CNP stoichiometry and productivity limitations in high-altitude wetland ecosystems of the Eastern Pamir

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SUMMARY

We studied two wetland plant community types that occur on flat lake terraces in the Eastern Pamir mountains (Tajikistan, Central Asia). We selected 13 homogeneous patches of salt marsh vegetation dominated by *Blysmus rufus* (Huds.) Link, and 20 homogeneous patches of saline small sedge meadow. From each patch we took soil and biomass samples which were analysed in the laboratory. We used $\delta^{13}C$ and $\delta^{15}N$ values for plant biomass to determine the type of nutrient limitation and to characterise dominant species, and we assessed the impact of detrital input on the CNP stoichiometry of biomass. Biomass $\delta^{13}C$ was typical for plants growing under low partial pressure of CO_2; while $\delta^{15}N$ was very high, especially in the leaves of *Carex orbicularis* Boott. N limitation was indicated for the majority of sampled sites, yet we found no significant correlation between $\delta^{13}C$ or $\delta^{15}N$ and N/P quotient. There were pronounced differences in $\delta^{15}N$ between species, the lowest values being recorded for *Carex microglochin* Wahlenb. No significant influence of detrital inputs on the chemical composition of plant biomass was detected.

KEY WORDS: Central Asia, N/P quotient, nutrient limitation, stable isotopes, Tajikistan

INTRODUCTION

Ecosystem succession and development is driven by the availability of resources such as light, water and nutrients, which strongly influence the structure of plant communities. Among the nutrients, nitrogen (N) and phosphorous (P) are considered to be the two most limiting elements in many terrestrial ecosystems (Koerselman & Meuleman 1996, Reich & Oleksyn 2004, Craine *et al.* 2015, Laiolo *et al.* 2015). The distributions of these key nutrients are uneven in space and time, and follow the variability of biotic and abiotic factors, thus modifying resource production and consumption (Laiolo *et al.* 2015). The N cycle is complex with many transformations, feedbacks and interactions with other elements; also, N cycling rates and predominant bioavailable forms differ among ecosystems. In general, however, dissolved organic forms of N dominate in colder ecosystems, and mineral forms (either NH_4^+ or NO_3^-) in warmer ecosystems. Bioavailable forms of N can be lost from the cycle as gaseous emissions (denitrification), particulate losses (erosion) or by leaching (Zech *et al.* 2011, An & Li 2015, Craine *et al.* 2015). Whereas N availability is linked to biological processes, available P originates mostly from rock (by weathering) and, to a lesser degree, from organic matter (by decomposition) (Jiao *et al.* 2015).

In arid and semi-arid regions, the highest influxes of detrital material - which provide extra nutrients to soils - are observed during warm and wet periods, when weathering is most intense (Manning *et al.* 2013, Yang *et al.* 2013). However, in regions characterised by low and/or highly seasonal precipitation, the main source of detrital material is short- and long-distance aeolian transport, which is most intense during dry periods (Wu *et al.* 2009, Wu *et al.* 2015). Detrital material subjected to various abiotic and biotic processes over prolonged periods is in general enriched in heavy isotopes of carbon (C), *e.g.* $\delta^{13}C$ is around -10 ‰ in dryland dust samples (Chen *et al.* 2015). Therefore, soil $\delta^{13}C$ can be used as an indicator of detrital material input to soils (Cao *et al.* 2004, Chen *et al.* 2015, Chen *et al.* 2016).

As leaf N and P typically reflect the availability of soil N and P, the N/P quotient of vegetation can be used as an indicator of nutrient limitation at community level (Koerselman & Meuleman 1996, Reich & Oleksyn 2004). The critical nutrient quotients established experimentally by Koerselman & Meuleman (1996) are commonly-used indicators; $N/P > 16$ indicates P limitation, while $N/P < 14$ indicates N limitation. In assessing a limitation type, N/P quotients can be complemented with critical values of the N and P contents of dry plant biomass, as proposed by Wassen *et al.* (1995), which are

particularly well-suited to wetland habitats; leaf N < 14 mg g^{-1} indicates N limitation and leaf P < 0.7 mg g^{-1} indicates P limitation. Changes in nutrient availability also influence the isotopic ratios of plant biomass; usually, plants discriminate against ^{15}N less in N-limited habitats than in N-rich habitats (Clarkson *et al.* 2005).

Temperature affects all physiological processes and controls cycling of the main nutrients. However, its global influence on plant nutrient content (greater content of leaf N and P under colder conditions due to the offset mechanisms) differs from its global influence on soil nutrients (reduced availability of N and P at low temperatures due to depression of microbial decomposition) (Xu *et al*. 2015, Reich & Oleksyn 2004). Because they are temperature-dependent, nutrient cycles and patterns might be disturbed by the current increase in global temperatures and the resulting widespread drying trend. First reports describe an aridity- and warming-related decline of soil C, N and P, which is most pronounced in arid and semi-arid regions. Such variations in CNP stoichiometry might alter ecosystem structure and function, and hence the provision of services to local inhabitants (Jiao *et al.* 2015, Reich & Oleksyn 2004).

In this study we investigated the issues of CNP stoichiometry and productivity limitation in high-altitude wetland ecosystems developed under cold semi-arid to arid climatic conditions. We posed two main research questions, listed below.

1. Can the values of $\delta^{13}C$ and $\delta^{15}N$ for plant biomass (at both community and species level) replace the critical values of Koerselman & Meuleman (1996) and Wassen *et al*. (1995) as identifiers of nutrient limitation type?
2. Which environmental factors best explain the variability of the investigated isotopes?

Additionally, we tried to determine typical isotopic ratios for three dominant plant species, and whether we can detect the impact of detrital input on the chemical composition of plant biomass at community level.

METHODS

Study area and sites

The Pamir Mountains are situated in the south-eastern part of Central Asia, mostly in Tajikistan but reaching into Kyrgyzstan, China and Afghanistan. Their climate is extreme and the growing season is rather short. Due to significant landscape differences, the Pamir range is divided into a western and an eastern part. The Western Pamir has alpine features with peaks up to 7,500 m a.s.l., steep slopes, deep ravines (denivelations above 4,000 m a.s.l.) and relatively intense precipitation at high altitudes (~1,500 mm p.a. above 3,000 m a.s.l. as opposed to ~200 mm p.a. below 3,000 m a.s.l). The Eastern Pamir is a plateau at 3,500–4,000 m a.s.l. surrounded by rounded peaks up to ~ 6,000 m a.s.l., with very low annual precipitation (50–150 mm above 3,000 m a.s.l.) which, in combination with high insolation, strong winds and monthly average air temperatures below zero from October to March, makes the Eastern Pamir a cold mountainous desert (Rojan 2007, Williams & Konovalov 2008, Kayumov 2010, Mętrak *et al*. 2015). The study sites were located in the Eastern Pamir, one within the catchment of Yashilkul Lake and the other in the joint catchment of Lakes Rangkul and Shorkul (Figure 1A), on wide, flat terraces around three small and medium-sized (< 10 km^2) shallow lakes (Bulunkul, Sasykkul and Rangkul).

