



Ecological stoichiometry and strategies of plants belonging different habitats in Kızılırmak Delta

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Kızılırmak Deltası'nda farklı habitatlara ait bitkilerin ekolojik stokiyometrisi ve stratejileri

Abstract: Kızılırmak Delta (Samsun, Türkiye) comprises a fine-scale mosaic of wetlands and saline/halophytic habitats, where strong environmental gradients may influence plant nutrient-use patterns and ecological strategies. Here, we evaluated how leaf stoichiometry (N, P, N:P) and CSR-based strategies vary across contrasting habitats and how these traits relate to measured soil and water chemistry. The dataset comprised 39 observations from nine terrestrial plant taxa sampled in three wetland localities (Balık, Cernek, and Liman lakes) and one saline area dominated by halophytes. Habitat differences were tested using Welch's t tests; trait–environment relationships were assessed using correlations and redundancy analysis (RDA). Halophyte sites exhibited markedly higher salinity indicators (EC, TDS) and higher soil phosphorus (P) levels. In contrast, wetlands had higher soil pH and higher inorganic N forms (NH₄ and NO₂+NO₃) and total soil N. Leaf N was significantly higher in wetlands. In contrast, leaf P and community-level N:P did not differ significantly between habitats, despite significant differences in soil P. Leaf N declined with increasing TDS and soil P. RDA separated habitats along a salinity–nutrient gradient, with environmental predictors explaining ~19% of the variance in stoichiometric responses. Competitive categories across taxa dominated CSR assignments. Overall, the results indicate that salinity and nutrient form/availability jointly structure habitat differences in plant stoichiometry in Kızılırmak Delta, with nitrogen showing the strongest habitat signal.

Key words: Nutrient limitation, functional traits, habitat filtering, salinity stress, coastal wetland

Özet: Kızılırmak Deltası (Samsun, Türkiye), sulak alanlar ile tuzlu/halofit habitatların iç içe geçtiği ve güçlü çevresel gradyanların görüldüğü bir mozaik sistemdir. Bu çalışmada, farklı habitatlarda yaprak stokiyometrisinin (N, P, N:P) ve CSR temelli stratejilerin nasıl değiştiği ve bu biyolojik örüntülerin toprak/su kimyasıyla nasıl ilişkili olduğu incelenmiştir. Veri seti, üç sulak alan lokalitesi (Balık, Cernek ve Liman gölleri) ile halofitlerin baskın olduğu bir tuzlu alandan örneklenen dokuz karasal bitki taksonuna ait toplam 39 gözlemi içermektedir. Habitat farkları Welch t testi ile değerlendirilmiş; özellik–çevre ilişkileri korelasyonlar ve redundans analizi (RDA) ile özetlenmiştir. Halofit habitatında EC ve TDS değerleri ile toprak P daha yüksek bulunurken; sulak alanlarda toprak pH'ı, inorganik N formları (NH₄ ve NO₂+NO₃) ve toplam toprak N daha yüksektir. Yaprak N sulak alanlarda anlamlı biçimde daha yüksekken, yaprak P ve topluluk düzeyinde N:P habitatlar arasında anlamlı farklılık göstermemiştir; bu durum, toprak P'deki büyük farklılıklara rağmen yaprak P'nin daha güçlü fizyolojik düzenleme/uyum mekanizmalarıyla kontrol edilebileceğine işaret etmektedir. Yaprak N, artan TDS ve toprak P ile azalma eğilimi göstermiş; RDA, örnekleri tuzluluk–besin gradyanı boyunca ayırmış ve çevresel değişkenler stokiyometrik varyansın yaklaşık %19'unu açıklamıştır. Sonuçlar, deltada özellikle azotun habitat farklılaşmasına en duyarlı stokiyometrik bileşen olduğunu göstermektedir.

Anahtar Kelimeler: Besin elementi sınırlılığı, işlevsel özellikler, habitat süzgeci, tuzluluk stresi, kıyı sulak alanı

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1. Introduction

Deltaic wetlands are dynamic landscapes that develop through the accumulation of suspended sediments as river flow enters a receiving basin and loses velocity (Roberts, 1997; Ameen et al., 2017). As deposition builds elevation and hydrological conditions shift, deltas support a mosaic of wetland and terrestrial plant communities whose distribution is strongly controlled by geomorphology and flooding regime (Mitsch and Gosselink, 1993; Cahoon et al., 2011). Such strong gradients create sharp transitions in salinity, nutrient availability, and disturbance regimes, which in turn shape plant functional composition.

