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

Pan, Y.

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Chapter 5

Adaptive strategies are decoupled from leaf economics traits and size-related traits in wetlands

Yingji Pan, Ellen Cieraad, Jean Armstrong,
William Armstrong, Beverley R. Clarkson, Ole Pedersen,
Eric J. W. Visser, Laurentius A.C.J. Voesenek,
Peter M. van Bodegom

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Abstract

- Plants may have to cope with specific stresses, in addition to dealing with water, nutrient and light limitations. 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.
- We analysed trait-based plant strategies in wetlands, with its unique hydrological regime and oxygen limitations, and evaluated 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. We evaluated how key trait dimensions are expressed along moisture gradients and between wetland habitats and life forms.
- Wetland adaptive traits are on different trait dimensions than leaf economics traits or size-related traits, indicating that there is no generic trade-off involved in adapting to wetland conditions. Moreover, we observed that adaptive traits themselves are to a large extent independent of each other. These results suggest that even plant strategies vital to surviving in stressful environments are species-specific without generic impacts on whole plant functioning.
- Hence, there are diverse strategies to promote plant adaptations and global plant distributions across multi-faceted stressful environments, such as wetlands. Our results provide a backbone for applying trait-based approaches in wetland ecology considering adaptive strategies as an additional key trait dimension. The decoupled trait dimensions in relation to environmental stressors and habitat resources may offer a promising path for a flexible wetland management approach for wetlands and stressful environments.

5.1 Introduction

To understand the functioning of organisms and the impacts of (a)biotic conditions thereupon, trait-based approaches are increasingly applied to surmount the boundaries across species groups of different life forms and habitat types. Trait-based ecology applies the concept of plant functional traits to study morphological, physiological, or phenological heritable features from the level of organisms to ecosystems (Lavorel & Garnier, 2002; Violle *et al.*, 2007, 2012), and to understand species strategies in terms of growth, production and survival (van Bodegom *et al.*, 2012; Reich, 2014). For plant species, the successful application of

trait-based approaches has resulted in the concept of the leaf economics spectrum (Wright *et al.*, 2004). This conceptual framework allows plant strategies to be distinguished based on investment and turnover of resources to leaves, ranging from conservative to acquisitive strategies (Reich *et al.*, 1997; Wright *et al.*, 2004; Reich, 2014). Additionally, size-related traits are considered as another important but independent trait dimension in competition for light and water. The quantitative analysis of these two trait dimensions helps us to understand the fundamental strategies for plant growth, survival and reproduction (Diaz *et al.*, 2016). Applications of these two trait dimensions have led to increased insights into critical ecosystem processes, such as the feedbacks between litter decomposition and fire regimes (Cornelissen *et al.*, 2017).

In addition to dealing with various habitat resources, as expressed in these two trait dimensions, many plants have to adapt to specific stresses in their environment. Wetlands constitute one such environment and are distinguished from terrestrial ecosystems by frequent or permanent flooding, and consequent anaerobic soil conditions. The biochemical processes and their products constrained to anaerobic metabolic pathways can cause adverse impacts on plants that inhabit wetlands (Greenway *et al.*, 2006; Voesenek *et al.*, 2006; Pezeshki & DeLaune, 2012). Wetland plants have specific traits to deal with these stressful conditions (as have plants in other stressful environments, such as waxy leaves in deserts or dauciform roots at extreme phosphate deficiencies, e.g. Bakker *et al.* 2005). Previous studies on wetland plant traits have focussed largely on the eco-physiological aspects of such adaptations (Armstrong *et al.*, 1994; Visser *et al.*, 2000b; Colmer & Voesenek, 2009; Voesenek & Bailey-Serres, 2013). Consequently, adaptive traits, including root porosity, decreased root/shoot ratios, shoot elongation, gas film formation, and underwater photosynthesis, have been intensively examined (Voesenek & Bailey-Serres, 2015; Winkel *et al.*, 2016; Moor *et al.*, 2017). These studies have mainly concentrated on the trait expression of a single or few species within the local species pool, which forms a major barrier to apply trait-based approaches in wetland ecology (Moor *et al.*, 2017; Pan *et al.*, 2019). Thus, we still do not have a comprehensive trait-based view on wetland plant strategies at a broader scale (Pan *et al.*, 2019).

Moreover, it is yet unclear whether and how these traits adaptive to specific habitat stresses relate to the two dominant trait dimensions (i.e. leaf economics traits and size-related traits) (Pan *et al.*, 2019). Since wetland plant adaptive traits, leaf economics traits and size-related traits play important but ramified roles in wetland plant functioning, it is critical to understand whether and how these different groups of traits generally relate to each other (Pan *et al.*, 2019). Therefore, quantitative analyses on the trait interrelationships are fundamental

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towards a comprehensive view of wetland plant strategies and will significantly improve our knowledge of wetland plant strategies that balance survival, growth, and competition under wetland conditions on a global scale. Moreover, it will provide a basis towards a fundamental understanding on the position of adaptations to specific environmental stresses in comparison to other key trait dimensions.

