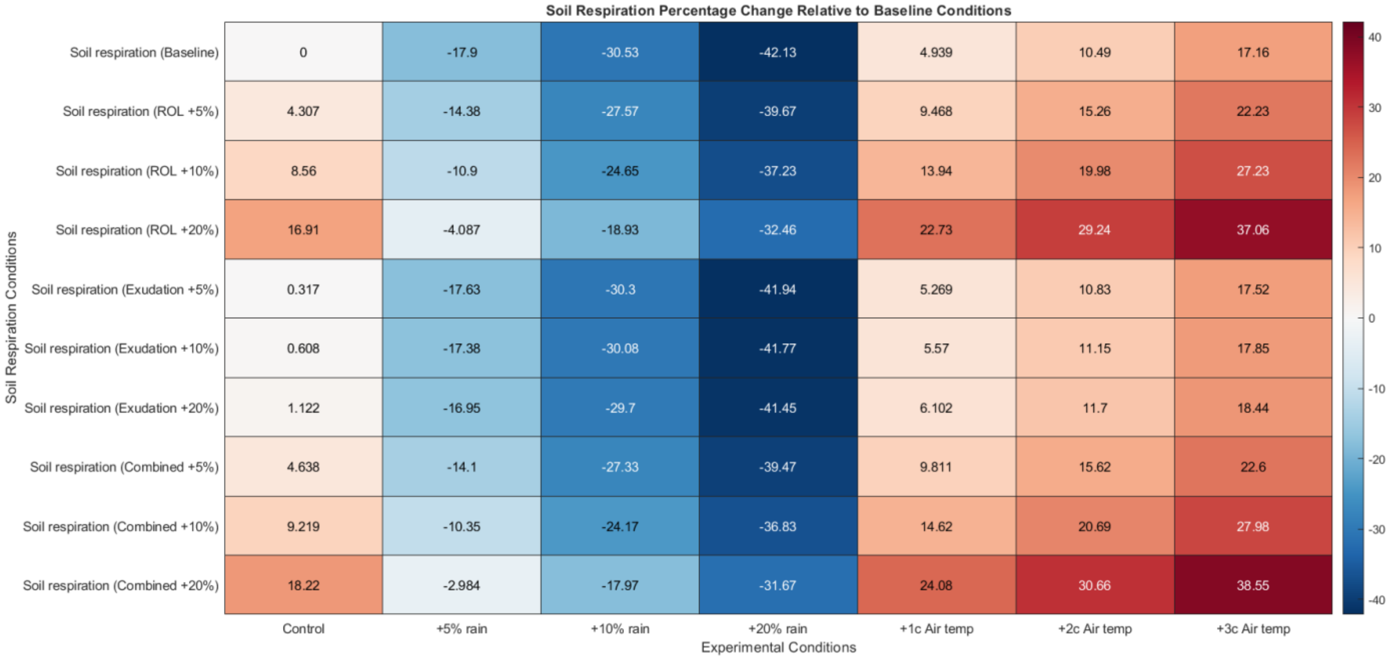
- Rainfall Increases (+5%, +10%, and +20%): Soil respiration consistently declines with increasing rainfall. For instance, in the control scenario without ROL or exudation, soil respiration drops from **1002.88** to ***823.38*** g C/m²/year at +5% rainfall and further decreases to 580.33 at +20% rainfall. This decline is observed across all ROL and exudation scenarios, indicating that higher moisture levels lead to reduced oxygen availability, thereby limiting microbial activity and decreasing soil respiration rates.
- Temperature Increases (+1°C, +2°C, and +3°C): Soil respiration increases significantly with rising temperatures. In the combined ROL and exudation scenario, soil respiration rises from ***1049.39*** at control to ***1229.57*** g C/m²/year at +3°C, reflecting a substantial increase of 17.15%. This trend is evident across all scenarios, highlighting that soil respiration is highly responsive to temperature changes, as warmer conditions enhance microbial metabolic activity.

The findings suggest that ROL plays a critical role in enhancing soil respiration, especially under warming scenarios where oxygen availability is not a limiting factor. However, under higher rainfall, even elevated ROL levels cannot compensate for the lack of oxygen in saturated soils, leading to reduced soil respiration rates.



Soil Respiration Parameters	Control	+5% Rain	+10% Rain	+20% Rain	+1°C Temp	+2°C Temp	+3°C Temp
Soil respiration (No Exudation or ROL)	1003	823.4	696.7	580.3	1052	1108	1175
Soil respiration (ROL +5%)	1046	858.7	726.4	605.1	1098	1156	1226
Soil respiration (ROL +10%)	1089	893.5	755.7	629.5	1143	1203	1276
Soil respiration (ROL +20%)	1172	961.9	813.1	677.3	1231	1296	1375
Soil respiration (Exudation +5%)	1006	826.1	699	582.3	1056	1112	1179
Soil respiration (Exudation +10%)	1009	828.5	701.2	584	1059	1115	1182
Soil respiration (Exudation +20%)	1014	832.9	705	587.1	1064	1120	1188
Soil respiration (Combined +5%)	1049	861.5	728.8	607.1	1101	1160	1230
Soil respiration (Combined +10%)	1095	899.1	760.5	633.5	1150	1210	1284
Soil respiration (Combined +20%)	1186	973	822.7	685.3	1244	1310	1389