Kızılırmak Delta (Samsun, Türkiye) is among the most important delta plains in Türkiye, recognized for its large extent and habitat diversity (Özhatay et al., 2005). The delta

includes lagoon systems and associated wetlands as well as saline/halophytic zones influenced by drainage and salinity dynamics (Arslan, 2012), providing an ideal setting for comparing plant strategies and nutrient-use patterns across contrasting habitats.

Trait-based frameworks interpret plant ecological strategies as outcomes of trade-offs among growth, persistence under stress, and reproduction under disturbance. Grime's CSR theory describes this as a continuum among competitors (C), stress-tolerators (S), and ruderals (R) (Grime, 1977). Operational CSR allocation approaches enable comparative assessment of species and communities along stress-disturbance gradients (Hodgson et al., 1999; Pierce et al., 2017), and have already been applied in Kızılırmak Delta habitats (Babur et al., 2021; Sürmen, 2021).

In parallel, ecological stoichiometry - particularly leaf nitrogen (N), phosphorus (P), and their ratios - provides a complementary lens for understanding nutrient status and potential limitation across habitats. Leaf N:P ratios have been widely used as indicators of nutrient limitation in wetlands and related ecosystems (Koerselman and Meuleman, 1996; Güsewell, 2004; 2005). Linking stoichiometry with CSR strategies offers a mechanistic perspective on how plants balance resource acquisition and stress tolerance across environments.

Moreover, foliar nutrient composition is not only a reflection of habitat nutrient pools but also of species-specific regulation, uptake costs, and allocation patterns under environmental stress (Aerts and Chapin, 2000; Sardans and Peñuelas, 2013). In wetlands, plant tissue nutrient “signatures” have been shown to respond predictably to nutrient availability, making stoichiometric traits informative for diagnosing habitat-level differences (Willby et al., 2001). Likewise, variability in N:P ratios across wetland vegetation has been linked to shifts in nutrient limitation and community structure (Güsewell et al., 2003; Güsewell, 2004). Under saline conditions, physiological constraints associated with salinity stress may further modify nutrient acquisition and internal balance, potentially decoupling leaf nutrient patterns from soil nutrient pools (Akcin and Yalcin, 2016). Despite the importance of these mechanisms, integrated assessments that combine stoichiometric patterns with plant strategy frameworks across fine-scale delta habitat mosaics remain comparatively limited.

Building on earlier delta-based strategy and habitat comparisons (Babur, 2018; Sürmen, 2021), this study compares plant stoichiometric patterns and CSR-based strategies across wetland and halophytic habitats in Kızılırmak Delta and relates these biological patterns to measured soil and water chemistry.

2. Materials and Method

The study was conducted in the Kızılırmak Delta (Samsun, Türkiye), using four localities that represent two habitat categories: Balık Lake, Cernek Lake, and Liman Lake (wetland), and a saline area dominated by halophytic vegetation (Fig. 1).

The dataset comprised 39 observations for nine plant taxa sampled across four localities (wetland, $n = 24$; halophyte, $n = 15$). For each observation, leaf N, leaf P, and leaf N:P were recorded, together with environmental variables including electrical conductivity (EC), total dissolved solids (TDS), soil pH, soil NH_4 , soil NO_2+NO_3 , soil total N, and soil P.

Soil and water chemical measurements followed standard protocols as applied in the previous delta study context (Rainwater and Thakcher, 1960; Tüzüner, 1990; Babur et al., 2021). Phosphorus determinations were consistent with commonly used soil extraction and assessment approaches (Bray and Kurtz, 1945), and N determinations followed established Kjeldahl-based workflows used in comparable studies (Allen et al., 1976).

Habitat differences in environmental and stoichiometric variables were evaluated using Welch’s two-sample t-tests. Relationships between leaf stoichiometry and environmental variables were assessed using Pearson correlation.