The relation between wetland adaptive traits and both leaf economics and size-related trait dimensions can have multiple outcomes (Fig. 5.1). For example, if wetland adaptive traits are decoupled (i.e. independent or orthogonal) from leaf economics traits, it suggests that adaptive traits are quite cheap to develop. Therefore, adaptation to wetland conditions would not intrinsically hinder plant functions in relation to the acquisition or allocation of resources (Fig. 5.1, A). Wetland plants should therefore not be constrained by habitat resources when adapting to habitat wetness. If, on the other hand, wetland adaptive traits are tightly coordinated with leaf economics traits, it indicates that either adaptation to wetlands facilitates the other leaf functions in terms of resources acquisition (positively related; Fig. 5.1, B), or that wetland plants have to optimise their adaptation to wetness with a considerable cost for leaf economics traits (trade-offs; Fig. 5.1, C). If wetland adaptive traits are tightly correlated with size-related traits, it suggests that either larger plants may more easily outgrow the water column and profit more from aerenchyma tissues (Fig. 5.1, D) or need less shoot elongation (Fig. 5.1, E).

So far, evidence from previous studies seem to support the case of decoupled relationships (as shown in Fig. 5.1, A). One line of evidence is that the environmental drivers for the different trait groups are different with nutrient and water availability driving leaf economics traits, and light availability steering size-related traits (Reich, 2014; Diaz *et al.*, 2016), while the water regime and the consequent availability of oxygen to belowground (waterlogging) and aboveground (submergence) tissues are general driving factors for wetland adaptive traits (Colmer & Voesenek, 2009). Also the observation that global wetland habitats cover a wide fertility range (e.g. from oligotrophic bogs to eutrophic floodplains) suggest that a trait decoupling prevails. If there would be significant trade-offs between adaptive traits and leaf economics traits, we would find wetland plants to be constrained to some specific wetland types (Pan *et al.*, 2019).

In this paper, we test the hypothesis that wetland adaptive traits constitute an independent trait dimension from the other two dominant trait dimensions (i.e. leaf economics traits and size-related traits) in wetlands. We also hypothesize that the prevalence of traits adaptive to wetland conditions is closely aligned to the stress gradient in wetlands, as represented by habitat affinities of plant species to wetness. We analysed 7 key wetland plant traits: root

porosity, root/shoot ratio and shoot elongation as representative of wetland adaptive traits based on their ecological importance and availability of quantitative records; leaf nitrogen (leaf N), leaf phosphorus (leaf P), and specific leaf area (SLA) to represent key leaf economics traits (Wright *et al.*, 2004; Diaz *et al.*, 2016); and plant height as representative of size-related traits. Through our analyses, we aim to understand the key trait dimensions related to wetland plant strategies across different species and biomes. We envision that this study may inspire research on the role of specific adaptations to habitat stress in trait-based strategies.

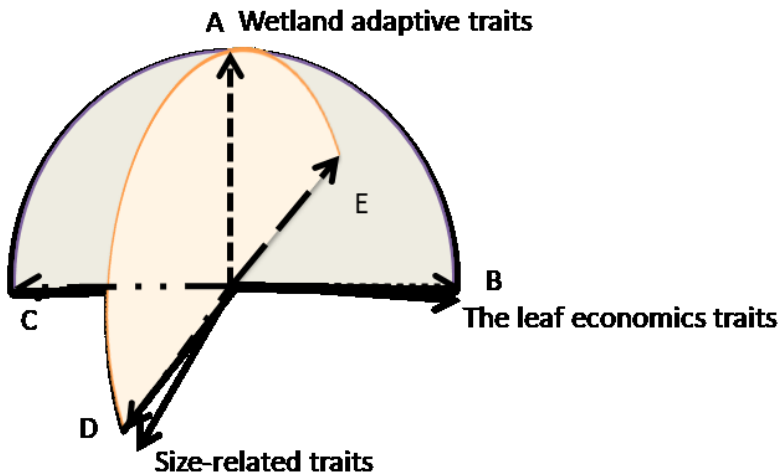


Figure 5.1 Possible positions of wetland adaptive traits (dashed lines) relative to the leaf economics trait and size-related trait axes (solid lines): A) wetland adaptive traits are decoupled from the leaf economics trait axis, indicating that adaptation to wetlands does not intrinsically hinder plant functions on resources acquisition or allocation; B) wetland adaptive traits are positively correlated to the leaf economics trait axis, suggesting that adaptation to wetlands facilitates plant functioning; C) wetland adaptive traits are negatively correlated to the leaf economics trait axis, implying costly trade-offs between adaptation and leaf functioning; D & E) wetland adaptive traits are correlated to the size-related trait axis, indicating the choices of varied wetland adaptive strategies depending on the plant size.

5.2 Materials and Methods

5.2.1 Data compilation

We compiled a global database of traits as prevailing in wetland plants. For this purpose, we defined wetland plants as those plants that occur in wetland habitats following the definition of the international Ramsar Convention (Ramsar Convention Secretariat, 2013). We compiled wetland plant traits under both field and laboratory measurements by a combination of expert knowledge of existing literature and systematic searches in Web of Science and Google Scholar (last search on the 5th of June 2018). The literature search included, but was not limited to, the following keywords: wetland, marsh, bog, floodplain, macrophytes, aquatic plants, hydrophyte, submerged, floating-leaved, emergent, isoetid, mangrove, root porosity, root/shoot ratio, shoot elongation, leaf N, leaf P, specific leaf area (SLA), leaf dry matter per unit area (LMA), plant height. We also checked the references of several important reviews of eco-physiological adaptive traits to wetlands and flooding events in the recent 15 years (e.g. Voesenek *et al.*, 2006; Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015). Moreover, we circulated enquiries around our network of wetland plant experts for recommendations for literature that we possibly had overlooked. We used The Plant List to eliminate synonyms in species names from our database (<http://www.theplantlist.org>). Our database is currently the largest database on wetland plant traits to our knowledge, containing more than 200 references for over 1200 species.