Figure 25*: Sensitivity Analysis Heatmap of Soil Respiration (g C/m²/year)*



Soil Respiration Conditions	Control	+5% rain	+10% rain	+20% rain	+1c Air temp	+2c Air temp	+3c Air temp
Soil respiration (Baseline)	0	-17.9	-30.53	-42.13	4.939	10.49	17.16
Soil respiration (ROL +5%)	4.307	-14.38	-27.57	-39.67	9.468	15.26	22.23
Soil respiration (ROL +10%)	8.56	-10.9	-24.65	-37.23	13.94	19.98	27.23
Soil respiration (ROL +20%)	16.91	-4.087	-18.93	-32.46	22.73	29.24	37.06
Soil respiration (Exudation +5%)	0.317	-17.63	-30.3	-41.94	5.269	10.83	17.52
Soil respiration (Exudation +10%)	0.608	-17.38	-30.08	-41.77	5.57	11.15	17.85
Soil respiration (Exudation +20%)	1.122	-16.95	-29.7	-41.45	6.102	11.7	18.44
Soil respiration (Combined +5%)	4.638	-14.1	-27.33	-39.47	9.811	15.62	22.6
Soil respiration (Combined +10%)	9.219	-10.35	-24.17	-36.83	14.62	20.69	27.98
Soil respiration (Combined +20%)	18.22	-2.984	-17.97	-31.67	24.08	30.66	38.55

Figure 26*: Soil Respiration Percentage Change Relative to Baseline Conditions*

Effect of Abiotic Factors on Carbon Balance

Figure 27 and **Figure 28** provides a comprehensive view of how these abiotic factors influence the carbon balance, defined as the net difference between carbon inputs (via photosynthesis) and outputs (via plant and soil respiration):

- Under increased rainfall (+5%, +10%, +20%), the carbon balance improves, as plant photosynthesis remains stable while soil respiration decreases due to oxygen limitations. This suggests that under higher moisture conditions, the marsh ecosystem can act as a stronger carbon sink, with less carbon lost through respiration. However, this effect is mitigated when ROL and exudation are combined at higher levels, where the carbon balance becomes increasingly negative due to higher microbial respiration rates.

- Temperature increases, by contrast, destabilize the carbon balance. As temperatures rise, the system shifts towards a net carbon source, especially at +3°C, where respiration losses outweigh the carbon gains from photosynthesis. The combined effect of ROL and exudation exacerbates this shift, as the enhanced microbial respiration driven by these biotic processes leads to greater CO_2 emissions from the soil.

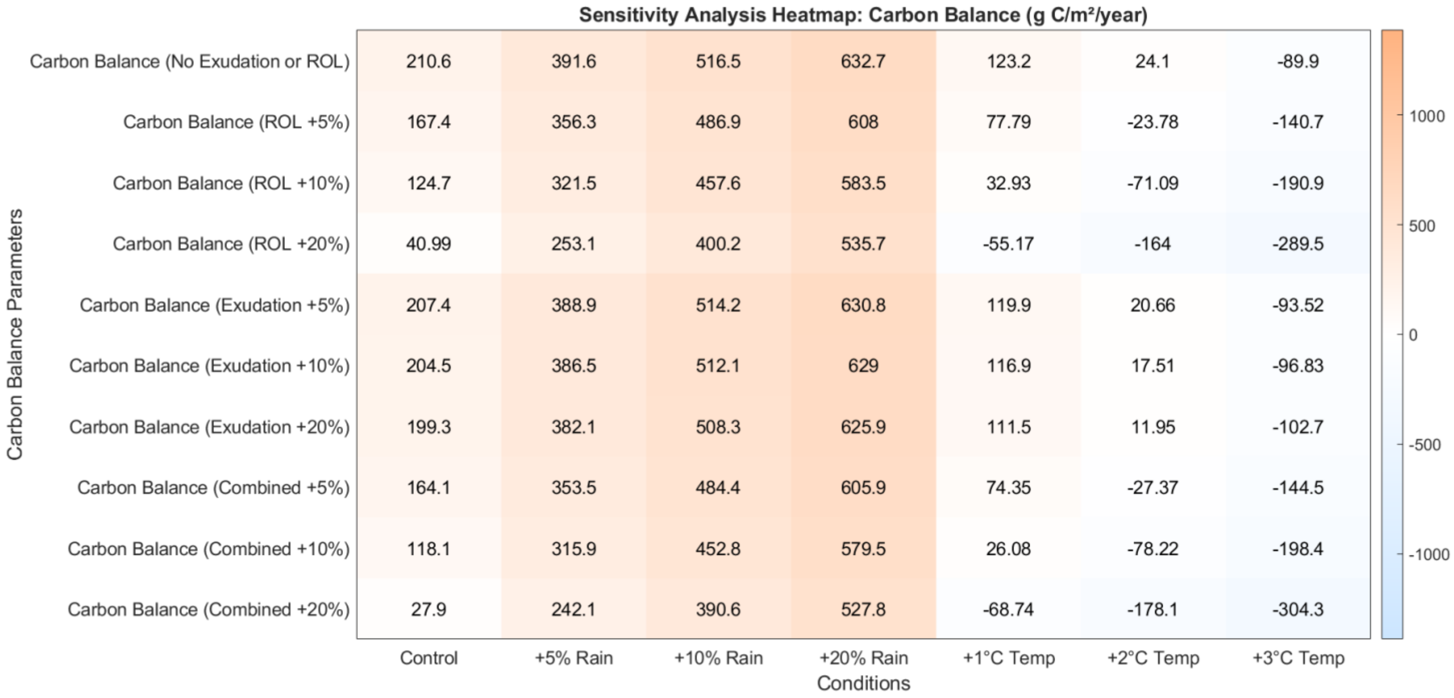
These results highlight the vulnerability of marsh ecosystems to warming, with the potential for significant carbon losses under higher temperatures, particularly when ROL and exudation are elevated. Thus, while increased rainfall alone may not drastically alter the carbon balance, rising temperatures pose a significant risk to the ecosystem's ability to sequester carbon.

