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Abstract

In wet peatlands, plant growth conditions are largely determined by local soil conditions, leading to locally adapted vegetation. Despite that *Carex* species are often the prevailing vascular plant species in fen peatlands of the temperate zone, information about how these species adapt to local environmental conditions is scarce. This holds true especially for below-ground plant traits and for adaptations to fen-typical nutrient level variations. To address this research gap, we investigated how different geographic origins (Germany, Poland, The Netherlands) of *C. acutiformis* and *C. rostrata* relate to their response to varying nutrient availability. We performed a common garden experiment with a controlled gradient of nutrient levels, and analyzed above- and below-ground biomass production of both *Carex* species from the different geographic origins. We related these traits to environmental conditions of the origins as characterized by vegetation composition-derived indicator values for ecological habitat conditions. While we detected high above-ground phenotypic plasticity of *Carex* from different origins, our data point to below-ground genotypic differences, potentially indicating local adaptation: Rhizome traits of *C. rostrata* differed significantly between origins with different nutrient indicator values. These results point towards differences in *C. rostrata* clonal spread behavior depending on local peatland conditions. Therefore, local adaptations of plant species and below-ground biomass traits should be taken into account when studying peatland vegetation ecology, as key functional traits can differ between genotypes within a single species depending on local conditions.

Keywords Rhizome growth · Azonal vegetation · Mire · *Carex rostrata* · *Carex acutiformis* · Genetic differentiation · Ellenberg indicator values · Ecotype

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Introduction

The composition of mire vegetation is impacted foremost by the local environmental conditions, where water-logging poses special challenges for plants to establish and flourish. Therefore, mire vegetation composition starkly differs from the typical zonal vegetation and is considered being azonal, i.e., similar species compositions form despite large geographic distances between peatlands (Mucina et al. 2006; Sieben 2019). Still, local conditions, e.g., water level depth, mineral and nutrient concentrations, and pH, can vary widely across and even within peatlands (Bridgham et al. 1996; Rydin and Jeglum 2013; Wheeler and Proctor 2000). It remains unclear whether the same species genetically adapt to the local conditions, or whether they exhibit high phenotypic plasticity, i.e., whether the same genotype produces different phenotypes in response to locally different environmental conditions.

Ground- and surface water-fed peatlands (fens) in the temperate zone are often dominated by *Carex* L. species. This genus consists of over 2,000 species, many of which occur sympatrically (GLOBAL CAREX GROUP 2015). Closely related *Carex* species – which supposedly have similar ecological niches – tend to not occur at the same sites, whereas sympatric *Carex* species often occupy well-distinguishable niches (Waterway et al. 2016). At the same time, *Carex* populations of the same species, but from different geographic origins, show local adaptations, for example with regard to their growth and phosphate absorption rates and, more generally, with regard to their realized ecological niches, and can also exhibit morphological differences (Chapin and Chapin 1981; Chapin III and Oechel, 1983; Choler and Michalet 2002; Hájková et al. 2008; Więclaw et al. 2021). While some studies about local adaptations of *Carex* species are thus available, we lack information about intra-specific adaptations of this fen-dominating genus to differences in nutrient availability. Nutrient levels can vary considerably within and between peatlands (Bridgham et al. 1996; Navrátilová et al. 2017; Rydin and Jeglum 2013; Wassen et al. 1990, 2002; Wheeler and Proctor 2000). Interspecific differences in the response of sedges to increasing nutrient levels are rather well understood and include species-specific increased biomass production and shoot:root ratios (Aerts et al. 1992; Hinzke et al. 2021; Pérez-Corona and Verhoeven 1996; Veerkamp et al. 1980), but how the same *Carex* species adapts to locally varying nutrient levels is as yet unknown.