Root porosity was measured mainly as either the percentage of the hollow area in the root cross-section or the ratio of hollow volume to the whole root volume (these two methods generally show agreement in air-filled root porosity, while subtle differences between the two methods are discussed in Van Noordwijk & Brouwer, (1988)). Root/shoot ratio was measured by the root dry mass divided by the shoot dry mass. Shoot elongation was calculated as the percentage of the maximum shoot length increase upon submergence (%). We are aware that there are many other wetland adaptive traits (e.g. radial oxygen loss, leaf gas films) that have been emphasized in eco-physiological studies. However, they are either qualitative, or represented in our database by too few consistently measured observations to be included in our statistical analysis. We recorded the habitat type where each wetland plant species occurs. We added life form to each wetland plant species based on the descriptions in the original literature. For this study, we took species mean trait values to allow analysing trait-trait relationships (the distribution map of the sampling sites across the globe is shown in Fig. 5.2). Our analysis included a total of 131 wetland species of six life form categories

(grass, sedge, emergent, submerged, floating-leaved and shrub/tree), with 113 species for root porosity, 60 species for root/shoot ratio, and 32 species for shoot elongation.

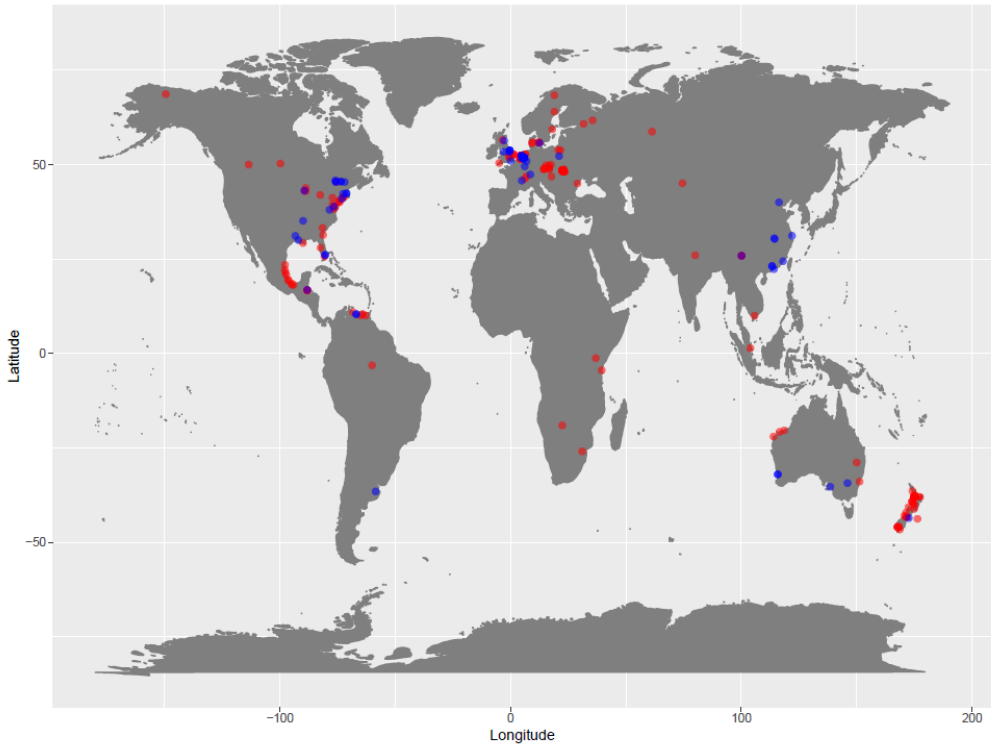


Figure 5.2 The location of the sampling sites. The field measurement data and laboratory measurement data are presented in red and blue dots, respectively. Note that the symbols are translucent and that brighter symbols indicate observations/studies at locations in close proximity of one another.

To investigate the effects of stress created by habitat wetness on trait expression, we applied the Ellenberg moisture indicator values (Ellenberg, 1988). These indicator values are based on expert knowledge of the distribution of plant species along a full gradient of habitat wetness, categorized into 12 levels from very dry habitats (level 1) to strictly aquatic (level 12). To make the Ellenberg moisture indicator applicable for a global analysis, we related the Ellenberg moisture indicator values to the USDA wetland plant classification to derive Ellenberg values for the flora of the USA (see details in Appendix 3B). In this study, the Ellenberg moisture indicator values were assigned to each wetland plant species for further analysis.

5.2.2 Data analysis

To reveal how wetland adaptive traits relate to the other two groups of traits at the inter-specific level, we conducted a principal component analysis (PCA) in R (R Core Team, 2018). Due to multiple gaps in the data set, we could not run a PCA on all of the traits selected in this study. Instead, we ran a PCA on each of the three adaptive traits separately with all leaf economics traits and size-related traits. The data points (one for each species) were labelled with their Ellenberg moisture indicator to represent each species' adaptation to habitat wetness, and their life form to present species' general characteristics of appearance. The data points labelled with habitat type are provided in Appendix 5A.

