General plant strategies and functions in wetlands: global trait-based analyses

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Issue Date: 2020-09-15

Chapter 1

General introduction

1.1 Wetland ecosystems

Wetlands are globally important ecosystems, which include various habitat types that depend on a variety of water regimes and nutrient supply features. As defined by the RAMSAR convention: "wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters" (Ramsar Convention Secretariat, 2016). Along this spectrum, bogs occur at long waterlogging periods and oligotrophic conditions, and floodplains and swamps stay at short waterlogging periods and eutrophic conditions, while shallow lakes are usually permanently inundated but at any nutrient conditions. The diverse wetland types at the global scale provide a natural laboratory to examine and extend established ecological theories (Moor *et al.*, 2017).

Wetlands support many kinds of life, including our human beings. Humans have managed and exploited wetlands for more than 8,000 years to harvest fish, waterfowl, fur-bearing animals and timber (McInnes, 2011; Mitsch & Gosselink, 2015). Nowadays, wetland ecosystems provide up to 40% of global renewable ecosystem services while covering less than 3% of the globe's surface (Costanza *et al.*, 1998; Zedler & Kercher, 2005). The ecosystem services provided by wetlands mainly include water purification, flood abatement, biodiversity support and carbon sequestration (Zedler & Kercher, 2005; Couwenberg *et al.*, 2010; Moor *et al.*, 2017).

The special role of wetland ecosystems in providing more and different ecosystem services than most other terrestrial ecosystems is related to their unique hydrological and soil conditions. Under water-saturated conditions, soil oxygen will be quickly depleted, which has profound impacts on the biogeochemical processes in wetland substrates and associated ecosystem functions. For example, wetlands improve water quality mainly through the microbial denitrification process and plants uptake. Both ammonium and nitrate can be directly taken up by wetland plants, removing nitrogen from the system. Nitrification of ammonium (NH_4^+) to nitrate (NO_3^-) occurs in the oxic rhizosphere of wetland plants. Then, the formed nitrogen can diffuse to the deeper anoxic sediments to be reduced to N_2 gas (denitrification) (Reddy *et al.*, 1989). The lack of oxygen impedes the decomposition processes in wetlands, which makes wetlands an important global carbon sink. Peatlands alone, as one of the typical wetland ecosystems, contain 500 to 700 billion tons of carbon (this equals to the total amount of atmospheric carbon) (Page & Baird, 2016).

In contrast to various positive ecosystem services provided, wetlands are also the main global source of two important greenhouse gases (GHG): methane (CH_4) and nitrous oxide (N_2O). Natural wetlands are considered as the main drivers of global inter annual variability of CH_4 emission (Stocker *et al.*, 2013). For the decade of 2000-2009, natural wetlands emitted 177×10^{12} to 284×10^{12} g methane (CH_4) per year, accounting for 32% of the total global methane emissions (Kirschke *et al.*, 2013). The release of CH_4 may counteract wetlands' positive role in GHG mitigation through carbon sequestration when considering the greater infrared absorptivity of CH_4 relative to CO_2 (Whiting & Chanton, 2001; Liu & Greaver, 2009). N_2O is released if the soil condition is not strictly anoxic during the denitrification processes (Schlesinger, 2009) and N_2O emissions increase by on average two folds through anthropogenic nitrogen enrichment (Liu & Greaver, 2009).