To address this research gap, we performed a common garden mesocosm experiment to detect genetic differentiation, which could indicate local genetic adaptations and phenotypic plasticity to variations in nutrient levels of two common *Carex* species, both sampled from different

geographic origins (Germany, Poland, The Netherlands). For our study, we chose two *Carex* species naturally adapted to different nutrient levels: the lesser pond-sedge *C. acutiformis* Ehrh. and the beaked sedge *C. rostrata* Stokes ex With. Both grow rhizomatous (Bernard 1990; Konings et al. 1992) and are common fen species throughout temperate and southern boreal Europe (Egorova 1999; Landucci et al. 2020; Mossberg and Stenberg 2003; Peterka et al. 2017).

We analyzed plant above- and below-ground biomass production, and determined biomass nutrient contents, as a measure for plant performance under different nutrient levels. We also performed vegetation surveys, based on which we calculated ecological indicator values for habitat conditions at the sampling sites of the *Carex* specimens used in this study, to relate reactions to nutrient level variations to conditions at the site of origin. We hypothesized (i) genetic adaptation of fen sedges with regard to nutrient levels. That is, we expected that plants from sites exhibiting high indicator values for nutrients would produce more biomass at higher nutrient levels, whereas those stemming from sites with lower indicator values for nutrients would show less biomass increase or even decrease with increasing nutrient levels. Additionally, we assumed that (ii) *Carex* species typically associated with different nutrient levels would show different reaction norms to variations in nutrient levels.

Methods

Sampling of *Carex* Specimens from Different Geographic Origins

For each of the two species *C. acutiformis* and *C. rostrata* we sampled specimens in November 2017 from three geographic origins (Table 1, see also Hinzke et al. 2021). We sampled in three to four different locations per geographic origin to collect different individuals rather than a single clone. For simplicity, we will refer to the geographic origins in the following by the names of the countries (Germany, Poland, The Netherlands). We chose these three geographic origins as they are sufficiently far away from each other to theoretically allow for site-specific genetic differentiation. In addition, they represent a gradient of nutrient status (mostly eu- to hypertrophic in The Netherlands and Germany, mesotrophic in Poland; Cabezas et al. 2014; Koch and Jurasinski 2015; Liu et al. 2021; Wassen and Olde Venterink, 2006), and different drainage histories (largely long-term drainage with partial rewetting in The Netherlands and Germany, mostly undrained in Poland). Drainage itself leads to increased peat mineralization and nitrogen release (Olde Venterink et al. 2009), and rewetting often to higher phosphorous mobilization (Emsens et al. 2017; Zak et al.

Table 1 *Carex* species used in this study, their geographic origins and sampling coordinates

Species	Geographic origin	Area	X coordinates	Y coordinates	
<i>C. acutiformis</i>	Germany	Gützkow Ost	53.92324	13.43534	
			53.92263	13.43151	
			53.92201	13.42732	
	Poland	Marlow Nowy Lipsk (Ostrowie, Biebrza)	54.15811	12.59101	
			53.73473	23.33013	
			53.91720	22.93098	
			Rospuda upper basin	53.28771	22.57058
	The Netherlands	Drentse Aa/ De Heest	53.03894	6.64080	
			53.03776	6.64047	
			53.03651	6.64340	
<i>C. rostrata</i>	Germany	Marlow	54.15899	12.58983	
			54.15936	12.59115	
			54.15859	12.59098	
	Poland	Ostrowie (Biebrza)	53.72089	23.30644	
			Rospuda lower basin	53.90399	22.95370
			Szuszalewo	53.71355	23.35722
	The Netherlands	Drentse Aa/ Gasterense Diep	53.02170	6.66989	
			53.02506	6.66748	
			53.02630	6.66360	

2010). Plants, consisting of one shoot and a few roots and rhizomes, were kept in small peat-filled pots in a common sand bed over winter.