Then, we analysed trait-trait relationships between wetland adaptive traits by standardized major axis (SMA) analysis (Warton *et al.*, 2006) to estimate how one trait scales against another across samples (Warton *et al.*, 2012). The standardized axis slopes and coefficients of determination (R^2) were calculated using the `sma()` function in SMATR package (Warton *et al.*, 2012) in R (version 3.6.0) software (R Core Team, 2018). The traits data were $\log_{10}$ transformed before analysis.

Finally, we ran an ordinary linear regression to examine how each adaptive trait contributes to plants' adaptation to habitat wetness (as represented by Ellenberg moisture indicator values).

5.3 Results

The PCA on each of the adaptive traits along with the other two groups of traits showed that leaf economics traits were strongly related to PCA axis 1, with size and adaptive traits on the other axes. The detailed PCA scores on PCA axis 1 and PCA axis 2 are shown in Table 5.1.

Table 5.1 The loading scores of wetland adaptive traits, leaf economics traits and size-related traits on the first two PCA axes.

Root porosity			Root/shoot ratio			Shoot elongation		
	Axis 1	Axis 2		Axis 1	Axis 2		Axis 1	Axis 2
Root porosity	0.40	-0.42	Root/shoot ratio	0.03	-0.80	Shoot elongation	0.06	-0.87
Leaf N	-0.61	0.14	Leaf N	0.58	0.26	Leaf N	0.63	0.13
Leaf P	-0.51	-0.21	Leaf P	0.44	0.15	Leaf P	0.50	-0.14
SLA	-0.46	-0.31	SLA	0.57	0.00	SLA	0.40	0.38
Plant height	0.00	0.81	Plant height	-0.37	0.52	Plant height	-0.44	0.24
Var. explained	42.0%	22.8%	Var. explained	33.3%	20.6%	Var. explained	39.2%	21.8%

The PCA on root porosity as adaptive trait shows that root porosity was to a large extent decoupled from the leaf economics trait axis (as represented by leaf N, leaf P and SLA; Fig. 5.3A). Plant height (as representative of the size-related trait) was positioned on the third trait axis. The first two PCA axes accounted for 42.0% and 22.8% of the total variation, respectively.

Also the root/shoot ratio was to a large extent decoupled from the leaf economics trait axis (represented by leaf N, leaf P and SLA) and plant height as size-related trait (Fig. 5.3B). The first two PCA axes accounted for 33.3% and 20.6% of the total variation, respectively. The same applies to shoot elongation, which was decoupled from leaf economics traits and plant height as size-related traits. The first two PCA axes accounted for 39.2% and 21.8% of the total variation, respectively (Fig. 5.3C).

The trait-trait relationships between leaf economics traits and wetland adaptive traits were further examined by the standardized major axis (SMA) analysis. SMA analysis confirmed the largely decoupled nature of the trait-trait relationships. There were significant correlations between root porosity-SLA and root porosity-leaf N ($P < 0.05$; Table 5.2). However, the root porosity-leaf N pair had only $R^2 = 0.22$, while the effect size of the root porosity-SLA pair was even smaller (only 9%). None of the other adaptive traits related significantly to any of leaf economics traits or size-related traits.

In addition, SMA analysis confirmed the significant strong correlations between the three leaf economics traits (SLA, leaf N and leaf P) (Table 5.2). However, there were no significant correlations among any of the pairs of wetland adaptive traits (i.e. of root porosity, root/shoot ratio and shoot elongation; $P > 0.05$) tested, and the effect size R^2 was only between 0.00 to 0.02 (Table 5.2).