The sensitivity analysis shows that abiotic factors, especially temperature, exert a powerful influence on both plant and soil respiration, modulated by ROL and exudation. The findings suggest that:

- Temperature Increase: Warming leads to a significant rise in both plant and soil respiration. While ROL enhances oxygen availability, which promotes aerobic microbial activity, the associated increase in respiration shifts the carbon balance towards a net source of emissions. This underscores the importance of temperature as a dominant driver of carbon cycling in marsh ecosystems.

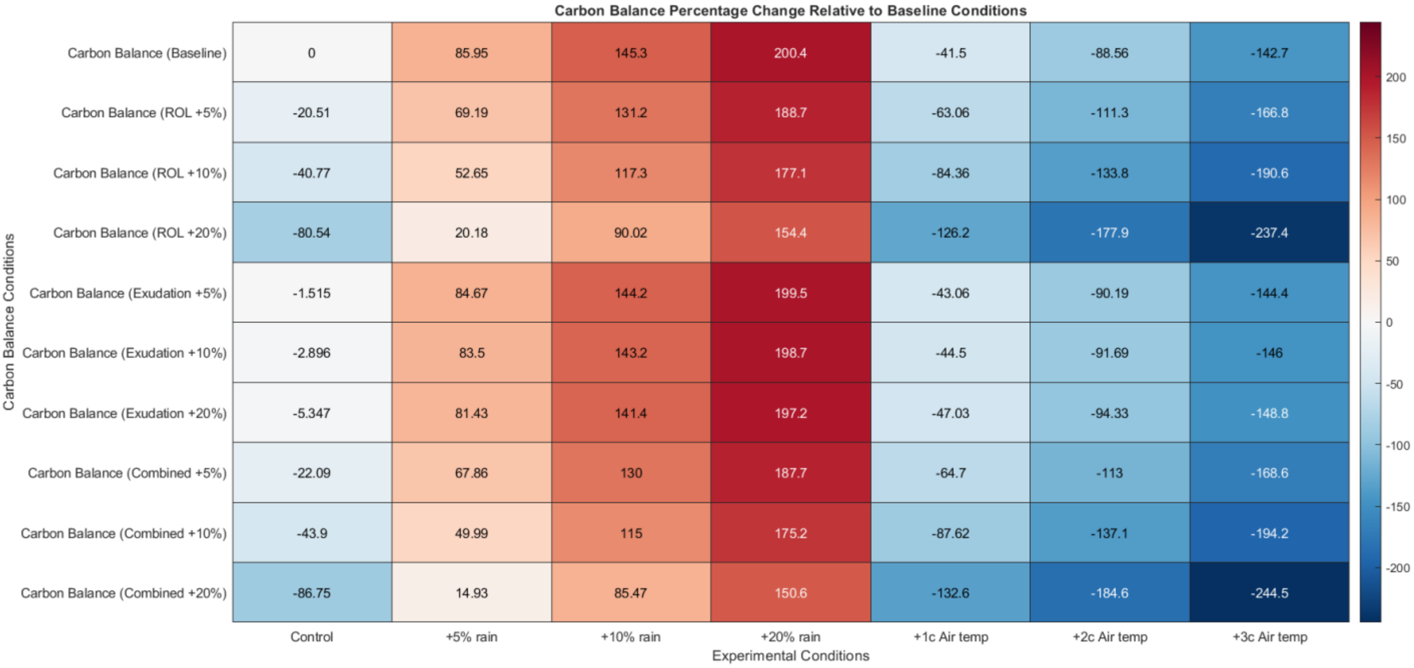
- Rainfall Variability: In contrast, increased rainfall reduces soil respiration due to oxygen limitations, allowing the marsh to retain more carbon. However, under extreme rainfall conditions, even ROL cannot fully mitigate the negative effects of water saturation on microbial respiration, leading to lower carbon turnover.

- Interaction of ROL and Exudation: While both ROL and exudation individually promote higher soil respiration under warm, oxygen-rich conditions, their combined effects under varying abiotic factors demonstrate the complexity of their interaction. Under saturated soils, their ability to enhance respiration is constrained, whereas in warmer, drier conditions, they amplify carbon losses.