Lakes Bulunkul (37° 43' 29" N, 72° 57' 45" E) and Sasykkul (37° 41' 48" N, 73° 10' 51" E) lie within the catchment of Yashilkul Lake and are situated in the east–west trending valley of the River Alichur (37° 43' 59" N, 73° 7' 47" E), in the climatic transition zone between the semi-arid Western Pamir and the arid Eastern Pamir (Figures 1A–C). This region currently receives approximately 50 mm of precipitation *per* year (average for the period 2009–2014 is 59 mm; unpublished data from the Bulunkul Meteorological Station of the Tajikistan National Agency for Hydrometeorology) and average annual air temperature is around - 4 ºC (average for the period 2009–2014 is - 4.3 ºC; data source as above). Lake Bulunkul (3,767 m a.s.l., area 3.5 km^2) is the smallest and least saline of the three lakes (concentration of salts up to 180 mg L^{-1}, pH 8–9), as it drains into Yashilkul Lake and the Alichur River (Achrorov 2006, Mętrak *et al.* 2015). The closed Lake Sasykkul, located at 3,825 m a.s.l., is the largest (8.9 km^2) and most saline (> 100,000 mg salts L^{-1}, pH around 10) (Achrorov 2006, Mętrak *et al.* 2015).

Lake Rangkul (38° 28' 51" N, 74° 15' 53" E, 3,784 m a.s.l.) is located in the Rangkul/Shorkul catchment, which is farther east and near the Chinese border (Figure 1A,D). During the period 1950–2005, this region was characterised by annual mean precipitation ~74 mm and annual average air temperature - 0.7 ºC (Kayumow 2010, Williams & Konovalov 2008). Lake Rangkul covers an area of approximately 8 km^2. Its pH is the same as that of Lake Bulunkul (~8) but its waters are slightly more saline, reaching 400 mg salts L^{-1} (Achrorov 2006, Mętrak *et al.* 2015).

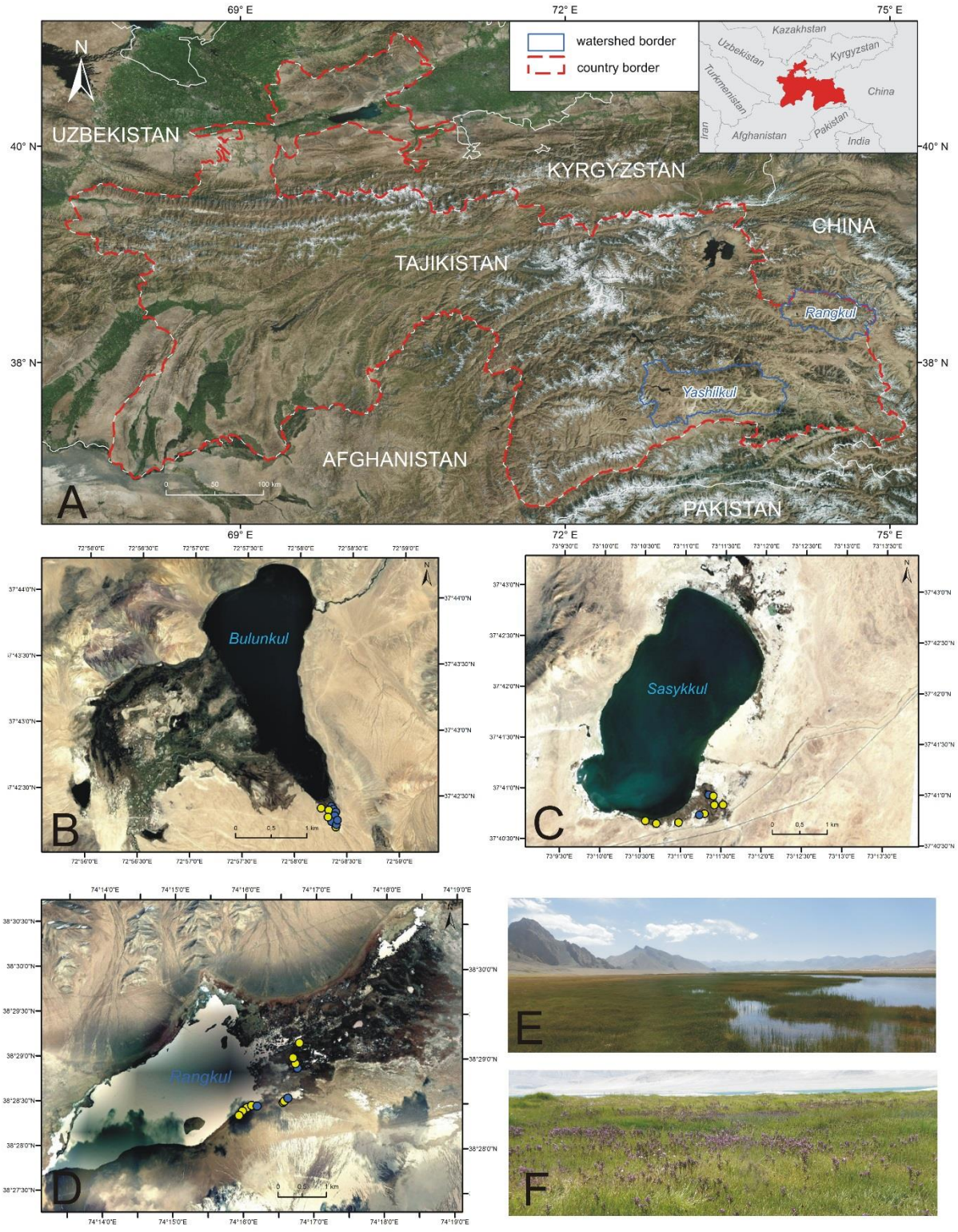

Figure 1. A: Locations of the Yashilkul and Rangkul/Shorkul catchments in the Eastern Pamir, Tajikistan. B–D: Locations of study sites on the terraces of Lakes Bulunkul (B), Sassykul (C) (both in the Yashilkul catchment) and Rangkul (D) (Rangkul/Shorkul catchment); blue dots = salt marsh, yellow dots = saline small sedge meadow. E: Salt marsh dominated by *Blysmus rufus*. F: Saline small sedge meadow dominated by *Carex microglochin* and *Carex orbicularis*. Sources: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, the GIS User Community, and Google Earth.

Plant communities and species studied

For the purpose of this study we selected two types of plant community, identified according to the vegetation survey described by Mętrak *et al.* (2017):

(1) salt marsh dominated by *Blysmus rufus* (Huds.) Link (Figure 1 E); and

(2) saline small sedge meadow dominated by *Carex microglochin* Wahlenb and/or *Carex orbicularis* Boott (Figure 1 F).

Salt marsh vegetation occurred mostly in the littoral zones of lakes, and in small ponds (stagnant water) that resulted from melting of ground ice. Saline small sedge meadow communities preferred locations near springs, outflows of subsurface waters (seepage/ spring zones), and small watercourses entering lakes (flowing water). For the detailed studies of foliar chemistry we chose three of the most abundant species, namely *Blysmus rufus*, *Carex microglochin* and *Carex orbicularis*, all of which belong to the *Cyperaceae* family and are characterised by C3 photosynthesis (Kukkonen 1970, Bruhl 1990).