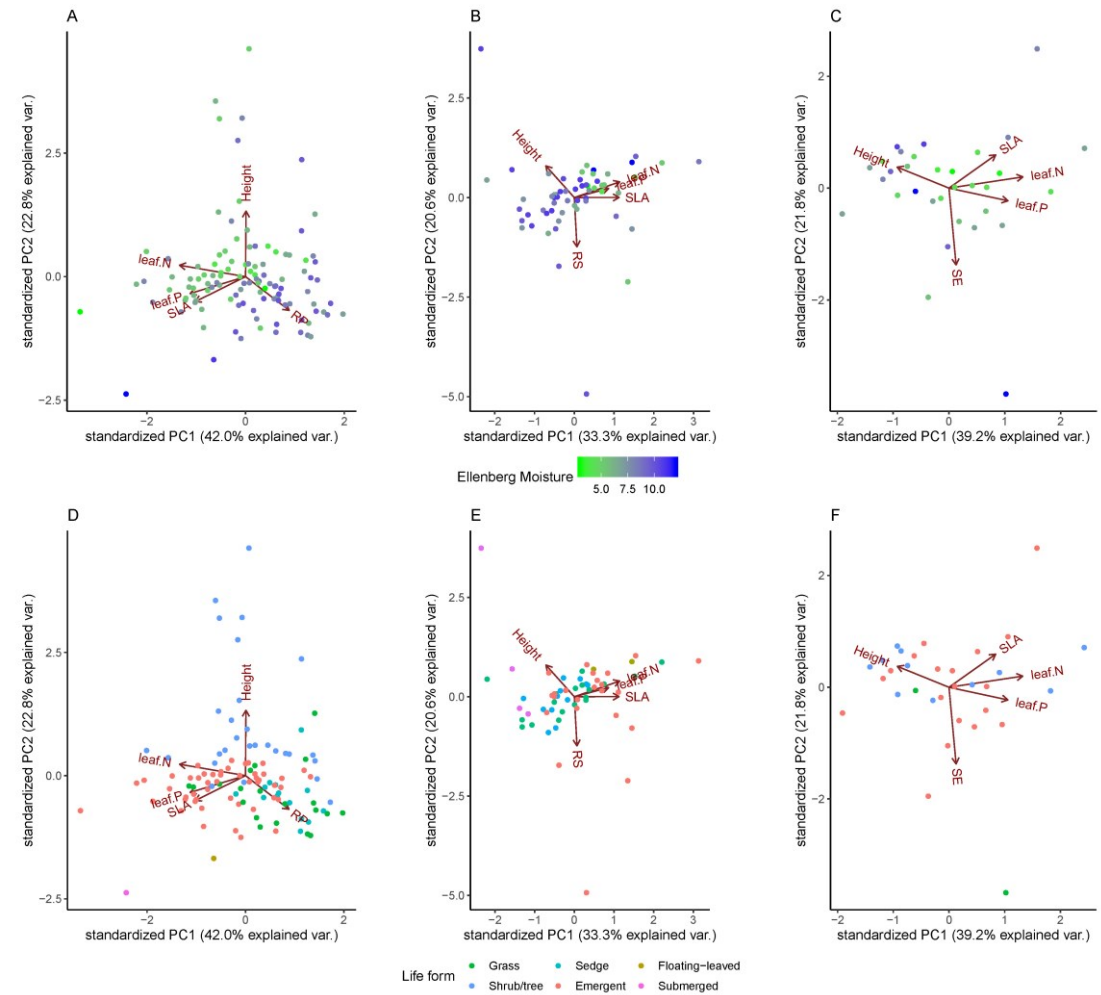


Figure 5.3 Principal Component Analysis (PCA) of leaf nitrogen (leaf N), leaf phosphorus (leaf P), specific leaf area (SLA), plant height (Height) and (A, D) root porosity (RP), (B, E) root/shoot ratio (RS) and (C, F) shoot elongation (SE) labelled by Ellenberg moisture indicator (A, B, C) and life form (D, E, F), respectively.

Table 5.2 Trait-trait relationships between leaf economics traits: specific leaf area (SLA), leaf nitrogen (leaf N), leaf phosphorus (leaf P); wetland adaptive traits: root porosity, root/shoot ratio, shoot elongation; and size-related trait: plant height. Traits were $\log_{10}$ transformed before analysis. The upper-right section shows standardized major axis slopes with 95% confidence intervals (referring to the y variable in the column and the x variable in the row). Coefficients of determination (R^2) and sample sizes are given in the lower-left section. Significant relationships ($P < 0.05$) are highlighted in bold.

	Root porosity	Root/shoot ratio	Shoot elongation	SLA	Leaf N	Leaf P	Plant height
Root porosity		0.50 (0.37, 0.68)	1.15 (0.74, 1.80)	-1.65 (-1.97, -1.38)	-2.74 (-3.23, -2.32)	-1.86 (-2.23, -1.54)	-0.77 (-0.92, -0.63)
Root/shoot ratio	0.00 (n=44)		-1.56 (-2.41, -1.01)	-1.68 (-2.17, -1.30)	-2.93 (-3.79, -2.27)	-1.94 (-2.51, -1.50)	-1.05 (-1.36, -0.81)
Shoot elongation	0.02 (n=22)	0.02 (n=23)		-2.04 (-2.90, -1.43)	-3.21 (-4.62, -2.23)	1.81 (1.26, 2.60)	-0.99 (-1.42, -0.69)
SLA	0.09 (n=113)	0.03 (n=60)	0.07 (n=32)		1.66 (1.43, 1.93)	1.07 (0.92, 1.26)	-0.47 (-0.56, -0.40)
Leaf N	0.22 (n=113)	0.03 (n=60)	0.00 (n=32)	0.28 (n=131)		0.65 (0.56, 0.75)	-0.28 (-0.34, -0.24)
Leaf P	0.02 (n=113)	0.02 (n=60)	0.01 (n=32)	0.17 (n=131)	0.25 (n=131)		0.44 (0.37, 0.52)
Plant height	0.00 (n=113)	0.02 (n=60)	0.02 (n=32)	0.07 (n=131)	0.00 (n=131)	0.00 (n=131)	

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None of the three adaptive traits seemed strongly related to differences in life form (Fig. 5.3D, E & F) or to the environmental conditions as summarized by wetland habitat type (Appendix 5A). To understand how an individual adaptive trait contributes to the prevalence of wetland plant species along a wetness gradient, we further tested the linear relationships between the Ellenberg moisture indicator and each adaptive trait (Fig. 5.4). Among the three adaptive traits, root porosity showed a significant relation with Ellenberg moisture indicator of a high effect size ($R^2=0.31$, $P<0.001$) and shoot elongation significantly explained 14% of the Ellenberg moisture indicator variance ($R^2=0.14$, $P<0.05$). There was no relationship detected between root/shoot ratio and Ellenberg moisture indicator ($R^2=0.00$, $P=0.830$). Hence, among the three adaptive traits, variation in root porosity and shoot elongation significantly contributed to the distribution of wetland plant species along a wetness gradient. Even though an increased root/shoot ratio is considered as an important wetland adaptive trait, it was not directly related to wetness adaptation.