Hydrology is also the main driver of the plant community composition in wetlands (Mitsch & Gosselink, 2015; Silvertown *et al.*, 2015). The waterlogged/submerged conditions of wetlands lead to a much lower gas diffusion rate (around 10,000 times slower than in atmosphere). Below the water surface, oxygen is quickly depleted to a reduced or weakly reduced environment. The degree of oxygen deficit in wetland substrates therefore largely depends on the duration of flooding event. The lack of oxygen as an electron acceptor directly impedes the aerobic respiration metabolism of plants and other organisms in the substrate. As a consequence, some plants may undergo cellular energy deficits, because the replacement of aerobic respiration by fermentation yields only 2 instead of 32 ATP units from each unit of glucose. When oxygen in the substrate has been depleted, alternative electron acceptors will be used in biogeochemical processes along the well-established dynamics of the redox sequence. Following oxygen, the alternative electron acceptors in the sequence are nitrate, manganese, iron, sulphate and carbon (Ponnamperuma, 1972). The utilization of alternative electron acceptors can result in the production of reduced chemical matter, such as ferrous iron and sulphide (Singer & Havill, 1993) and low-weight monocarboxylic acids (e.g. acetic, propionic, butyric and hexanoic acids) (Armstrong & Armstrong, 2001; Pezeshki, 2001). Those chemical compounds are often phytotoxic to wetland plants. In addition, the return to oxic conditions after flooding does not necessarily mean salvation from the adverse situation for the oxygen-depleted wetland plants tissues. When at low oxygen conditions and upon re-aeration, accumulated electrons at electron transport chain in the mitochondria are donated to O_2, which produces reactive oxygen species (ROS) (Colmer & Voesenek, 2009). The accumulation of reactive oxygen species can cause damage to cellular macromolecules and membranes (Yordanova *et al.*, 2004; Bailey-Serres & Voesenek, 2008; Colmer & Voesenek, 2009). The above-mentioned adverse conditions form major challenges for plants to survive and prosper in wetland habitats. As a consequence, wetlands contain plant communities that are unique to these ecosystems.

1.2 Adaptations of plants to wetland conditions

To survive in the anoxic wetland environment with the abundant phytotoxic compounds and the lack of oxygen, plants have developed special ecophysiological adaptive strategies. For example, the development of spongy tissue (i.e. aerenchyma tissue) that forms spaces or air channels in the leaves, stems and roots can facilitate internal oxygen transportation from leaves/stems to roots and ameliorate the oxygen shortage in the rhizosphere (Visser *et al.*, 2000b; Mcdonald *et al.*, 2001; Colmer, 2003b). Oxygen can also be released to the rooting substrate through root radial oxygen loss (ROL). This process improves the oxygen content in the rhizosphere and induces detoxification of soil-borne phytotoxins such as ferrous iron and sulphide (Armstrong & Armstrong, 2001). To avoid excessive oxygen loss before it reaches the root tip, wetland plants developed ROL barriers to reduce diffusion of precious oxygen to the rhizosphere (Armstrong *et al.*, 2000; Colmer, 2003a). Shoot elongation under submergence allows leaves to access atmospheric oxygen. Varied root/shoot ratios of different plant species allow the optimal balance between gas transport capacity (as an oxygen source) and root oxygen consumption (as an oxygen sink) in different habitats (Van Bodegom et al., 2005; Jung et al., 2009). For plants undergoing long-term submerged conditions of low HCO_3-/CO_2 concentrations and low light intensity, underwater photosynthesis is an important process to allow for continued growth and survival (Mommer & Visser, 2005; Pedersen *et al.*, 2006, 2016; Colmer *et al.*, 2011). Adaptive traits involved in maintaining an optimal underwater photosynthetic rate include gas film formation (Colmer & Pedersen, 2008), modified leaf morphological structure to become thinner, narrower leaves with reduced cuticles, and rearranged chloroplasts closer to the epidermis (Voesenek *et al.*, 2006; Konnerup & Pedersen, 2017).

1.3 Trait-based approaches in ecology

To quantitatively study the response and effect of plants to their ambient abiotic environments, trait-based approaches apply the concept of plant functional traits to present plants' performance (such as growth, reproduction and survival) and strategies (such as adaptation and resources management) across organizational and spatial scales (Violle *et al.*, 2007; Shipley *et al.*, 2016). Trait-based ecology is promising in synthesising, integrating, and predicting general patterns in ecological niche, community assembly and ecosystem functioning (Violle & Jiang, 2009; van Bodegom *et al.*, 2012; Shipley *et al.*, 2016). The trait-based approaches advance over the traditional plant functional types (PFTs) by a better capability of capturing the variation/acclimation of individual plants along the environmental gradient.