Estimation of Ecological Habitat Conditions Based on Vegetation Indicator Values

Our characterization of ecological habitat conditions of the *Carex* sampling sites was based on site-specific vegetation. We performed vegetation surveys at the sampling locations of both *Carex* species, and assigned the plant species ecological indicator values for ecological habitat conditions as given by Ellenberg indicator values. Ellenberg indicator values assign numeric values (1–9) to species-specific optima estimates observed along gradients of environmental conditions (Ellenberg et al. 2001). This expert system of vegetation-derived indicator values has the important advantage to represent long-term conditions, rather than a snapshot of highly dynamic environmental parameters (Bartelheimer and Poschlod 2016; Schaffers and Sýkora 2000). To give an example for our study, *C. acutiformis* has an Ellenberg indicative value for nutrients (Ell_N) of 5, whereas

C. rostrata has an Ell_N of 3 (Ell_N according to GermanSL, Jansen and Dengler 2008; see below). This means that *C. acutiformis* prefers more nutrient-rich soils than *C. rostrata*.

Vegetation surveys of 4 m² plots including both vascular plants and mosses were conducted in June/July 2017 in Poland (2 relevés for *C. acutiformis*, 9 for *C. rostrata* sampling locations) and 2021 in Germany (4 relevés for *C. acutiformis*, 2 for *C. rostrata* sampling locations) and The Netherlands (3 relevés each for *C. acutiformis* and *C. rostrata*) on the sampling sites of the *Carex* specimens used in this study. Site-specific ecological indicator values were then calculated using the Ellenberg indicator values as given in the “ecodbase” database of the “GermanSL v. 1.5”, which contains taxonomic reference lists for vegetation databases in Germany (Jansen and Dengler 2008), and using novel indicator values for nutrients for bryophytes (Simmel et al. 2021). We weighted the indicator values by the respective species’ coverage to generate cover-weighted indicator values. “Indifferent” assignments were not used for indicator value calculation. For entries in the ecodbase database marked as “doubtful” (i.e., indicator value with question mark), the indicator value given was used. In order to assess representativeness of the indicator value calculation, we also calculated the coverage of plants with a numeric indicator value relative to the total coverage per plot.

Mesocosm Experiments

Our study was conducted in the course of a 12-week mesocosm common garden experiment from May to September 2018 (Hinzke et al. 2021). A nutrient level gradient with 12 steps was created via fertilization combined with watering, with each mesocosm corresponding to one nutrient level (Supp. Table 1), resulting in a total of 24 mesocosms. In each mesocosm (a 125 l pot filled with peat), nine specimens of the same species and geographic origin were planted. Pots were fertilized every two weeks to adjust the specific nutrient level per pot. Additionally, pots were watered twice a week initially and then daily. Each pot was connected via a tube to one canister, and water from that canister was used to water the same pot again. This way, the water level was kept within a few centimeters below the peat surface and nutrients stayed in the same mesocosm. At the typical end of the below-ground growing season in temperate ecosystems (i.e., September; Schwieger et al. 2019), plants were harvested, separated into below- and above-ground parts, dried, and weighed, rhizomes were counted and their length was measured. Shoot C and N contents, as well as shoot and root P and K contents were determined as described in Hinzke et al. (2021).