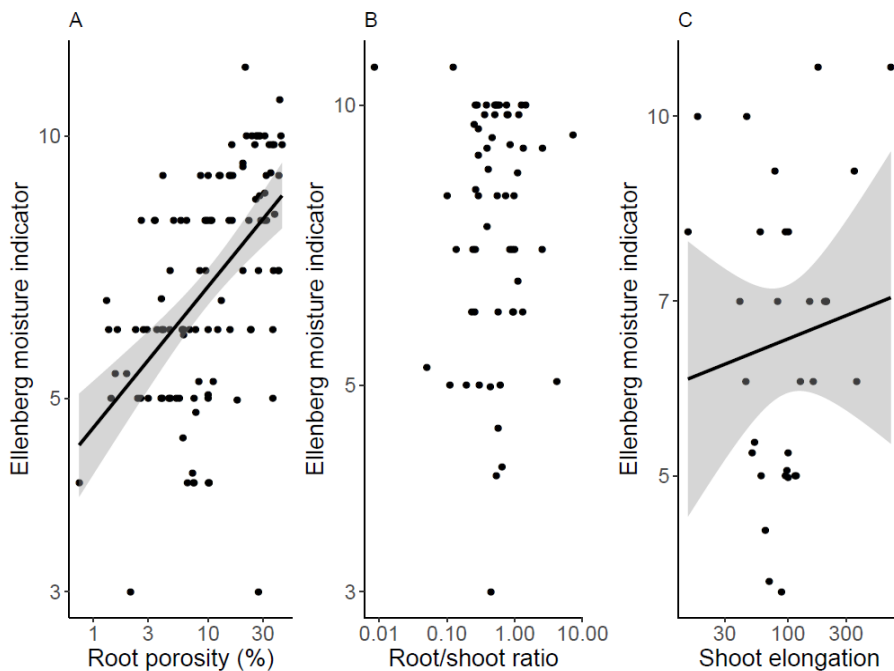


Figure 5.4 The linear relationships between Ellenberg moisture indicator and the three wetland plant adaptive traits. For root porosity ($R^2=0.31$, $P<0.001$, $n=113$), root/shoot ratio ($R^2=0.00$, $P=0.830$, $n=60$) and shoot elongation ($R^2=0.14$, $P<0.05$, $n=32$).

5.4 Discussion

5.4.1 Wetland adaptive traits as key component in wetland plant strategies

Based on the currently largest available dataset for wetland plant traits, our research explores the strategies of wetland plant species based on trait-trait relationships. Understanding the relationships between wetland adaptive traits, leaf economics traits and size-related traits will not only help us to understand wetland plant strategies in coping with the complex wetland conditions (including nutrient, light and flooding stress), but also provides a benchmark for upscaling the wetland plant traits to wetland ecosystems functioning (Moor *et al.*, 2017; Pan *et al.*, 2019).

Our research reveals that the three important wetland adaptive traits are, to a large extent, decoupled from the leaf economics and size-related trait dimensions (Fig. 5.3). Moreover, similar to the pattern in terrestrial systems, leaf economics traits and size-related traits also remain largely decoupled from each other in wetland ecosystems. This pattern suggests that besides leaf economics traits and size-related traits, wetland adaptive traits play an important but different ecological role in the adaptation to wetlands. As leaf economics traits relate to habitat fertility, and size-related traits confer a competitive power for light (and water), wetland adaptive traits mainly contribute to coping with the stressful aspects of wetland environments. Considering the tight associations between leaf economics traits and the root, stem and whole-plant economics spectra (Freschet *et al.*, 2010), we expect that wetland adaptive traits may also be decoupled from these traits of the whole plant. Together, these results indicate that the wetland adaptive strategies are a key dimension independent of other plant strategy components, such as growth and competitive strategies in wetlands.

The generally decoupled relationships between wetland adaptive traits and leaf economics traits provide an explanation for the broad distribution of aquatic plants (Santamaría, 2002; Chambers *et al.*, 2008) as they allow wetland plants to cope with both flooding stressors and habitat fertility limitations in a flexible fashion. This decoupling of adaptive traits from leaf economics traits may suggest that adaptation to wetland conditions is either cheap, or sufficiently beneficial to offset the costs of such adaptation on the wetland plant's overall resource budget. For example, with shoot elongation extra access to light, CO₂ and O₂ is gained (Colmer & Voesenek, 2009). However, the benefit of such extra access for the functioning of the underwater organs can still be limited (Rich *et al.*, 2013), and sometimes can be risky if leaves do not reach the air (Colmer & Voesenek, 2009). If flood is fast or deep, the cost for shoot elongation may offset the benefit from such adaptation from a nutrient acquisition and investment perspective (Voesenek *et al.*, 2004; Loreti *et al.*, 2016).