To summarize multivariate trait-environment structure, redundancy analysis (RDA) was computed by regressing standardized leaf stoichiometric variables (N, P, N:P) on standardized environmental predictors (EC, soil pH, NH_4 , NO_2+NO_3 , soil total N, and soil P), followed by principal component analysis of fitted values; results were visualized as an RDA biplot.



Figure 1. General views of studied habitats

3. Results

Across the 39 samples, habitat categories showed clear differentiation in environmental chemistry (Fig. 2; Table 1). Halophyte sites displayed higher salinity-related metrics: EC increased from 4.04 ± 1.41 ms (wetland) to 7.34 ± 0.67 ms (halophyte) and TDS from 1696 ± 815 to 4597 ± 1168 (both Welch's t-tests $p < 0.001$).

In contrast, wetland sites had higher soil pH (8.38 ± 0.60 vs. 7.77 ± 0.15 ; $p < 0.001$) and higher inorganic N forms, with NH_4 (1.49 ± 1.29 vs. 0.14 ± 0.21 ; $p < 0.001$) and NO_2+NO_3 (0.506 ± 0.75 vs. 0.055 ± 0.01 ; $p = 0.007$). Soil

total N was also higher in wetland samples (1.39 ± 1.11 vs. 0.165 ± 0.04 ; $p < 0.001$), whereas soil P was markedly higher in halophyte samples (4.13 ± 0.60 vs. 0.157 ± 0.24 ; $p < 0.001$) (Table 1).

Leaf stoichiometric traits differed between habitats primarily in nitrogen content (Fig. 3; Table 1). Leaf N was higher in wetland samples (3.74 ± 1.71) than in halophyte samples (2.44 ± 0.77) ($p = 0.0026$). Leaf P showed no significant habitat-level difference (0.37 ± 0.14 vs. 0.27 ± 0.21 ; $p = 0.131$), and leaf N:P was also not significantly different between habitats ($p = 0.530$) (Fig. 3).

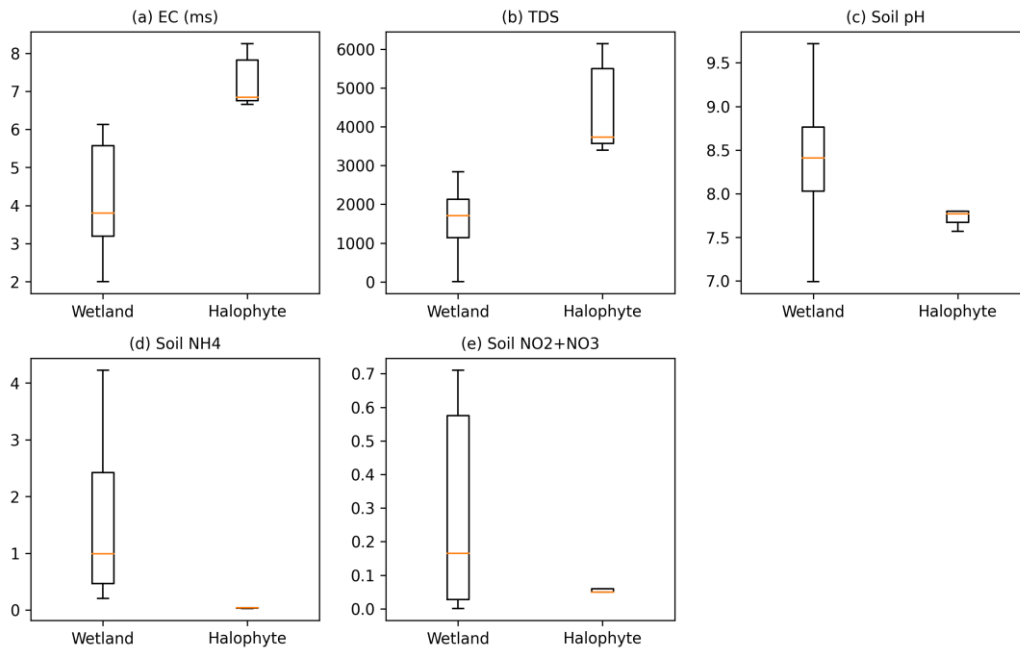


Figure 2. Environmental variables by habitat category (combined panel): (a) EC, (b) TDS, (c) soil pH, (d) soil NH_4 , (e) soil NO_2+NO_3 . Boxplots show median, interquartile range and whiskers