Species were identified using a key developed for the Eastern Pamir by Ikonnikov (1963) and verified against specimens in the herbaria of the Experimental Station of the Academy of Sciences of the Republic of Tajikistan in Chechekty and the Pamir Biological Institute in Khorog. Species names were checked against the database of Kew Royal Botanic Gardens (RBG-MBG 2013).

Sampling

We selected 13 homogeneous patches of salt marsh dominated by *Blysmus rufus* and 20 homogeneous patches of saline small sedge meadow. Within each patch we randomly established a 50 cm square plot from which soil and biomass samples were collected in July 2014. Soil samples were taken from the effective root penetration zone typical for saturated soils (0–30 cm). There were only 19 soil samples from saline small sedge meadow because we were unable to collect a sample in one patch. Soil moisture was assessed in the field as the difference in mass between wet (immediately after sampling) and air dried samples. Above-ground biomass was collected by clipping the vegetation 1 cm above ground level, leaving the moss layer below untouched. Only living biomass was retained for analysis.

In July 2015 we sampled living biomass of *Blysmus rufus*, *Carex microglochin* and *Carex orbicularis* (separately) within all of the previously established plots. Biomass samples consisted of healthy green leaves collected from approximately ten individuals *per* plot.

Laboratory analyses

Soil samples were oven dried at 50 °C, ground manually with a mortar, and sieved (< 0.25 mm). Biomass samples were oven dried at 50 °C and pulverised in an automatic mill. For soil samples we measured the following: (1) electrical conductivity (EC) with a HQ40d Portable Multi Meter (Hach, Loveland, CO, USA), in water extract (soil : water ratio 1 : 5) and recalculated to electrical conductivity of saturated soil extract (ECe) at 25 °C (dS m^{-1}) (Shirokova *et al.* 2000); (2) total carbon (TC) and total nitrogen (TN) with a CHNS Elemental Analyser NA 2500 (Carlo Erba, Milan, Italy); and (3) available phosphorous content (P_{av}) by the Olsen method (do Carmo Horta & Torrent 2007). Additionally, we measured total organic carbon (TOC) after digestion with HCl using a FLASH 2000 CHNS Elemental Analyzer (Thermo Fisher Scientific, Bremen, Germany), and nitrates and ammonia ions in 0.03 M acetic acid extract with a San^{++} Continuous Flow Analyzer (Skalar Analytical, Breda, The Netherlands). Soil moisture content assessed in the field was calculated as the difference in mass between wet (immediately after sampling) and air dried samples, expressed as a percentage of the water content of the air dried sample.

In biomass samples we measured the following: (1) total carbon (TC) and total nitrogen (TN) (FLASH 2000 CHNS Elemental Analyzer); (2) total phosphorous (TP) (San^{++} Continuous Flow Analyzer) after mineralisation in HNO_3.

Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of both soil and biomass samples were measured with a Delta V Plus Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Bremen, Germany) linked with a FLASH 2000 CHNS Elemental Analyser (approximately 1 mg of soil and 0.5 mg of biomass weighed into tin capsule). Isotope ratios were calculated as:

$$\delta[13C, 15N]\ samples = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1{,}000$$

where R_{sample} and $R_{standard}$ are $^{13}C/^{12}C$ and $^{15}N/^{14}N$ molar abundance quotients of samples, with the internationally accepted standard (V-PDB) and the free atmosphere (^{15}N) serving as references.

Statistical analyses

Differences in productivity, in CNP stoichiometry of community and foliar biomass, and in characteristics of soil types were determined either with the Student's t test and ANOVA (in the cases of foliar $\delta^{15}N$ and foliar C/P with Tukey HSD tests); or with the non-parametric Kruskal-Wallis test when studied

parameters failed to meet the assumptions of a parametric test (normal distribution and/or equal variances). PCA analyses of soil samples and biomass samples were performed to assess the variability of soil and biomass chemistry. Spearman's correlation coefficients were calculated to assess correlations between soil features.

Biomass stoichiometry (dependent variables) was related to physical and chemical soil properties (explanatory variables) using multiple regression. Only non-collinear explanatory variables were included. In the case of total P in plant biomass, one outlying sample was removed in order to improve homoscedasticity of residuals. Trends in frequency distribution of different plant communities according to limitation type were determined with a permutation-based χ^2 statistic.

All analyses were performed with Statistica for Windows v. 12 and with CANOCO for Windows, Version 4.5 (ter Braak & Smilauer 1998).

RESULTS

Composition, productivity, and biomass stoichiometry of the studied plant communities

On sites with salt marsh vegetation, the average cover of *Blysmus rufus* was 25 % and *Carex orbicularis*, *Triglochin palustris* and *Eleocharis quinqueflora* were relatively abundant (Figure 2). Other species with individual cover below 4 % together formed 19 % of the plant cover on average. The average cover of bryophytes was 21 % and these were always accompanied by tracheophytes; we recorded no patches covered exclusively with mosses. Sites with small sedge meadow vegetation were dominated by *Carex* species, namely *Carex orbicularis* (25 % of the plant cover), *Carex microglochin* (12.8 %) and *Carex pycnostachya* (6.75 %) (Figure 2). Another species with relatively high occurrence was *Blysmus rufus* (5 %). Other species with individual cover > 4 % together made up 20 % of the plant cover on average. The average cover of bryophytes was 26 % and, again, no patches covered exclusively with mosses were recorded.

Although the studied plant communities were characterised by divergent dominating species, we recorded no significant differences in productivity between salt marsh with *Blysmus rufus* (115–492 g m^{-2}, median 266 g m^{-2}) and small sedge meadow with *Carex* species (56–574 g m^{-2}, median 253 g m^{-2}; p in Kruskal-Wallis test > 0.50). Similarly, we observed no significant differences in the CNP stoichiometry of their biomass. However, it is worth noting that $\delta^{15}N$ values were always above 2 ‰ in sedge communities where the cover of *Carex orbicularis* was higher than that of *Carex microglochin*, whereas negative $\delta^{15}N$ values were quite common in other communities. Detailed characteristics of plant biomass from the two plant communities are provided in Table A1 (in the Appendix).