From a trait-based perspective, the decoupled wetland adaptive strategy from other plant strategy components may have wide implications for other stressful ecosystems. In nature, environment stressors, including drought, heat, freeze, shading, infertility and soil salinity, impose pronounced challenges to the adaptation and survival of plants (Bohnert *et al.*, 1995; Wolfe & Tonsor, 2014). While various adaptive mechanisms have been carefully examined from genetic, morphological to community points of view (Wolfe & Tonsor, 2014; Bechtold, 2018; Liu *et al.*, 2018), an integral perspective on plant's strategies as a whole is missing. We propose that other stressful environments may have similarly decoupled adaptive strategy components in response to those specific environmental stressors mentioned above. Such decoupled trait dimensions would allow plants to adapt to multifarious niche dimensions and facilitate species coexistence in stressful habitats (Westoby *et al.*, 2002; Li *et al.*, 2015).

5.4.2 Diverse plant strategies enable adaptations to a multi-faceted stressful environment

Despite their analogous functional roles in adaptations to wetland conditions, the interrelationships within the three wetland adaptive traits were all non-significant and weak (Table 5.2, $P > 0.05$ with R^2 ranges from 0.00 to 0.02). Moreover, while root porosity and shoot elongation significantly contribute to the adaption of wetland plants along the gradient of stress induced by increasing wetness, root/shoot ratio is not directly linked to the patterns of the Ellenberg moisture indicator, life form or habitat type (Fig. 5.3, 5.4 & Appendix 5A). This suggests that the different adaptive traits are not similarly aligned to a wetness gradient, while these adaptive traits may contribute concordantly or accumulatively to the different aspects of the stressful wetland environment. We conclude that the driving mechanisms behind these different adaptive traits are complicated and likely highly case-specific for different wetland conditions, including the occurrence of anoxic substrate, phytotoxic compounds, and flooding events. For example, root porosity can be induced by waterlogging and provides more oxygen transport to the rooting system (Armstrong, 1980; Colmer, 2003a; Garssen *et al.*, 2015). Likewise, shoot elongation helps plants to reach above the water surface from fully submerged conditions to gain access to oxygen (Voesenek *et al.*, 2003; Nagai *et al.*, 2010), while root/shoot ratio is a proxy for oxygen balance within wetland plant tissues (Mommer *et al.*, 2004; Winkel & Borum, 2009).

Moreover, while mostly decoupled, some links were observed between wetland adaptive traits and leaf economics traits. For example, we detected an apparent trade-off between root porosity and leaf N at the inter-specific level ($R^2 = 0.22$, $P < 0.05$; Table 5.2). The ecological causal links between root porosity and leaf N are complicated and experimental evidence has

often been contradictory. On the one hand, the formation of root porosity impedes the nutrient acquisition efficiency and will lead to trade-offs (Kirk, 2003; Hu *et al.*, 2014). On the other hand, the production of large numbers of laterals in response to flooding conditions may increase the root surface area for nutrient acquisition (Lissner *et al.*, 2003). In addition, root porosity may positively coordinate with leaf N, because the oxygen released from the root, induced by increased root porosity, can oxidize nutrients such as NH_4^+ to NO_3^- , as the main source of stable and storable nitrogen for plants (Kirk, 2003). In our case, a reduced efficiency of nutrient transport by an incremented root porosity may exist at the inter-specific level, while evidence showed that such trade-offs seems extremely weak at the intra-specific level (Pan *et al.*, 2019).

We also observed weak but significant relations between root porosity-SLA ($R^2=0.09$, $P<0.05$; Table 5.2) and between plant height-SLA ($R^2=0.07$, $P<0.05$; Table 5.2). Even though the effect sizes are small (with 9% and 7%, respectively), it suggests SLA is a key trait interrelating with the three different trait dimensions simultaneously. Previous studies indicated that the relationships between SLA and to the position on flooding gradients could be either positive or negative depending on life form, season and community weighted SLA (Huber *et al.*, 2009; Violle *et al.*, 2011; Douma *et al.*, 2012; Wright *et al.*, 2017a). Even so, in general, amphibious/aquatic plants have a higher SLA than terrestrial plants (Mommer & Visser, 2005; Pierce *et al.*, 2012).

In combination, the specific connections between the traits of different trait dimensions indicate that the adaptation to wetland conditions involves rather complex and multifarious plant strategies as expressed in different plant trait dimensions. Apparently, multiple plant strategies across multiple trait dimensions have been developed to deal with these stressful environments.

5.4.3 Implications for ecosystem functioning & ecosystem management

Disentangling the relationships between wetland adaptive traits and leaf economics traits are also important for upscaling plant functional traits to wetland ecosystem processes, such as denitrification and methane emissions (Pan *et al.*, 2019). For instance, root porosity (an adaptive trait) helps to develop an aerobic rhizosphere (Engelaar *et al.*, 1993; Colmer, 2003b; Lai *et al.*, 2011) and affects both denitrification and methane emission processes, while leaf N and leaf P (leaf economics traits) are indicative of organic matter quality to support decomposition processes (Hobbie, 2015) and may hence enhance methane production (van Bodegom & Scholten, 2001; Bhullar *et al.*, 2013a). This may be further enhanced by the “chimney effect” of wetland plants, which is created by increased root and stem porosity,

mediating methane transport to the atmosphere (Bhullar *et al.*, 2013a). The opposite driving forces complicate quantifying the facilitation vs. suppression role of wetland plants in methane emissions and denitrification. The decoupling between leaf economics traits (stimulating production) and adaptive traits (both stimulating and suppressing) further adds to the variation in impacts of wetland plants on these processes. Indeed, those influences are often considered to be species-dependent (Joabsson & Christensen, 2001; Laanbroek, 2010; Sutton-Grier & Megonigal, 2011). Our results thus highlight that precise and separate measurements are required of both adaptive traits and other key traits to adequately predict methane emission (Sutton-Grier & Megonigal, 2011; Bhullar *et al.*, 2013b).