Carbon Balance Parameters	Control	+5% Rain	+10% Rain	+20% Rain	+1°C Temp	+2°C Temp	+3°C Temp
Carbon Balance (No Exudation or ROL)	210.6	391.6	516.5	632.7	123.2	24.1	-89.9
Carbon Balance (ROL +5%)	167.4	356.3	486.9	608	77.79	-23.78	-140.7
Carbon Balance (ROL +10%)	124.7	321.5	457.6	583.5	32.93	-71.09	-190.9
Carbon Balance (ROL +20%)	40.99	253.1	400.2	535.7	-55.17	-164	-289.5
Carbon Balance (Exudation +5%)	207.4	388.9	514.2	630.8	119.9	20.66	-93.52
Carbon Balance (Exudation +10%)	204.5	386.5	512.1	629	116.9	17.51	-96.83
Carbon Balance (Exudation +20%)	199.3	382.1	508.3	625.9	111.5	11.95	-102.7
Carbon Balance (Combined +5%)	164.1	353.5	484.4	605.9	74.35	-27.37	-144.5
Carbon Balance (Combined +10%)	118.1	315.9	452.8	579.5	26.08	-78.22	-198.4
Carbon Balance (Combined +20%)	27.9	242.1	390.6	527.8	-68.74	-178.1	-304.3

Figure 27*: Sensitivity Analysis Heatmap of Carbon Balance (g C/m²/year)*



	Control	+5% rain	+10% rain	+20% rain	+1c Air temp	+2c Air temp	+3c Air temp
Carbon Balance (Baseline)	0	85.95	145.3	200.4	-41.5	-88.56	-142.7
Carbon Balance (ROL +5%)	-20.51	69.19	131.2	188.7	-63.06	-111.3	-166.8
Carbon Balance (ROL +10%)	-40.77	52.65	117.3	177.1	-84.36	-133.8	-190.6
Carbon Balance (ROL +20%)	-80.54	20.18	90.02	154.4	-126.2	-177.9	-237.4
Carbon Balance (Exudation +5%)	-1.515	84.67	144.2	199.5	-43.06	-90.19	-144.4
Carbon Balance (Exudation +10%)	-2.896	83.5	143.2	198.7	-44.5	-91.69	-146
Carbon Balance (Exudation +20%)	-5.347	81.43	141.4	197.2	-47.03	-94.33	-148.8
Carbon Balance (Combined +5%)	-22.09	67.86	130	187.7	-64.7	-113	-168.6
Carbon Balance (Combined +10%)	-43.9	49.99	115	175.2	-87.62	-137.1	-194.2
Carbon Balance (Combined +20%)	-86.75	14.93	85.47	150.6	-132.6	-184.6	-244.5

***Figure 28**: Carbon Balance Percentage Change Relative to Baseline Conditions*

The percentages presented in **Table 11** indicate the percentage differences relative to the Carbon Balance Baseline of each respective abiotic scenario. For instance, in the abiotic scenario of "+5% rain," all biotic scenarios are evaluated in comparison to the baseline value of +5% rain *391.62* g C/m²/year. Similarly, the percentage differences in other abiotic scenarios are calculated using their respective baselines. For the heat maps **Figure 26** and **Figure 28**, the values represent the percentage differences compared to the control baseline values: *1002.88* g C/m²/year for soil respiration and *210.60* g C/m²/year for the carbon balance.

Summary of Findings

The results indicate that:

- The Elbe Estuarine Marsh currently functions as a net carbon sink under baseline conditions.
- Plant traits such as ROL and root exudation significantly influence soil respiration and carbon balance.
- Increased ROL has a more substantial impact on carbon emissions than root exudation.

- Abiotic factors like temperature and rainfall modulate these effects, with warming potentially transforming the marsh into a net carbon source.
- The interplay between plant traits and environmental conditions is critical for predicting future carbon dynamics in marsh ecosystems.

The findings highlight the importance of incorporating plant trait variability and environmental factors into models assessing carbon dynamics in marsh ecosystems. Understanding how ROL and root exudation influence carbon cycling, especially under changing climatic conditions, is essential for predicting the future role of marshes in global carbon sequestration and for informing conservation and management strategies.

Chapter 5 General Discussion

1. Overview

The primary objective of this study was to investigate the role of plant-microbe interactions, particularly through Root Oxygen Loss (ROL) and root exudation, in regulating carbon dynamics within the Elbe Estuarine Marsh. The findings highlight the significant role that these biotic interactions, modulated by abiotic factors such as temperature and rainfall, play in influencing carbon sequestration or release within marsh ecosystems. In this chapter, I will discuss the implications of the results in the broader context of marsh carbon cycling and how these insights align with or challenge current understandings of wetland ecosystem function. I will also revisit the research questions posed in the introduction to provide comprehensive answers based on the outcomes of this study.