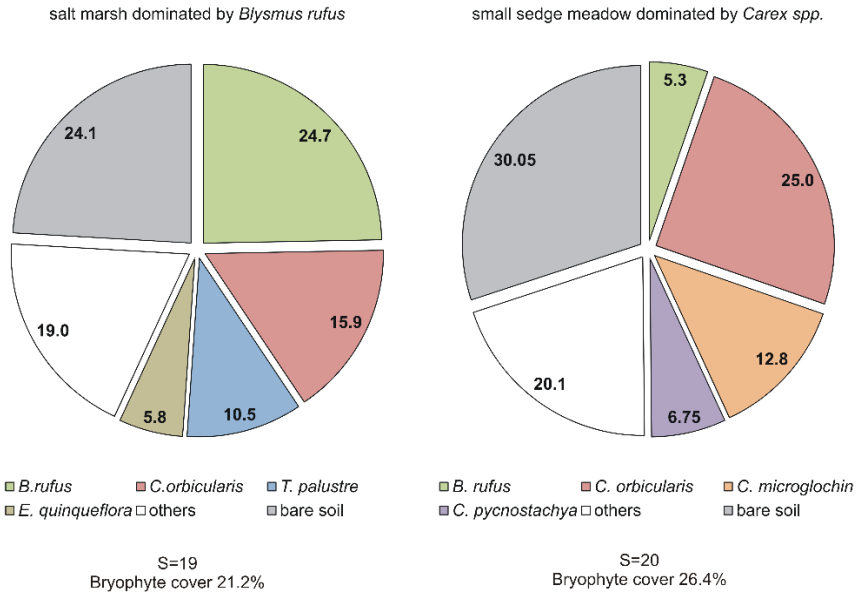

Figure 2. Average cover (%) of the most abundant species in salt marsh dominated by *Blysmus rufus* (N=13) and saline small sedge meadow dominated by *Carex microglochin* and *Carex orbicularis* (N=20). S = number of species recorded.

General characteristics of soils from the studied plant communities

On the basis of our own observations (Mętrak *et al*. 2017) and the World Reference Base for Soil Resources classifaction (FAO 2015), we divided the soils on which the studied plant communities were growing into three categories:

(1) high-mountain silty clay soils with soil organic carbon (SOC) content < 6 %, developed on mineral or lacustrine deposits;

(2) high-mountain wet meadow soils with SOC content 6–12 % and a melanic horizon; and

(3) high-mountain peaty soils with SOC content > 12 % and a histic horizon.

Chemical characteristics of these three soil types are presented in Table A2 (Appendix). Both studied plant communities most often developed on peaty soils (61 % of *Blysmus rufus* communities and 53 % of *Carex* communities), yet they were also quite frequent on silty clay soils (23 % of *Blysmus rufus* communities and 31 % of *Carex* communities).

The soil types we distinguished differed significantly in moisture, electric conductivity, content of nutrients (TC, TN, P_{av}) and nutrient quotients (C/N). The highest values of all these properties were recorded for peaty soils and the lowest for silty clay soils. No significant differences were observed in isotopic composition of the studied soils. Concerning salinity, 67 % of the peaty soils, 60 % of the wet meadow soils and only 20 % of the silty clay soils can be classified as saline (ECe > 4 dS m^{-1}). Detailed characteristics of these soil types are provided in Table A2.

Relationships between biomass and soil properties

A PCA analysis including both soil properties and chemical characteristics of plant biomass showed a clear division of the samples according to soil type (Figure 3). Regardless of vegetation, the samples of mineral soils formed a distinct group characterised by lower soil moisture, lower content of organic matter (TN_s, TC_s, SOC), lower ECe and higher values of $\delta^{13}C$ than the samples of organic soils. These observations were confirmed by calculating Spearman coefficients for soil properties. According to these results, there were positive correlations between soil moisture and total N ($r = 0.75$, $p < 0.0001$), total C ($r = 0.63$, $p < 0.0001$) and available P ($r = 0.44$, $p = 0.0097$); and a negative correlation between soil moisture and soil $\delta^{13}C$ ($r = -0.39$, $p = 0.0289$).

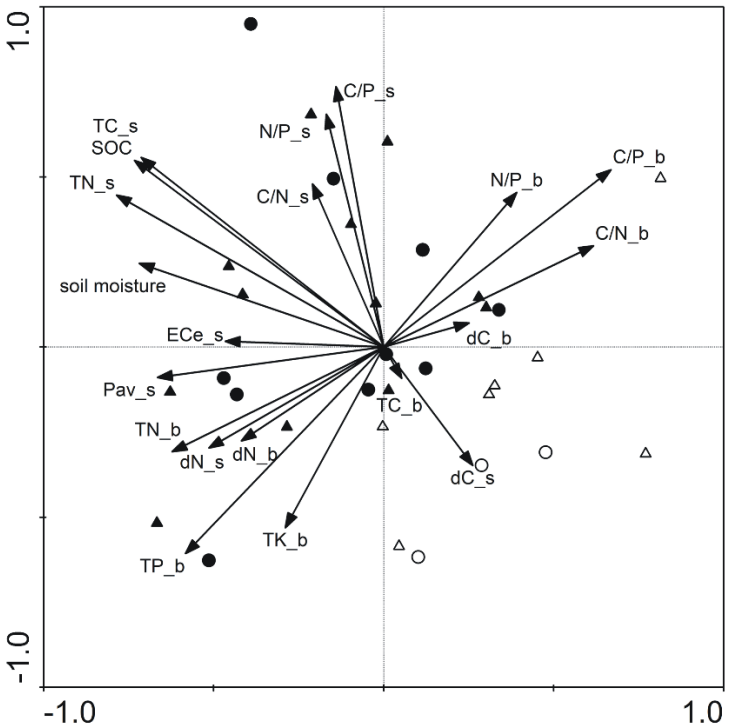

Figure 3. PCA of soil (suffix s) and biomass (suffix b) properties, $\lambda_1 = 0.264$, $\lambda_2 = 0.189$, $\lambda_3 = 0.129$, $\lambda_4 = 0.101$. Filled circles: *Blysmus rufus* communities on organic soils (SOC content > 6 %); unfilled circles: *Blysmus rufus* communities on mineral soils (SOC content < 6 %); filled triangles: *Carex* communities on organic soils; unfilled triangles: *Carex* communities on mineral soils.

Content of biogenic elements in plant biomass was positively correlated with their content in soil (with the exception of total C), and with soil moisture and ECe. Calculation of Spearman coefficients confirmed positive correlations between available phosphorus (P_{av}) in soil and total phosphorus in plant biomass (TP_b) ($r = 0.46$, $p = 0.0072$) and between electric conductivity (ECe) and total nitrogen in plant biomass (TN_b) ($r = 0.50$, $p = 0.0045$). Spearman coefficients also verified the strong positive correlations observed in the PCA diagram between soil $\delta^{15}N$ and plant $\delta^{15}N$ ($r = 0.69$, $p < 0.0001$), TN_b ($r = 0.42$, $p = 0.0167$) and TP_b ($r = 0.48$, $p = 0.0053$). Although the samples showed substantial variability (Figure 3), we observed no visible trends relating chemical characteristics of biomass to identified vegetation types.

In order to better assess the relationships between biomass and soil properties, we performed multiple regression analyses (Figure 4). The variability observed in content of biogenic elements and their quotients in biomass was best explained by $\delta^{13}C$ in soil (β values ranging from -1.18 to -0.64). Moreover, we recorded a weak ($\beta = 0.18$) positive relationship between soil ECe and TN_b. Plant $\delta^{15}N$ was strongly correlated to $\delta^{15}N$ in soil ($r^2 = 0.79$).