Varied plant functional traits can enhance ecosystem management goals (Laughlin, 2014), and the decoupled patterns of adaptive, leaf economics and size-related traits can be useful for wetland environment management. Previous studies relate wetland adaptive traits to methane oxidation (Bhullar *et al.*, 2013b), water purification (Li *et al.*, 2013b) and heavy metal removal (Yang *et al.*, 2014). Leaf economics traits determine the biomass production and carbon sequestration potential of wetland ecosystems (Meerburg *et al.*, 2010; Lavorel, 2013; Doherty *et al.*, 2014). While size-related traits relate to the flooding abatement and storage potential (Bardgett *et al.*, 2014; Moor *et al.*, 2017). When adaptive traits, leaf economics traits and size-related traits are largely decoupled and correlated to different environmental drivers (such as water depth, fertility supply and plant community construction design, respectively), this implies that a flexible wetland management approach can serve different management goal by controlling different subsets of environmental conditions.

5.5 Conclusions

Our results reveal that wetland adaptive traits are largely decoupled from leaf economics trait and size-related trait dimensions, which suggests that traits adaptive to wetlands constitute an independent plant strategy dimension. This trait decoupling allows wetland plant species to cope with the multi-faceted stressful wetland environment (in terms of flooding, resources and competition). Our study indicates that no integral general strategy exists that explains the adaptation of wetland plants in coping with the complex wetland environments. Instead, the multiple facets of wetland plant strategies, as shown by the combination of functional traits including adaptive traits, leaf economics traits and size-related traits, allow wetland plants to survive in complex wetland environments and to prosper globally across a wide range of habitat fertilities. These insights provide a foundation to trait-based approaches towards

understanding the general wetland plant strategies and the distributions of wetland plants worldwide and as well as to understanding adaptations to habitat stress in general.

5.6 Acknowledgements

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5.7 Authors' contributions

PvB initialized this research; YP, PvB and EC designed and planned the research. YP and PvB compiled the data with inputs from all co-authors. YP ran all analyses with inputs from all co-authors. YP, PvB and EC wrote the first drafts of the manuscript that was further improved by inputs from all co-authors, and finalized by YP. All authors contributed critically to the drafts and gave final approval for publication.

5.8 Data accessibility statement

Data used in this paper for analysis will be deposited in the Dryad Repository once accepted.

5.9 Supporting information

Appendix 5A

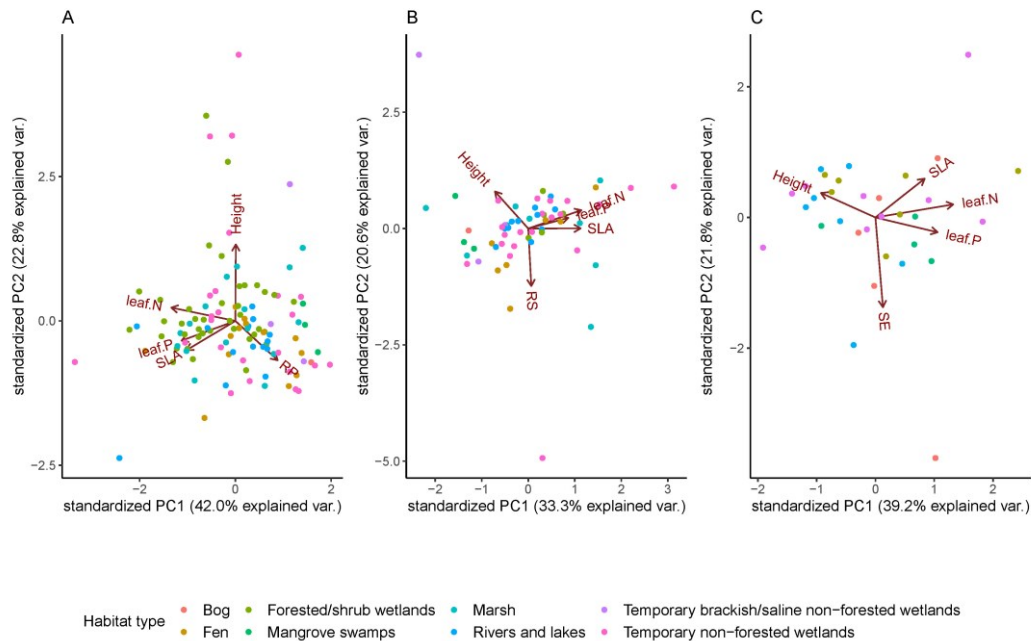


Figure 5S1 Principal Component Analysis (PCA) of leaf nitrogen, leaf phosphorus, specific leaf area, plant height and (A) root porosity, (B) root/shoot ratio and (C) shoot elongation labelled by habitat type.