2. Discussion of Results

The baseline carbon balance simulation, which excludes the interactions from ROL and root exudation, indicated that the high marsh of the Elbe Estuary serves as a net carbon sink, with a carbon balance of 210.60 g C/m^2/year. This finding aligns with existing research, which underscores the vital role that marsh ecosystems play in sequestering atmospheric CO_2, contributing to climate change mitigation (Waldo et al. 2019; Zhang et al. 2017). This baseline scenario reflects the overall carbon dynamics and productivity of the marsh, where carbon inputs from photosynthesis exceed carbon losses through plant and soil respiration. The accurate simulation of this carbon balance provides a solid foundation for assessing how different plant traits and environmental factors might alter carbon cycling in the marsh.

3. Role of Plant-Microbe Interactions

Plant-microbe interactions, particularly ROL and root exudation, were central to this study. These processes, occurring predominantly in the rhizosphere, are key determinants of microbial activity and, consequently, soil respiration. The sensitivity analysis revealed that even modest increases in ROL can lead to substantial increases in soil respiration. For example, a 20% increase in ROL resulted in a marked reduction in the marsh’s carbon balance, demonstrating how increased oxygen availability stimulates microbial activity, accelerating organic matter decomposition and CO_2 emissions (Waldo et al. 2019). This highlights the critical role that ROL plays in shaping carbon dynamics, suggesting that shifts in plant traits could significantly alter the marsh's role in carbon sequestration.

Conversely, increases in root exudation had a more moderate effect on soil respiration and overall carbon balance. Even with a 20% increase in exudation, soil respiration rose only modestly, and the marsh retained most of its carbon sink capacity. This suggests that while root exudates provide additional substrates for microbial decomposition, their overall impact is less pronounced compared to ROL. The high soil organic carbon (SOC) content in marshes likely buffers the effect of exudation, as the microbial community already has ample organic material available for decomposition. Consequently, the addition of root exudates does not significantly amplify respiration rates.

The combined effect of elevated ROL and root exudation was more profound. When both processes were increased simultaneously, soil respiration rates surged, and the marsh transitioned from a net carbon sink to a carbon source. This finding underscores the importance of considering multiple plant traits and their interactions in assessments of marsh carbon dynamics. It also suggests that ROL and root exudation may have synergistic effects that can drastically alter the carbon balance, potentially undermining the marsh’s capacity to mitigate climate change. (Waldo et al. 2019).

4. Modulation of Plant-Microbe Interactions by Abiotic Factors

Abiotic factors, particularly temperature and rainfall can significantly modulate the effects of plant-microbe interactions. For example, increased rainfall reduced soil respiration rates, particularly in the +20% rainfall scenario where soil respiration dropped to 580.33 g C/m^2/year. This reduction is likely due to the saturation of the soil, which limits oxygen diffusion and thereby suppresses aerobic microbial processes. Under such conditions, the marsh enhances its carbon storage potential by maintaining anaerobic conditions that favor long-term organic matter preservation.

In contrast, rising temperatures had a pronounced impact on soil respiration, amplifying the effects of both ROL and exudation. A +3°C increase in air temperature led to a sharp increase in soil respiration across all scenarios, with the rate reaching 1175.0 g C/m^2/year under baseline conditions. This outcome is consistent with the broader literature, where elevated temperatures are known to accelerate microbial activity, thereby increasing soil respiration and CO_2 emissions (Davidson & Janssens, 2006). When combined with elevated ROL, the increased temperatures further exacerbate CO_2 release, which could compromise the marsh's role as a carbon sink. This sensitivity to temperature suggests that even small climatic shifts could disproportionately influence the carbon dynamics of marsh ecosystems, leading to significant shifts in their contribution to the global carbon cycle.

5. Broader Ecological and Climate Implications

This study underscores the complex interplay between biotic and abiotic factors in marsh carbon dynamics. Marshes are often significant carbon sinks due to their high productivity and anaerobic conditions that slow decomposition. However, their role as carbon sinks is highly influenced by various environmental stressors. The sensitivity of these ecosystems to shifts in plant traits and environmental conditions highlights potential vulnerabilities. In addition to temperature-induced changes in ROL and root exudation, marsh ecosystems are also significantly affected by sea level rise and coastal erosion, which threaten their stability and carbon storage capacity. Factors such as increased salinization, habitat loss, and erosion can diminish the carbon sequestration potential of marshes and, under certain conditions, even turn them into net carbon sources. It is therefore crucial to understand the balance of these processes to ensure the resilience of marsh ecosystems in the context of global climate change.

These findings have significant implications for conservation strategies. Preserving the current state of marsh ecosystems may be insufficient to maintain their carbon sink functions as climate conditions change. Increased ROL under rising temperatures, for example, could reduce or even negate the carbon sequestration potential of the Elbe Estuarine Marsh. Such a transformation would undermine the marsh's role in mitigating climate change and contribute to global greenhouse gas emissions. Therefore, adaptive management strategies that address both biotic and abiotic factors are essential for sustaining the carbon sink function of marsh ecosystems.

6. Study Limitations

While this study provides valuable insights, several limitations must be acknowledged. First, the exclusion of anaerobic respiration and methane emissions represents a significant gap in the model. Marsh soils, particularly in the low-oxygen conditions typical of wetland environments, are known to generate methane (CH_4) and nitrous oxide (N_2O) through anaerobic microbial processes. Both CH_4 and N_2O are potent greenhouse gases, and their exclusion likely underestimates the total greenhouse gas emissions from the ecosystem. However, the focus of this study was on the aerobic processes in the rhizosphere, where ROL and root exudation predominantly occur, making the exclusion of methane and nitrous oxide emissions a deliberate decision to prioritize the interactions most relevant to the research objectives.