At the species level (Table 2), wetland taxa spanned a broad range of N and N:P values. *Apium nodiflorum* had the highest mean leaf N (7.57 ± 0.15) and N:P (32.87 ± 6.03), whereas *Samolus valerandi* showed relatively low N (2.06 ± 0.08) and low N:P (6.75 ± 2.15). Among halophytes, *Artemisia santonicum* had the highest mean leaf P (0.61 ± 0.02) and the lowest N:P (6.01 ± 0.37), while *Spergularia media* showed a comparatively high N:P (22.49 ± 8.09) despite low leaf N (1.79 ± 0.04). CSR strategy assignments were dominated by competitive types: halophyte taxa were classified as C, while wetland taxa included C and competitive subtypes (C/CR; C/CSR) (Table 2).

Trait-environment relationships supported the dominance of the salinity-nutrient gradient (Table 3; Fig. 4). Leaf N was negatively correlated with TDS ($r = -0.334$, $p = 0.0378$)

and Soil P ($r = -0.386$, $p = 0.0151$), while leaf P was positively correlated with Soil NH_4 ($r = 0.391$, $p = 0.0139$) (Table 3). In standardized multiple regression models, Soil P remained a significant predictor of leaf N (standardized beta = -0.691 , $p = 0.043$), whereas overall model fit was modest ($R^2 = 0.19$).

The RDA indicated that environmental predictors explained 19.2% of the variance in standardized stoichiometric responses; RDA1 and RDA2 accounted for 62.2% and 36.1% of the constrained component, respectively. Samples tended to separate by habitat category, with halophyte samples aligning with higher EC and soil P, and wetland samples aligning with higher soil pH and nitrogen variables (Fig. 4).

Table 1. Habitat-level summary of environmental variables (mean \pm SD; min-max)

Habitat	EC (ms) (mean \pm SD; min-max)	TDS (PPT) (mean \pm SD; min-max)	Soil_pH (mean \pm SD; min-max)	Soil_NH ₄ (mean \pm SD; min-max)	Soil_NO ₂ -NO ₃ (mean \pm SD; min-max)	Soil_N (mean \pm SD; min-max)	Soil_P (mean \pm SD; min-max)
Halophyte	7.34 ± 0.67 ; 6.66–8.25	4596 ± 1167 ; 3401–6143	7.77 ± 0.15 ; 7.57–8.00	0.14 ± 0.21 ; 0.030–0.550	0.06 ± 0.01 ; 0.05–0.06	0.17 ± 0.04 ; 0.11–0.20	4.13 ± 0.60 ; 3.59–5.11
Wetlands	4.04 ± 1.41 ; 2.00–6.13	1696 ± 815 ; 3.10–2835	8.38 ± 0.59 ; 6.99–9.72	1.50 ± 1.29 ; 0.20–4.22	0.51 ± 0.75 ; 0.00–2.41	1.39 ± 1.11 ; 0.31–4.21	0.16 ± 0.24 ; 0.01–0.90

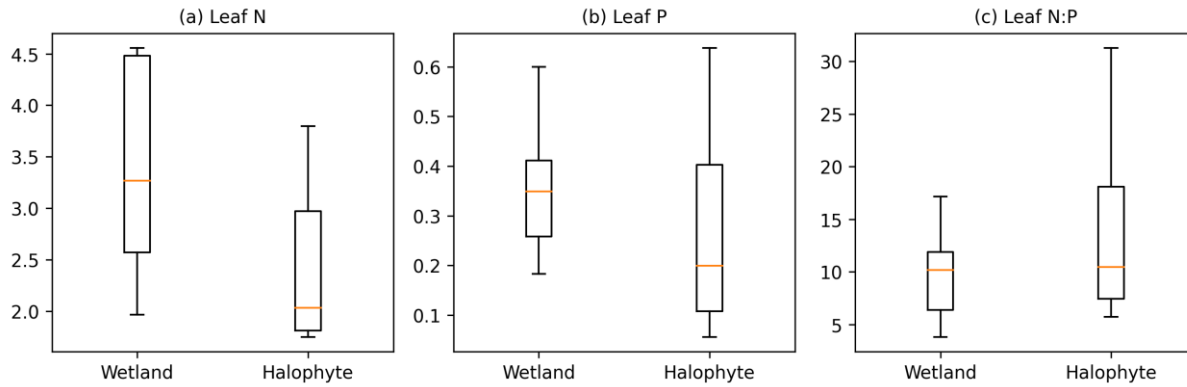


Figure 3. Leaf stoichiometry by habitat category (combined panel): (a) leaf N, (b) leaf P, (c) leaf N:P. Boxplots show median, interquartile range and whiskers