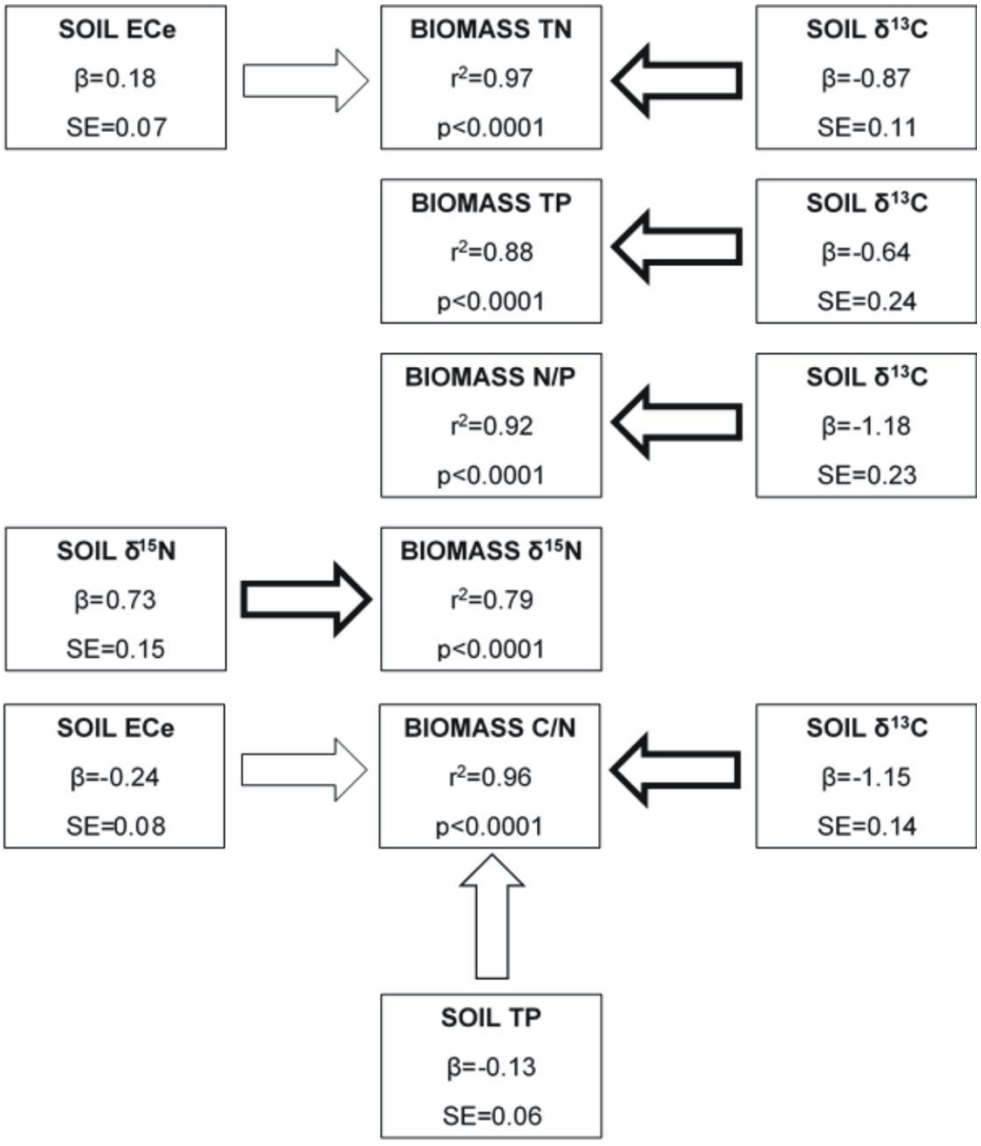

Figure 4. Results of multiple regression of chemical properties of biomass (dependent variables) and physical and chemical properties of soil (explanatory variables). Only statistically significant explanatory variables are shown. Coefficients of determination (r^2) and p values are given for regression of all non-collinear independent variables, namely soil moisture, electric conductivity, soil phosphorous content, soil $\delta^{15}N$ and soil $\delta^{13}C$. Bold arrows indicate $|\beta| > 0.5$.

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CNP stoichiometry of leaves

According to the statistical analysis, leaf samples from the three studied species were characterised by rather uniform chemical features. There were significant differences between the studied species in terms of $\delta^{15}N$ and C/P. The highest $\delta^{15}N$ was observed for *Carex orbicularis* leaves (on average 6.01), with lower values for *Blysmus rufus* (on average 2.76) and *Carex microglochin* (on average 1.00, $p < 0.0001$) (Table A1). The highest C/P values were observed for *Carex microglochin* leaves (on average 455.36), with lower values for *Blysmus rufus* (on average 324.20) and *Carex orbicularis* (on average 309.87, $p < 0.05$).

Productivity limitations

We compared the total content of nitrogen and phosphorous and the N/P quotient in the biomass with the critical values defined by Koerselman & Meuleman (1996) and Wassen *et al.* (1995) (Figure 5). For the majority (20 out of 33) of the biomass samples N/P was below 14, indicating N deficiency; for five biomass samples N/P was above 16, indicating P limitation; and for eight biomass samples N/P was between 14 and 16, which suggests co-limitation or no limitation at all. No significant relationship was found between type of plant community and type of limitation ($p = 0.2074$ in permutation-based χ^2 test). In the case of critical N