Additionally, this study focused solely on the freshwater marsh zone, excluding the brackish and saltwater zones of the Elbe Estuary. These zones exhibit different salinity levels, flooding frequencies, and plant species compositions, all of which can significantly influence carbon cycling. Including these zones would provide a more comprehensive understanding of how the entire estuary functions as a carbon sink under varying environmental conditions. Time constraints limited the scope of this study, but future research should incorporate these additional zones to better capture the estuarine marsh’s full carbon sequestration potential.

Moreover, the gas exchange field data used for model validation were limited to three-time points, all collected within a single day in May 2022. While the close alignment between the observed CO_2 fluxes and model predictions suggests that the model can accurately simulate soil respiration dynamics, the limited temporal scope of the data restricts the robustness of the validation. Seasonal variations in temperature, moisture, and plant growth are likely to significantly affect soil respiration, and longer-term data are necessary for a more thorough validation of the model across different environmental conditions.

The model also excludes several important aspects of plant-microbe interactions. Higher decomposition rates by soil microbes under certain conditions could release more nutrients, potentially increasing plant productivity. This represents a mechanism through which ROL and root exudation might lead to enhanced carbon sequestration, contrary to current model predictions. It also suggests a potential negative feedback loop under climate change, where increased nutrient availability could partially offset carbon losses. Microbial pathogens, as well as the general diversity of microbial communities, are also not considered in the current model, despite their significant influence on plant health and productivity.

Additionally, the role of fauna in marsh ecosystems, as highlighted in the original project proposal, is not currently included in the model. Animals can influence marsh carbon dynamics through herbivory, bioturbation, and other ecological interactions, which may affect both carbon sequestration and emissions.

Finally, the model relies on input data from local weather stations and does not dynamically simulate climatic parameters, limiting its ability to capture complex interactions and feedback among climatic variables. For instance, changes in air temperature can influence relative humidity, wind speed, and precipitation. In this study, we used statistical models to estimate the relationship between air temperature and relative humidity to adjust for temperature increases.

While practical, this approach has limitations:

- **Static Relationships**: The statistical relationship assumes constancy over time, which may not hold under climate change.
- **Simplified Climatic Interactions**: It excludes other climatic factors like cloud cover and solar radiation that affect plant and soil processes.
- **Lack of Feedback Mechanisms**: The model does not account for feedback loops where changes in one parameter influence others.

Incorporating a dynamic climate model or coupling with a regional climate model could improve predictions by capturing these intricate interactions more accurately.

These limitations underscore the importance of future research to incorporate missing biotic and abiotic processes, including methane and nitrous oxide emissions, nutrient feedback from increased microbial activity, and the role of fauna, to improve the model's ability to predict the carbon balance in the marsh ecosystems under varying environmental scenarios.

7. Strengths and Contributions

Despite these limitations, this study contributes valuable knowledge about the role of plant-microbe interactions in marsh carbon cycling. The process-based model developed for this research incorporates detailed representations of plant traits and microbial processes, providing a more nuanced understanding of how ROL and exudation affect soil respiration and carbon balance. Traditional models often simplify or omit these interactions, but by explicitly modeling them, this study offers a more accurate representation of the biotic interactions that regulate carbon fluxes in marsh ecosystems.

Additionally, the sensitivity analysis highlights the significant impact that small changes in plant traits can have on the ecosystem’s carbon balance. The finding that increased ROL can nearly eliminate the marsh’s carbon sink function underscores the importance of understanding plant-soil interactions in the context of climate change and wetland management.

8. Future Directions

Future research should aim to address the limitations identified in this study. Incorporating anaerobic processes and methane emissions into the model would provide a more comprehensive assessment of the marsh's carbon emissions. Expanding the study to include brackish and saltwater zones, as well as collecting longer-term field data, would improve the model's accuracy and applicability. Additionally, further exploration into the variability of ROL and exudation across different plant species and environmental conditions could refine the model's ability to predict carbon cycling under changing climatic conditions.

In conclusion, this study underscores the complex interactions between plants and microbes that regulate carbon dynamics in marsh ecosystems. While the Elbe Estuarine Marsh acts as a significant carbon sink under baseline conditions, changes in plant traits such as ROL and exudation can drastically alter this balance. Understanding these interactions is crucial for predicting how marsh ecosystems will respond to future environmental changes and for developing strategies to maximize their role in mitigating climate change.