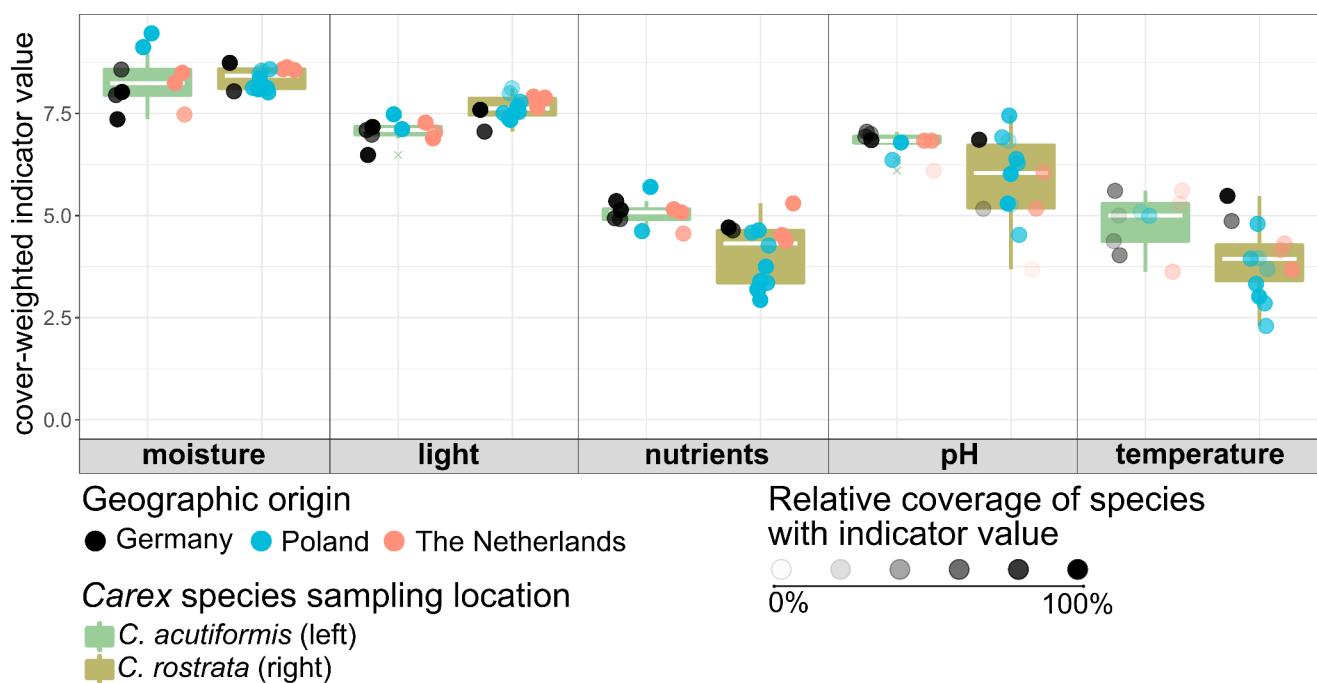


Fig. 1 Ecological indicator values for moisture, light, nutrients, pH, and temperature of sampling locations of *Carex acutiformis* and *C. rostrata*. Indicator values were weighted by species coverage. Dots: Indicator values of individual plots, colored by geographic origin.

Statistical Evaluation of Plant Biomass Characteristics

Data evaluation for *Carex* biomass characteristics was based on the best models identified in a former study (Hinze et al. 2021). In brief, we fitted total, shoot, root, and rhizome biomass production using a Gompertz growth model. Likewise, we used a Gompertz growth model to model data of total rhizome lengths and total rhizome numbers. For the ratio of above- to below-ground biomass, we used a logistic growth model. To model specific rhizome length (total rhizome length divided by total rhizome weight) and shoot C:N ratios, we employed linear models (see Hinze et al. (2021) for C:N ratio) and compared model performance with predictors “total N” only, “geographic origin” only, and combining both, using ANOVA (Supp. Table 2). Additionally, we modelled %P and %K in root and shoot biomass with linear models, and %N in shoot biomass using a logistic growth model. These models were selected based on model evaluation with diagnostic plots. Non-overlap of 95% confidence bands was interpreted as significant difference. Analyses were done in R 4.0.5 (R Core Team, 2021), using for data reformatting the packages dplyr 1.0.5 (Wickham et al. 2021a), purrr 0.3.4 (Henry and Wickham 2020), and tidyr 1.1.3 (Wickham 2021), for statistical analysis the packages AICcmodavg 2.3-1 (Mazerolle 2020), boot 1.3–27 (Canty and Ripley 2021), broom 0.7.6 (Robinson et al.