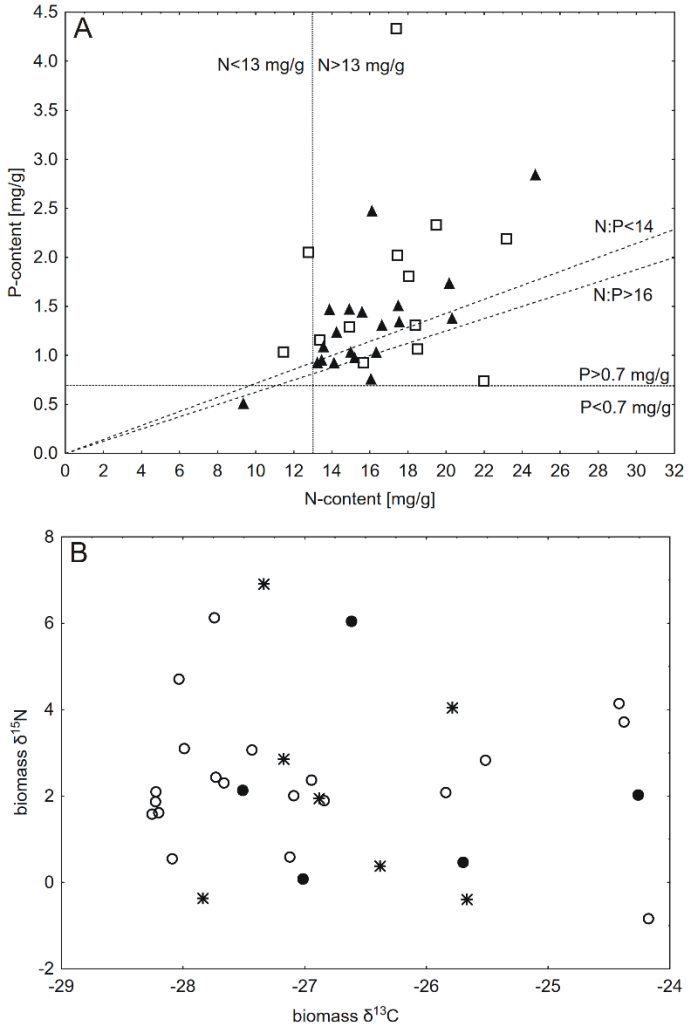

Figure 5. A: Relationship between vegetation TN and TP content and the nature of nutrient limitation in salt marsh with *Blysmus rufus* (squares) and small sedge meadow with *Carex* species (triangles). Dashed lines depict N/P quotients of 14 and 16, by mass (as in Koerselman & Meuleman 1996); dotted lines depict N and P contents of, respectively, 13 mg g^{-1} and 0.7 mg g^{-1} (as in Wassen *et al.* 1995). B: Relationship between $\delta^{15}N$ and $\delta^{13}C$ in biomass samples according to limitation type, following Koerselman & Meuleman (1996). Unfilled circles denote N limitation, filled circles denote P limitation, and asterisks denote N and P limitation or no limitation.

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and P content in the biomass (as in Wassen *et al.* 1995), only three sites could be classified as limited by N (< 13 mg g^{-1}) and only one site as limited by P (< 0.7 mg g^{-1}) (Figure 4A). As far as biomass is concerned, we found no significant correlations between $\delta^{15}N$ and N/P ($p = 0.8637$), yet we found a weak positive correlation for $\delta^{13}C$ and N/P ($r^2 = 0.34$, $p = 0.05$). However, the biomass samples are distributed randomly in Figure 5B, forming no clusters.

DISCUSSION

Under the cold desert conditions of the Eastern Pamir, the abundance and diversity of species are controlled predominately by the availability of water. Due to the scarcity of precipitation in this area (60–70 mm annually) (Williams & Konovalov 2008, Kayumov 2010), wetland communities depend on other sources of water. High mountain meadows and fens are usually located on alluvial plains or lake terraces and are characterised by high groundwater level or associated with springs and seepages (Sidorov 1961, Agakhanjanz 1966, Rusyeva 1970, Ikonnikov 2013, Vanselow *et al.* 2016). They can also develop on slopes where they receive meltwater from glaciers and snow (Sidorov 1961). In our case, the soils on which the studied plant communities were established formed on Quaternary sediments, mostly on silty and/or loamy alluvial deposits and on peats that developed in post-glacial endorheic hollows with persistent permafrost (Baranov & Klunnikov 1936, Loskutov 1968, own data). With low cover of glaciers and permanent snow - 0.2 % of the Rangkul catchment and 2 % of the Yashilkul catchment (own data) - and low winter precipitation - around 50 mm in both catchments (from October to March, according to Kuzmina (1968) and Latipova (1968)) - ground ice and thawing permafrost are the main sources of water for plant communities. Soils formed under such conditions are subject to thermokarst processes, resulting in the development of frost mounds (Kimble 2004), which enhance the patchwork character of the study area. This diversification of the topography of flat terraces around lakes in the glacial valleys of the Eastern Pamir shapes water and nutrient relationships at local scale, with wetter hollows becoming highly enriched in organic matter and simultaneously more saline due to intense evaporation.

Under arid climatic conditions, greater soil moisture usually enhances microbial activity, leading to enrichment of soil organic matter in heavy isotopes of C and N (*via* highly fractionating pathways of microbially mediated gaseous C and N losses) (Davidson *et al.* 2000, Zech *et al.* 2011, Ruiz-Navarro *et al.* 2016). However, we observed no positive correlations between soil moisture and either soil $\delta^{13}C$ or soil $\delta^{15}N$. On the other hand, we must remain aware of the potential influence of the relatively small number of analysed soil samples ($N = 32$) on the results of statistical analyses under circumstances where environmental determinants may also play a role in shaping the soil isotopic composition. First, on some sites - especially salt marshes with *Blysmus rufus* - fully aquatic species such as *Potamogeton pectinatus* or *Chara canescens* were present, indicating stable high water level (permanently flooded habitats). Under such conditions access to oxygen remains limited, resulting in reduced microbial activity. Secondly, the studied communities were located at high altitude, where mean annual temperatures are relatively low. Low temperature is widely known to suppress decomposition and mineralisation of organic matter and reduce the availability of nitrogen and phosphorous (Reich & Oleksyn 2004). Moreover, microorganisms in the surface layers of the Pamir's soils are exposed to rapid shifts in temperature, with differences between day and night as high as 60 ºC (Kayumov 2010). Relatively low temperatures combined with high daily amplitudes disturb functioning of the N cycle, since the temperature optimum for nitrification and denitrification processes is 25–30 ºC and few nitrifiers and denitrifiers are able to grow at temperatures below 8 °C or above 50 °C (Saad & Conrad 1993, Vijaya Bhaskar & Charyulu 2005). In the case of the soils studied here, the content of ammonia ions in the inorganic N fraction (overall mean 10.01 mg *per* 100 g) was more than ten times that of nitrate/nitrite ions (overall mean 0.61 mg *per* 100 g). Ammonia accumulation and predominance over NO_3^- is often viewed as an indicator of a conservative closed nitrogen cycle with limited gaseous N losses and relatively low soil $\delta^{15}N$ (Davidson *et al.* 2000, Brearley 2013). N losses are usually enhanced by intense grazing (Frank *et al.* 2004, An & Li 2015), however we chose only marginally grazed sites in order to properly assess the taxonomic diversity of the plant communities.

Turning to the influence of detrital material on plant biomass, soil $\delta^{13}C$ was an important explanatory variable for the total contents of nitrogen and phosphorous and their quotients (N/P and C/N) in biomass. Yet, instead of the expected positive influence (especially in case of phosphorous), we

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observed a negative influence of detrital input on the nutrient content of biomass. This observation links better nutrient availability to soils in which organic matter input (depleted in heavy carbon isotopes, as in the PCA analysis in Figure 3) exceeds detrital input (rich in heavy carbon isotopes). Hence we can assume that, although huge amounts of deflated aeolian dust are transported over the Eastern Pamir from the deserts of West and Central Asia (Wu *et al*. 2009, Wu *et al*. 2015), this additional influx of nutrients has no significant impact on production of plant biomass in communities dominated by *Blysmus rufus*, *Carex microglochin* and *Carex orbicularis*.