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10. Appendix

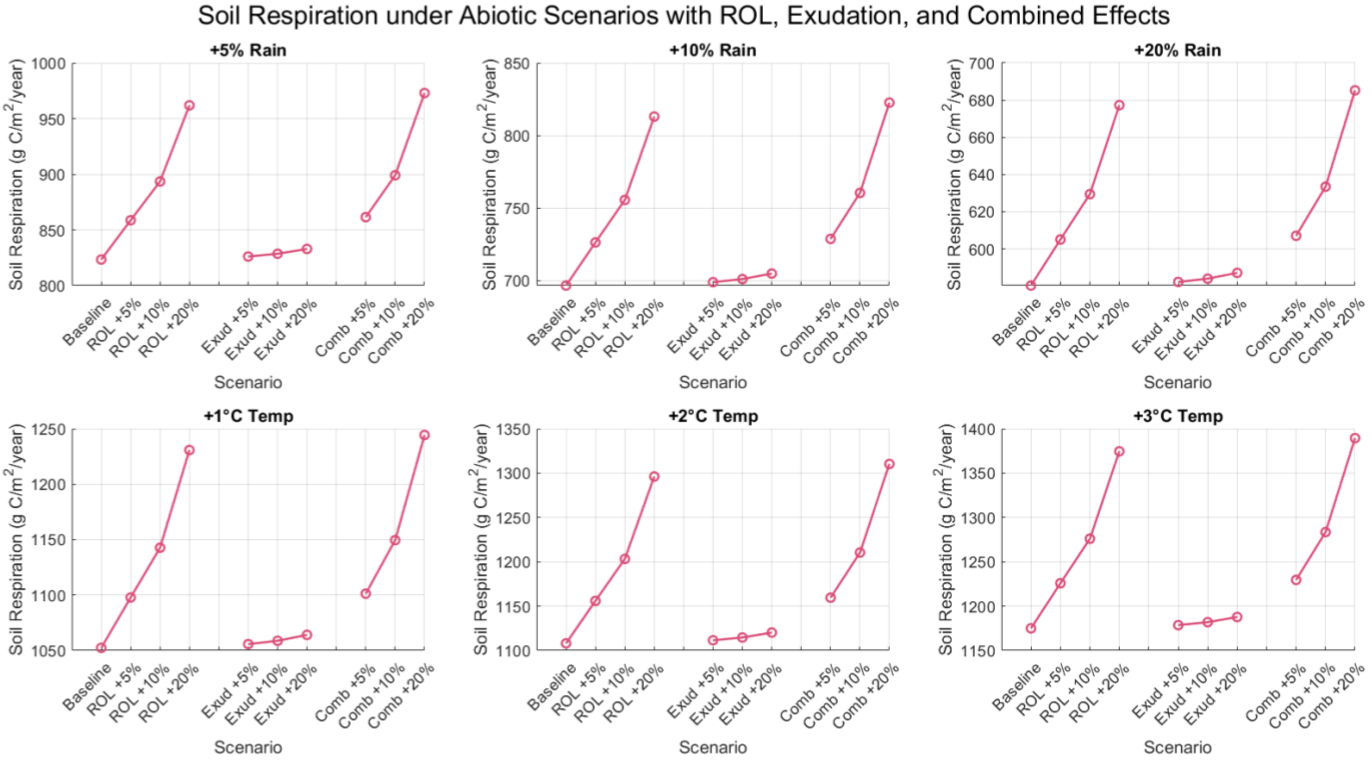

***Figure 29**: Soil Respiration under Abiotic Scenarios with Root Oxygen Loss (ROL), Exudation, and Combined Effects*

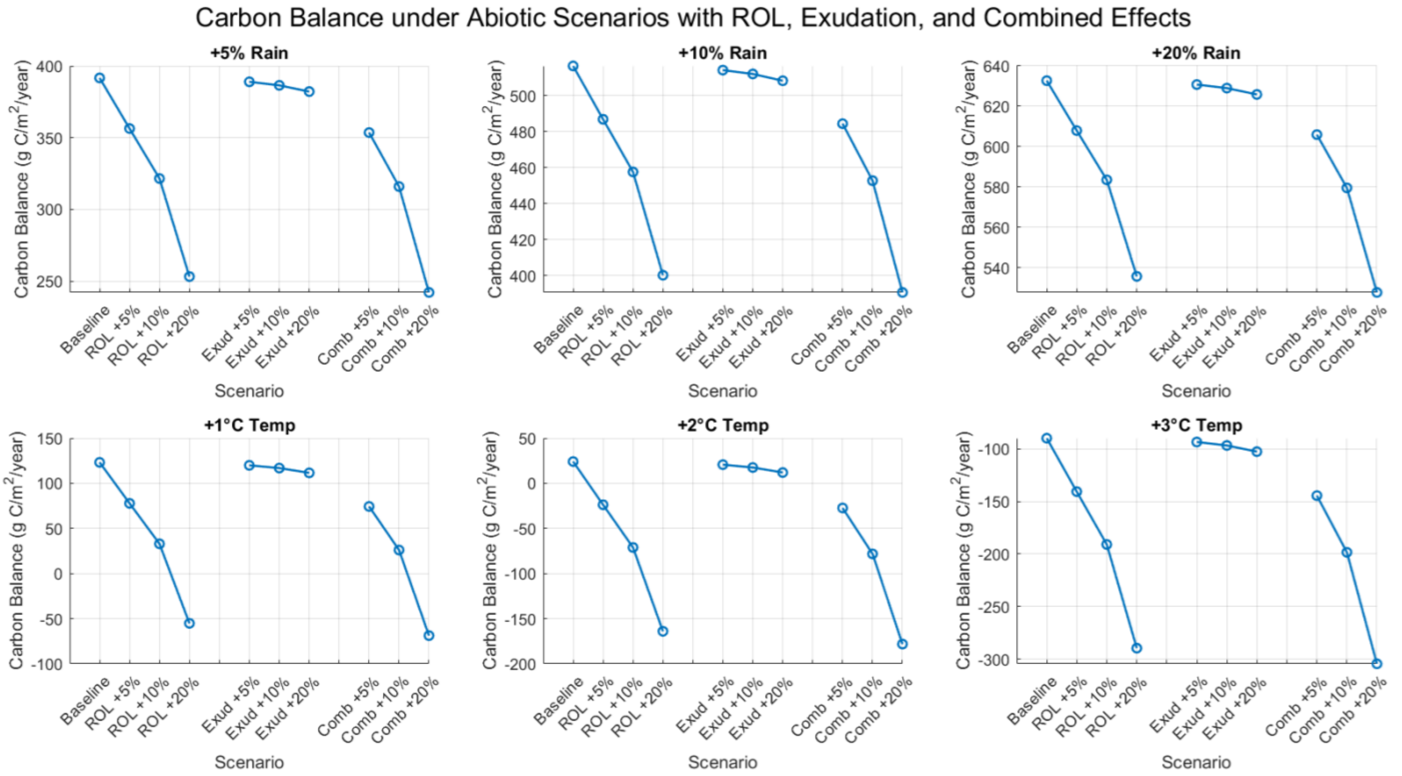