Table 2. Species list with habitat affiliation and CSR category, and species-level leaf N, P and N:P (mean ± SD)

Species	Habitat	CSR	N (mean±SD)	P (mean±SD)	N:P (mean±SD)
<i>Apium nodiflorum</i> Lag.	Wetland	C/CR	7.57 ± 0.16	0.236 ± 0.05	32.87 ± 6.02
<i>Artemisia santonicum</i> L.	Halophyte	C	3.67 ± 0.12	0.612 ± 0.02	6.01 ± 0.37
<i>Calystegia sepium</i> (L.) R.Br.	Wetland	C/CR	4.53 ± 0.04	0.431 ± 0.09	10.80 ± 2.14
<i>Euphorbia villosa</i> Willd.	Wetland	C/CSR	3.68 ± 0.61	0.513 ± 0.13	7.73 ± 2.89
<i>Geranium robertianum</i> L.	Wetland	C/CR	3.19 ± 0.26	0.275 ± 0.06	12.09 ± 2.91
<i>Salicornia prostrata</i> Pall. subsp. <i>prostrata</i>	Halophyte	C	2.02 ± 0.10	0.199 ± 0.02	10.16 ± 0.31
<i>Samolus valerandi</i> L.	Wetland	C/CR	2.06 ± 0.08	0.338 ± 0.13	6.75 ± 2.15
<i>Spergularia media</i> (L.) C.Presl	Halophyte	C	1.79 ± 0.04	0.090 ± 0.04	22.49 ± 8.09
<i>Suaeda maritima</i> (L.) Dumort.	Halophyte	C	2.94 ± 0.06	0.356 ± 0.09	8.60 ± 2.14

4. Discussions

This study shows that terrestrial plant assemblages within Kızılırmak Delta are structured along a strong habitat gradient that links salinity-related conditions to nutrient forms and availability. Halophyte sites exhibited higher EC and TDS and higher soil P, whereas wetland sites had higher pH and higher inorganic N (NH₄ and NO₂+NO₃) as well as higher soil total N (Fig. 2; Table 1). Deltaic wetlands often exhibit such coupled gradients because sediment deposition, inundation frequency, and freshwater-saltwater mixing control soil chemistry and plant establishment (Mitsch and Gosselink, 1993; Cahoon et al., 2011). Vegetation development on delta-splay surfaces can also be closely linked to physical conditions and sediment dynamics (Ameen et al., 2017). In the coastal plain adjacent to the delta, groundwater salinity varies spatially and temporally, providing an additional mechanism that can reinforce habitat differentiation (Arslan, 2012).

Leaf stoichiometric responses mirrored this environmental differentiation mainly through nitrogen. Leaf N was significantly higher in wetland samples than in the halophyte habitat (Fig. 3a), consistent with higher soil inorganic and total N in wetlands (Table 2) and indicating that N uptake and assimilation are more strongly supported under wetland conditions. Because foliar nutrient concentrations reflect both external supply and plant-level regulation (Aerts and Chapin, 2000), higher wetland leaf N likely reflects both greater N availability and differences in species-level nutrient-use strategies. In contrast, leaf P did not differ significantly between habitats, despite the much higher soil P levels in the halophyte habitat (Table 2). This pattern suggests that foliar P is buffered by physiological control and internal allocation and that stressful conditions

associated with salinity may constrain nutrient acquisition or alter allocation priorities (Akcin and Yalcin, 2016; Sardans and Peñuelas, 2013).