Trait-based approaches have been widely applied to study a variety of ecosystem types at different spatial scales, such as the prediction of community assembly in forests, grasslands and shallow lakes (Shipley *et al.*, 2006; Ackerly & Cornwell, 2007; Pan *et al.*, 2017), and the modelling of global vegetation distribution maps (van Bodegom *et al.*, 2014). One important component of trait-based ecology is the generation of global leaf economics spectrum (LES) (Wright *et al.*, 2004). The LES provides convincing evidence of a consistent and continuous relationship among the so-called leaf economics traits, reflecting a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources (Reich *et al.*, 1997; Shipley *et al.*, 2016; Funk *et al.*, 2017). This spectrum seems to represent an important axis of variation in plant strategies.

In the meantime, many global plant trait databases have been established through the compilation of trait data contributed from different countries and regions (e.g. Kleyer et al. 2008, Kattge et al. 2011, Forbes et al. 2018). This has systematically increased the accessibility of plant trait data over wide scales (Kattge *et al.*, 2011) and provided a promising basis for understanding various ecological questions from species to ecosystem levels (McGill *et al.*, 2006; Diaz *et al.*, 2016).

1.4 Trait-based wetland ecology

Despite the significant progress that have been achieved in trait-based ecology in many different ecosystems, there are still barriers towards a trait-based wetland ecology (Moor et al. 2017). On the one hand, the majority of trait-based studies have focused on terrestrial ecosystems, such as forests and grasslands. Most of the trait studies in wetlands have only concentrated on comparisons of trait expression within the local species pool under laboratory conditions (Pedersen *et al.*, 2011; Colmer *et al.*, 2013). This makes it difficult to understand the wetland plant strategies and functioning at a broader scale in the context of functional ecology. On the other hand, the unique hydrological regimes and the consequent environmental conditions in wetlands (as discussed in section 1.1) make it difficult to directly apply the ecological theories and concepts from other ecosystems to wetlands. For example, the leaf economics spectrum may be deformed if the cost of adaptation to wetland conditions is expensive from a resource utilization perspective (Kirk, 2003). Therefore, it requires special attention to both commonly measured traits (such as leaf nitrogen, specific leaf area and photosynthetic rate) and those unique wetland adaptive traits (such as root porosity, root/shoot ratio, radial oxygen loss and shoot elongation) when applying trait-based approaches to wetlands.

Important wetland plant functional traits include, but not limited to, wetland plant ecophysiological adaptive traits, leaf economics traits and size-related traits. Those wetland plant traits do not only play a critical role in the survival and prosperity of plants in wetland conditions, but also have important effects on the wetland ecosystem functioning (Engelhardt, 2006; Alldred & Baines, 2016; Moor *et al.*, 2017). For example, some wetland adaptive traits can help to transport oxygen to the rhizosphere to relieve the oxygen shortage in the substrate and allows plants to endure the flooding events. Leaf economics traits reflect resources acquisition and allocation strategies of the plants and considerably correspond to habitat fertility. Size-related traits are a proxy for competition and reproduction capacity. Considering the various ecological roles that different groups of traits play, it is imperative to apply trait-based approaches to wetlands for a better understanding of plant strategies, ecological niches, community assembly and ecosystem functioning in wetlands.

One example of how different wetland plant traits affect ecosystem functioning can be found in the complex interactions between wetland plants and methane emission (Ding *et al.*, 2005). On the one hand, plants can facilitate the methane emission through transporting the methane through the aerenchyma tissue (known as the chimney effect) and providing carbon sources through aboveground and belowground litter (Laanbroek, 2010; Bhullar *et al.*, 2013a). Conversely, plants can inhibit methane production by transporting oxygen to the rhizosphere, inhibiting the activity of methanogens, and oxidizing produced methane to carbon dioxide (Segers, 1998; Bhullar *et al.*, 2013a; Bridgham *et al.*, 2013). The application of trait-based approaches is promising to quantify these complex processes in wetlands through wetland plant functional traits (Sutton-Grier & Megonigal, 2011).