Figure 30: *Carbon Balance under Abiotic Scenarios with Root Oxygen Loss (ROL), Exudation, and Combined Effects*

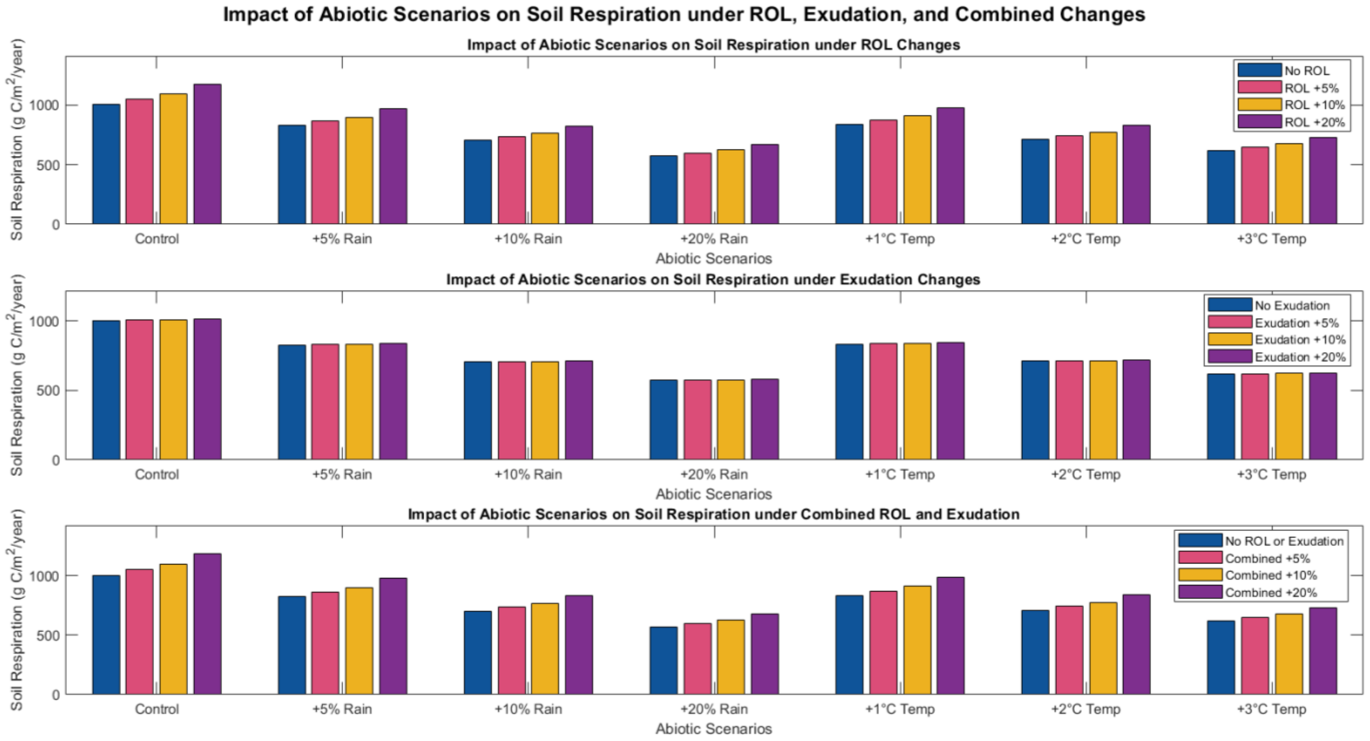

Figure 31: *Bare Plot Impact of Abiotic Scenarios on Soil Respiration under ROL, Exudation, and Combined Changes*