Table 3. Pearson correlation summary and standardized regression coefficients linking leaf stoichiometric traits to environmental variables

Species	Habitat	CSR
N	EC (ms)	-0.268 (p=0.0992, n=39)
N	Soil_N	+0.141 (p=0.392, n=39)
N	Soil_NH ₄	+0.130 (p=0.431, n=39)
N	Soil_NO ₂ -NO ₃	+0.101 (p=0.541, n=39)
N	Soil_P	-0.386 (p=0.0151, n=39)
N	Soil_pH	+0.065 (p=0.696, n=39)
N	TDS (PPT)	-0.334 (p=0.0378, n=39)
N:P	EC (ms)	+0.133 (p=0.42, n=39)
N:P	Soil_N	-0.192 (p=0.242, n=39)
N:P	Soil_NH ₄	-0.290 (p=0.0731, n=39)
N:P	Soil_NO ₂ -NO ₃	-0.124 (p=0.453, n=39)
N:P	Soil_P	+0.096 (p=0.56, n=39)
N:P	Soil_pH	-0.263 (p=0.106, n=39)
N:P	TDS (PPT)	-0.041 (p=0.803, n=39)
P	EC (ms)	-0.270 (p=0.097, n=39)
P	Soil_N	+0.160 (p=0.331, n=39)
P	Soil_NH ₄	+0.391 (p=0.0139, n=39)
P	Soil_NO ₂ -NO ₃	+0.100 (p=0.544, n=39)
P	Soil_P	-0.238 (p=0.144, n=39)
P	Soil_pH	+0.281 (p=0.0828, n=39)
P	TDS (PPT)	-0.061 (p=0.711, n=39)

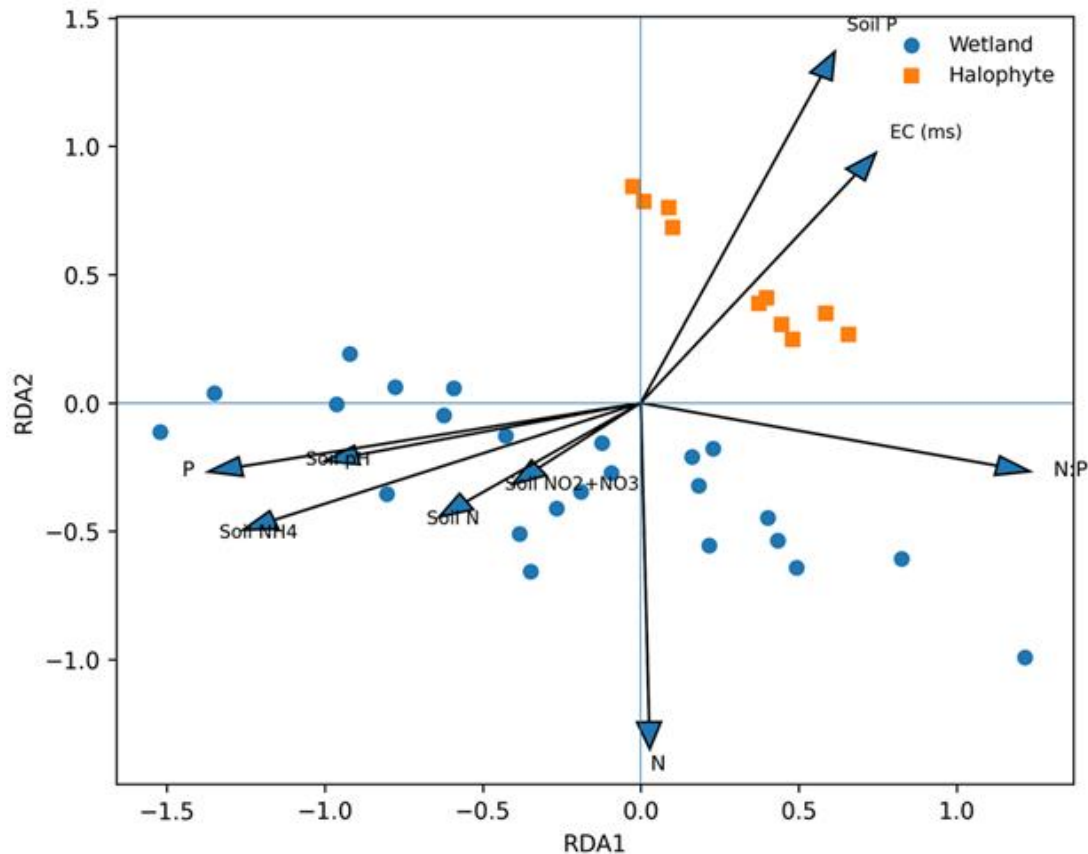


Figure 4. RDA biplot relating leaf stoichiometry (N, P, N:P) to environmental variables (EC, soil pH, NH₄, NO₂+NO₃, Soil N, Soil P). Points represent samples (symbol = habitat category) and arrows indicate standardized environmental gradients