To fill the knowledge gaps and explore the ecological theories in wetlands, one powerful solution is the compilation of a wetland plant trait data to quantitatively understand the wetland plant strategies and functioning on the regional to global scale (Kattge *et al.*, 2011; Pan *et al.*, 2019). When compiling a wetland plant trait database, we should keep in mind that in addition to the traditionally studied plant functional traits, the important wetland adaptive traits should also be taken into consideration for their unique but fundamental roles in helping plants to survive in wetlands and affecting wetland ecosystem functioning.

1.5 Research aims and questions

The aim of this research is to develop trait-based approaches that enhance our understanding of general wetland plant strategies on a global scale. In this thesis, the following questions will be addressed (see also Figure 1.1 for a conceptual scheme of the thesis):

1. What are the general potential drivers for wetland adaptive traits? (Chapter 2)
2. What is the global leaf economics spectrum (LES) in wetlands? (Chapter 3)
3. How can we integrate both wetland adaptive traits and leaf economics traits for a better understanding of functional wetland ecology? (Chapter 4)
4. What are general plant strategies in wetlands? (Chapter 5)

To answer these questions, an original wetland plant trait database has been compiled for this study. The wetland plant trait data were compiled through systematic searches in Web of Science and Google Scholar for wetland plant ecophysiological adaptive traits, leaf economics traits and size-related traits. The references presented in important reviews that focused on the ecophysiological studies of how wetland plants adapt to flooding conditions published in the past 15 years were also checked for traits records. In addition, enquiries were sent around our network of colleagues working on the ecophysiology of wetland plants for recommendations for possible literature that may have been missed. Finally, several unpublished data sources along with contributions from our network were added. In total, around 8000 observations of more than 1200 species from over 200 references were included. Besides the functional trait data, the available plant species information that presents the characteristics and habitat information, such as life form, Ellenberg moisture indicator, as well as details of the habitat including habitat type, hydrological regime and geographic reference (coordinates) was recorded.

1.6 Thesis content

The wetland plant trait database compiled for the purpose of this thesis enables, for the first time, the quantitative analysis of the wetland plants strategies on a global scale. For instance, we can test the potential drivers for wetland plant traits by analysing the correlations between wetland plant traits and their environmental factors. We can also examine whether the global leaf economics spectrum exists in wetlands by analysing the trait-trait relationships between wetland plant leaf economics traits. Last but not the least, we can understand the wetland plant strategies by analysing the relationships between wetland adaptive traits and leaf economics traits to see whether facilitations or trade-offs occur among different groups of traits.

The conceptual scheme of trait-based relations in wetlands with links to each chapter is shown in Figure 1.1