Recorded values of $\delta^{15}N$ in both community and species biomass (overall mean values 2.27 and 3.36 ‰) were rather high, covering a range from -1.15 up to 10.30 ‰, which is high even for the *Cyperaceae* family. According to Yang *et al.* (2015), values for two *Carex* species (*Carex foetida* and *Carex sempervirens*) in alpine vegetation were roughly between -1.5 and 2.5 ‰. Makarov *et al.* (2014) reported overall means of -1.47 ‰ for *Carex sempervirens* and -1.17 ‰ for *Carex umbrosa* in alpine lichen heath, and Michelsen *et al.* (1996) gave a range of -0.5 to +2.5 ‰ for *Carex* spp. and *Luzula acurata* in northern Swedish Lapland. On the other hand, Zech *et al.* (2011) gave a $\delta^{15}N$ value of 9.4 ‰ for the biomass of heavily grazed spring turf, specifically in the Eastern Pamir. As in other nutrient-poor environments (*e.g*. Michelsen *et al*. 1996, Nadelhoffer *et al*. 1996, Clarkson *et al*. 2005), we observed large differences in $\delta^{15}N$ amongst co-habiting species, especially between *Carex orbicularis* (range 2.94–10.30 ‰) and *Carex microglochin* (range -1.15–3.99). Alpine plants from the *Cyperaceae* family are known for effective acquisition of ^{15}N enriched organic forms of nitrogen, their uptake rates for glycine being similar or even greater than for inorganic N. Therefore, species specific $\delta^{15}N$ in this family is substantially higher than in species from other taxonomic groups (Raab *et al*. 1999, Makarov *et al*. 2014). Concerning inorganic N uptake by plants from the *Cyperaceae* family, Miller & Bowman (2002) reported proportions of NO_3^- uptake to NH_4^+ uptake around unity (0.79 for *Carex rupestris* and 0.99 for *Kobresia myosuroides*). However, NH_4^+ uptake by saline soils can be reduced by direct competition from sodium ions (MacTavish & Cohen 2017), which could be another reason for ammonia accumulation in the studied soils.

Since differences in community biomass $\delta^{15}N$ show no relationship with N availability across the sites (range 0.10– 2.54%), we may assume that the species in question exhibit relatively fixed traits with respect to N utilisation, regardless of the site characteristics (as in Miller & Bowman 2002), and/or there are other factors influencing biomass chemistry. As two of the studied species, namely *Blysmus rufus* and *Carex orbicularis*, were identified by Khan (2003) as hydrohalophytes, we believe that there are certain differences in their physiological response (including N utilisation) to high soil salinity in comparison with *Carex microglochin*. Hence, soil salinity (expressed here as ECe) might be an important factor influencing the chemistry of biomass from the two studied plant communities. As *Carex orbicularis* (hydrohalophyte) and *Carex microglochin* co-occur in different proportions in the small sedge meadow communities studied here, potential salinity-dependent differences in biomass chemistry are not easy to grasp. However, ECe was positively related to the N content of biomass from the studied communities, which indirectly suggests higher biomass production on saline soils.

Recorded values of $\delta^{13}C$ in both community and species biomass (overall mean values -26.97 ‰ and -27.23 ‰) corresponded well with typical ranges for C3 plants, which range from approximately -34 ‰ to -20 ‰ (*e.g*. Diefendorf *et al*. 2010, Basu *et al*. 2015, Yang *et al*. 2015) and include data for high-altitude vegetation with an overall $\delta^{13}C$ mean of -26.15 ‰ (Yang *et al*. 2015). Considering that, and in contrast to findings in the available literature (*e.g.* Xu *et al*. 2015, Yang *et al*. 2015), we can conclude that low temperatures did not strongly affect $\delta^{13}C$ in plant biomass.

Critical values of N and P content in biomass given by Wassen *et al*. (1995) turned out to be much more conservative than critical values of biomass N/P defined by Koerselman & Meuleman (1996). According to the latter, on the sites we studied N-limitation of plant growth predominated, as confirmed by high $\delta^{15}N$ values in both community biomass (up to 6.91 ‰) and leaves (up to 10.30 ‰ for *Carex orbicularis*). In line with the common plant isotopic fractionation model, in N-limited habitats (P in excess of demand), uptake of N will show no discrimination against ^{15}N because all available N must be assimilated (*e.g*. McKee *et al*. 2002, Clarkson *et al*. 2005, Sorrell *et al.* 2011). Therefore, plant $\delta^{15}N$ becomes more enriched with decreasing N availability and with increasing N limitation. Isotope-nutrient relations can be influenced by mycorrhizal fractionation (Clarkson *et al*. 2005, Makarov *et al*. 2014), yet in our case the dominating species can be regarded as non-mycorrhizal (Brundrett 2009, Druva-Lusite & Ievinsh 2010, Akhmetzhanova *et al*. 2012).

Amongst the three species studied, *Carex microglochin* was characterised by the lowest foliar $\delta^{15}N$. This could be interpreted as an indication of well-balanced nutrient management resulting in high biomass production *per* unit of limiting nutrient; or be attributed to inhibited growth on saline soils, since *Carex microglochin* was the only non-halophilous species investigated. *Blysmus rufus* and *Carex orbicularis* were characterised by higher foliar $\delta^{15}N$ values, which can result from maximised N uptake and biomass production. The amounts of biomass produced *per* unit of limiting nutrient taken up (nutrient productivity *sensu* Garnier & Aronson 1998) in small sedge meadow dominated by *Carex microglochin* were 19 g *per* mg N/100 g dry soil and 280 g *per* mg P/100 g dry soil; whereas lower values (approximately 16 g *per* mg N/100 g dry soil and 190 g *per* mg P/100 g dry soil) were obtained for *Blysmus rufus* and *Carex orbicularis*. However, these results must be regarded as approximate because we assessed only the spatial domination of certain species, not their participation in harvested biomass.

CONCLUSIONS

1. For the majority of sampled sites N limitation was recorded on the basis of the criterion set by Koerselman & Meuleman (1996), yet we found no significant correlation between $\delta^{13}C$ or $\delta^{15}N$ and N/P.
2. Species-specific differences in $\delta^{15}N$ were pronounced, the lowest values being recorded for *Carex microglochin*. This could indicate well balanced N management in this species or result from inhibited growth on saline soils, as *Carex microglochin* is the only non-halophilous species described here.
3. We recorded no significant influence of detrital input on chemical composition of plant biomass from salt marsh dominated by *Blysmus rufus* and saline small sedge meadow dominated by *Carex microglochin* and/or *Carex orbicularis.*

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Appendix

Table A1. CNP stoichiometry and isotopic composition of biomass from salt marsh with *Blysmus rufus* and from small sedge meadow with *Carex* species; and of leaves from three dominant species in these plant communities - *Blysmus rufus*, *Carex microglochin* and *Carex orbicularis*.