Although community-level leaf N:P did not differ significantly between habitats (Fig. 3c), species means revealed substantial stoichiometric spread (Table 2). N:P is widely used as a comparative indicator of relative nutrient balance and potential limitation in wetlands and related ecosystems (Koerselman and Meuleman, 1996; Güsewell, 2004; 2005). Additionally, biomass N:P ratios have been proposed as indicators of nutrient limitation in wetland plant populations (Güsewell et al., 2003). Species-level contrasts in N:P observed here, therefore, likely reflect differences in nutrient acquisition and allocation. Comparable work has shown that tissue nutrient signatures can predict herbaceous wetland community responses to nutrient availability (Willby et al., 2001).

CSR strategy assignments were dominated by competitive types, with halophyte taxa classified as C and wetland taxa spanning competitive subtypes (C/CR; C/CSR) (Table 2). Within the CSR framework, competitive strategies are expected where resource capture and growth remain advantageous and where stress and disturbance do not overwhelmingly constrain biomass accumulation (Grime, 1977; 2002). Because CSR allocation depends on trait syndromes and is sensitive to the trait set used, interpretation is strengthened when based on standardized allocation approaches (Hodgson et al., 1999; Pierce et al., 2017). The dominance of competitive categories in both habitats reflects the particular taxa included and the relatively stable microsites sampled within each habitat.

Trait-environment statistics reinforced the importance of the salinity-nutrient gradient. Leaf N decreased with increasing TDS and soil P in bivariate correlations and remained negatively associated with soil P in the

multivariate model (Table 3). The RDA biplot summarized these relationships by positioning halophyte samples closer to the EC and soil P vectors and wetland samples closer to soil pH and nitrogen variables (Fig. 4). The constrained ordination explained a modest fraction of the total variance, which is consistent with evidence that plant responses to similar soil conditions can vary among regions and that local resource gradients interact with broader-scale context (Seidling and Rohner, 1993; Cornwell and Grubb, 2003). Moreover, deviations in nitrogen-related indicator expectations can be linked to atmospheric inputs and other external sources of N, potentially adding noise to soil-plant relationships (Seidling and Fischer, 2008).

From an applied perspective, the results suggest that shifts in hydrology and salinity - driven by drainage, canal leakage, or changes in freshwater inflow - may alter not only species composition but also community nutrient balances in the delta. Hydrological processes underpin wetland functioning and biogeochemical cycling (Mitsch and Gosselink, 1993), while salinity dynamics in the Bafra Plain can influence the spatial distribution of saline conditions (Arslan, 2012). Deltaic wetland accretion and sediment redistribution can further modify habitat chemistry and vegetation patterns (Cahoon et al., 2011; Ameen et al., 2017). Therefore, maintaining hydrological heterogeneity and limiting salinization of wetland zones are likely important for sustaining both biodiversity and functional diversity across the habitat mosaic.

A limitation of the present analysis is that it is based on a relatively small set of species and observations with unbalanced habitat sample sizes. In addition, the dataset represents a single sampling context and does not explicitly

address seasonal variability, which can be substantial in wetland systems (Mitsch and Gosselink, 1993). Future studies would benefit from replicated sampling across seasons and years, the inclusion of additional functional traits (e.g., SLA, leaf dry matter content, and tissue ion concentrations), and the explicit quantification of the hydrological regime. These expansions help clarify whether the observed patterns reflect persistent habitat filtering or short-term environmental conditions during the sampling period.

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Conflict of Interest

No potential conflict of interest was reported by the authors.

Authors' Contribution

Hakan Yılmaz: conceptualization of the study, statistical analysis and interpretation, and critical revision and editing of the manuscript. Burak Sürmen: sampling design support, field sampling, laboratory measurements, data curation, and drafting of the manuscript.

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