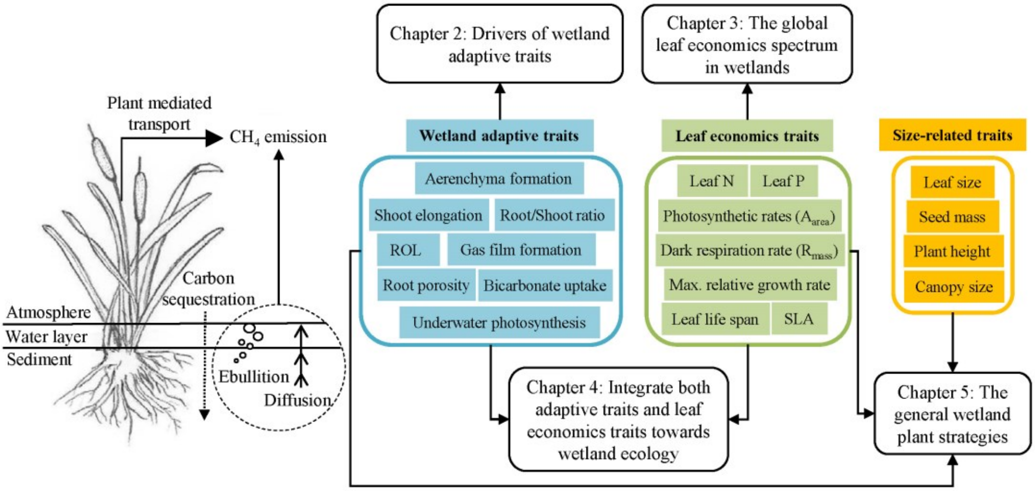

Figure 1.1 Conceptual scheme of the topics of chapters 2, 3, 4 and 5, and the plant functional traits involved with a brief illustration on how a wetland plant affects ecosystem functioning.

The principal content of each chapter is as follows:

Chapter 1: General introduction

This chapter provides a general introduction on wetland ecosystems, wetland adaptive strategies and trait-based approaches in wetland ecology. The major research questions and outline of the thesis are outlined.

Chapter 2: Drivers of plant traits that allow survival in wetlands

This chapter explores the potential driving factors of three important wetland adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate) at a broader scale beyond the local species pool. The results show that in addition to bioclimatic variables (temperature and precipitation), each adaptive trait is also influenced by different driving factors (hydrological regime, habitat type and life form), which indicates a variety of driving mechanisms affecting the expression of different adaptive traits.

Chapter 3: The leaf economics spectrum revisited: global trait patterns in wetlands

The leaf economics spectrum (LES) reflects a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources. However, whether and how the LES exists in wetlands at the global scale is still unclear. Based on a large wetland plant trait database, this chapter reveals a shifted LES in wetlands compared to other non-wetland terrestrial habitats, reflecting the special strategies of wetland plants in coping with resources. Wetland plants tend to hold a fast-return strategy with a relatively low respiration rate due to their unique leaf structure and plant functioning. This analysis provides a first step to bringing trait-based approaches to wetland ecology.

Chapter 4: Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands?

This chapter continues to advance trait-based approaches in wetland ecology, by incorporating both wetland adaptive traits and LES traits. First, it carefully reviews their distinct but important ecological roles and effects on ecosystem functioning, such as methane emission and denitrification processes. Moreover, this chapter addresses the importance of combing the two suites of traits within wetland ecology by understanding their trait-trait relations. Based on an exploratory analysis, it reveals that trait-trait relationships between wetland adaptive traits and LES traits are largely decoupled (i.e. are orthogonal in trait space), which provides an important premise for understanding the wetland plant strategies as well as the wetland ecosystem functioning from a trait-based perspective.

Chapter 5: What are general plant strategies in wetlands?

While trait-based approaches have provided critical insights in general plant functioning, we lack a comprehensive quantitative view on the role of adaptations to stressful habitats in plant strategies. This chapter uses the newly compiled wetland plant trait dataset, to explore adaptive strategies to wetlands in relation to other plant strategy components. As LES traits and size-related traits are considered as two major (but decoupled) trait axes representing the strategies for growth and resources competition in terrestrial ecosystems, this chapter evaluates the relationships between three key traits indicative of adaptations to wetland conditions (root porosity, root/shoot ratio, shoot elongation) vs. leaf economics traits and size-related traits on a global scale. The chapter reveals that the adaptive traits are largely independent of the other two dominant trait axes, and adaptive traits themselves are largely independent of each other. The pattern indicates that there are multiple mechanisms involved in plant adaptive strategies to deal with the multi-faceted wetland conditions, which include waterlogging, submergence and a range of nutrient conditions.

Chapter 6: General discussion

This chapter synthesizes the principal findings of this research project. It emphasizes the significance of bringing the trait-based approaches to wetland ecology to understand wetland plant strategies, wetland ecosystem functioning and ecosystem management. Based on the findings of previous chapters, this chapter discusses the implications for future ecosystem management.