		BIOMASS		**LEAVES**		
		Salt marsh with *Blysmus rufus* (N=13)	Small sedge meadow with *Carex microglochhin* and *Carex orbicularis* (N=20)	*Blysmus rufus* (N=13)	*Carex microglochhin* (N=9)	*Carex orbicularis* (N=11)
N_{tot} (%)	mean (SD)	1.71 (0.34)	1.59 (0.32)	1.90 (0.58)	1.82 (0.53)	1.91 (0.47)
	median	1.74	1.54	1.85	1.81	1.96
	min–max	1.14–2.32	0.93–2.47	1.16–2.93	1.19–2.78	0.93–2.43
	Statistics		p_{ttest}=0.305612			p_{ANOVA}=0.9116
$\delta^{15}N$	mean (SD)	1.98 (1.59)	2.46 (2.07)	2.76 (1.52) **A**	1.00 (1.68) **A**	6.01 (2.29) **B**
	median	1.9	2.22	2.25	0.82	6.22
	min–max	(-0.39)–6.04	(-0.83)–6.91	0.90–5.67	(-1.15)–3.99	2.94–10.30
	Statistics		p_{ttest}=0.483273			**p_{ANOVA}<0.00001**
C_{tot} (%)	mean (SD)	42.02 (2.50)	43.23 (1.24)	40.71 (5.89)	44.34 (3.07)	43.98 (5.83)
	median	42.15	43.17	41.07	44.62	44.45
	min–max	34.60–44.39	40.93–45.27	30.51–52.50	38.61–48.96	35.12–56.91
	Statistics		$p_{Kruskal-Wallis}$=0.1405			p_{ANOVA}=0.2027
$\delta^{13}C$	mean (SD)	(-26.88) (1.27)	(-27.26) (1.68)	(-27.15) (0.49)	(-27.12) (0.37)	(-27.43) (0.52)
	median	-26.95	-27.26	-26.93	-26.95	-27.57
	min–max	(-28.26)–(-24.26)	(-31.79)–(-24.18)	(-28.03)–(-26.48)	(-27.76)–(-26.61)	(-28.24)–(-26.89)
	Statistics		$p_{Kruskal-Wallis}$=0.9706			p_{ANOVA}=0.2560

continued overleaf.....

Table A1 (continued)

		BIOMASS		**LEAVES**		
		Salt marsh with *Blysmus rufus* (N=13)	Small sedge meadow with *Carex microglochhin* and *Carex orbicularis* (N=20)	*Blysmus rufus* (N=13)	*Carex microglochhin* (N=9)	*Carex orbicularis* (N=11)
P_{tot} (%)	mean (SD)	0.17 (0.09)	0.13 (0.05)	0.15 (0.09)	0.11 (0.04)	0.15 (0.04)
	median	0.13	0.13	0.11	0.09	0.14
	min–max	0.07–0.43	0.05–0.28	0.06–0.38	0.06–0.18	0.11–0.25
	Statistics		$p_{Kruskal-Wallis}$=0.3022			$p_{Kruskal-Wallis}$=0.0754
C/N	mean (SD)	25.63 (6.12)	28.22 (5.77)	22.53 (4.64)	26.22 (8.00)	24.04 (5.46)
	median	23.66	27	22.50	24.57	22.85
	min–max	17.92–37.48	17.97–46.66	15.11–30.10	16.63–40.97	18.22–37.91
	Statistics		$p_{Kruskal-Wallis}$=0.1728			$p_{Kruskal-Wallis}$=0.5270
C/P	mean (SD)	305.74(141.76)	357.83 (150.06)	324.20 (135.04)	455.36 (163.32)	309.87 (98.99)
	median	313.38	338.48	347.81	452.56	258.95
	min–max	94.78–581.96	155.95–847.62	139.34–652.03	247.09–751.49	167.46–527.56
	Statistics		$p_{Kruskal-Wallis}$= 0.8290			**p_{ANOVA}=0.0414**
N/P	mean (SD)	12.28 (6.43)	13.08 (3.34)	15.08 (7.11)	18.94 (8.90)	13.32 (4.54)
	median	11.05	12.85	12.46	18.40	14.15
	min–max	4.01–29.65	6.50–21.09	6.02–27.90	7.44–33.99	6.39–22.57
	Statistics		$p_{Kruskal-Wallis}$=0.1728			p_{ANOVA}=0.2048

Table A2. Chemical characteristics of the soil types associated with the three plant communities studied.

		Mineral soil (N = 10) (SOC < 6 %)^{A}	**Meadow soil (N = 5)** (6 % < SOC < 12 %)^{B}	**Peaty soil (N = 17)** (SOC > 12 %)^{C}
Moisture (%)	mean (SD)	49.25 (16.23)^{C}	64.66 (11.26)	71.42 (19.72)^{A}
	median	47.6	60.1	76.6
	min–max	28.10–77.30	53.90–77.10	19.70–86.20
	Statistics			**$p_{Kruskal\text{-}Wallis}$=0.0120**
Ece (dS m^{-1})	mean (SD)	2.99 (1.80)^{C}	4.79 (1.88)	5.63 (2.77)^{A}
	median	2.91	4.06	6.69
	min–max	0.62–7.30	3.13–7.97	1.30–9.29
	Statistics			**$p_{Kruskal\text{-}Wallis}$=0.0395**
N_{tot} (%)	mean (SD)	0.34 (0.26)^{C}	0.56 (0.18)^{C}	1.41 (0.52)^{AB}
	median	0.28	0.58	1.41
	min–max	0.10–1.03	0.32–0.80	0.71–2.54
	Statistics			**$p_{Kruskal\text{-}Wallis}$<0.0001**
$\delta^{15}N$	mean (SD)	1.32 (1.91)	2.41 (1.23)	2.48 (1.88)
	median	1.96	2.86	2.48
	min–max	(-2.22)–3.91	0.29–3.24	(-1.21)–5.52
	Statistics			$p_{Kruskal\text{-}Wallis}$=0.3055
C_{tot} (%)	mean (SD)	7.90 (4.50)^{C}	11.98 (1.62)^{C}	24.32 97.09)^{AB}
	median	7.39	11.39	22.44
	min–max	2.02–18.18	10.67–14.66	15.97–37.33
	Statistics			**$p_{Kruskal\text{-}Wallis}$<0.0001**
SOC (%)	mean (SD)	3.22 (1.38)^{C}	9.34 (1.98)	22.16 (8.46)^{A}
	median	3.37	9.54	18.75
	min–max	0.75–5.16	6.67–11.77	13.22–38.10
	Statistics			**$p_{Kruskal\text{-}Wallis}$<0.0001**
$\delta^{13}C$	mean (SD)	-26.68 (1.12)	-27.17 (0.78)	-27.71 (1.58)
	median	-26.74	-27.09	-27.86
	min-max	(-28.10)–(-24.06)	(-28.28)–(-26.43)	(-31.06)–(-24.02)
	Statistics			$p_{Kruskal\text{-}Wallis}$=0.0991
P_{av} (%)	mean (SD)	0.11 (0.07)^{C}	0.15 (0.12)	0.33 (0.24)^{A}
	median	0.08	0.1	0.28
	min–max	0.03–0.21	0.07–0.36	0.06–0.87
	Statistics			**$p_{Kruskal\text{-}Wallis}$=0.0148**
C/N	mean (SD)	11.13 (4.03)^{BC}	17.16 (2.24)^{A}	16.04 (3.29)^{A}
	median	11.53	16.38	16.13
	min–max	3.57–15.79	14.68–20.67	11.25–24.54
	Statistics			**$p_{Kruskal\text{-}Wallis}$=0.0043**
Frequency of salt marsh communities		**23.10 %**	**15.40 %**	**61.50 %**
Frequency of small sedge meadow communities		**31.30 %**	**15.60 %**	**53.10 %**