2021), nlstools 1.0–2 (Baty et al. 2015), and for graphics generation and export egg 0.4.5 (Auguie 2019), ggnewscale 0.4.5 (Campitelli 2021), ggplot2 3.3.3 (Wickham 2016), and svglite 2.0.0 (Wickham et al. 2021b).

Results

Carex Sites of Origin Differ in Ecological Indicator Values for Nutrients

Ecological indicator values for site conditions calculated from vegetation surveys of *C. acutiformis* and *C. rostrata* sampling locations were mostly similar for the same species between geographic origins, with the notable exceptions of nutrient and temperature values for *C. rostrata*, and of moisture values for *C. acutiformis* (Fig. 1). Cover-weighted nutrient and temperature values of *C. rostrata* sampling locations in Poland were often lower than those for the other two origins. With regard to moisture values for *C. acutiformis* sampling locations, these were highest for Poland. Overall, differences between sampling locations of the two different species were more pronounced. Except for soil reaction values (pH), the relative coverage of plants with “indifferent” indicator value assignment was always below 11% (Supp. Table 3).

Biomass Production in *Carex* Depends on Nutrient Level and Geographic Origin

Carex from different geographic origins generally did not differ significantly in their overall and organ-specific biomass production (Fig. 2). However, root biomass production and number of rhizomes at intermediate to high nutrient levels were lower for *C. acutiformis* from The Netherlands as compared to the other origins. Moreover, for Polish *C. rostrata*, number of rhizomes and total rhizome lengths were significantly lower than were those of the other origins. At the highest nutrient level, *C. rostrata* from Poland had a total of 512 rhizomes with a total rhizome length of 91 m, whereas *C. rostrata* from Germany had 556 rhizomes (104 m) and *C. rostrata* from The Netherlands 709 rhizomes (124 m). At intermediate nutrient levels, Polish *C. rostrata* had 150 to over 200 rhizomes less than those from Germany and The Netherlands, corresponding to a total length difference of 24 to 37 m (Supp. Table 4). Concomitantly, specific rhizome length of *C. rostrata* differed significantly between origins, with the lowest specific rhizome length observed for Polish *C. rostrata*. In addition, *C. rostrata* specific rhizome length showed a significant interaction between origins and nutrient levels, with specific rhizome length decreasing stronger across nutrient levels for *C. rostrata* from Poland and Germany as compared to those from The Netherlands. Length of individual rhizomes did not show a clear pattern or difference between either nutrient levels or origins, aside from *C. acutiformis* from The Netherlands producing a somewhat higher number of long rhizomes than those from the other origins (Supp. Figure 1).

In addition, the above-/below-ground biomass ratio of *C. acutiformis* from The Netherlands was slightly higher at intermittent nutrient levels than those of the other origins. Above-/below-ground biomass ratio also appeared to be intermittently higher for *C. rostrata* with Polish origin than for those of the other origins, but this difference was driven by only one data point.

While for *C. acutiformis* no significant difference in shoot C:N ratios between origins was found, shoot C:N ratio of *C. rostrata* from The Netherlands was significantly lower, and, correspondingly, %N in shoot was higher, than were those of the other origins (Supp. Figure 2, Supp. Table 2).

Specimens from different origins did not differ significantly in their %P or %K in root and shoot biomass across the nutrient gradient, apart from %P in *C. rostrata* roots from Poland being higher than in the other origins at the highest nutrient level (Supp. Figure 3).

Maximum differences of plant biomass metrics of the same species from different origins occurred mostly at very high to highest nutrient levels for *C. acutiformis*, but also at intermediate nutrient levels for *C. rostrata* (Fig. 2, Supp.

Table 4). For *C. acutiformis*, maximum differences always occurred between Germany and the other origins, and for *C. rostrata*, between Poland and the other origins. Differences between *C. acutiformis* and *C. rostrata* from the same origin were almost always highest at intermediate to high nutrient values. Maximum within-species differences for biomass traits were mostly about half to two thirds as high as between-species differences.

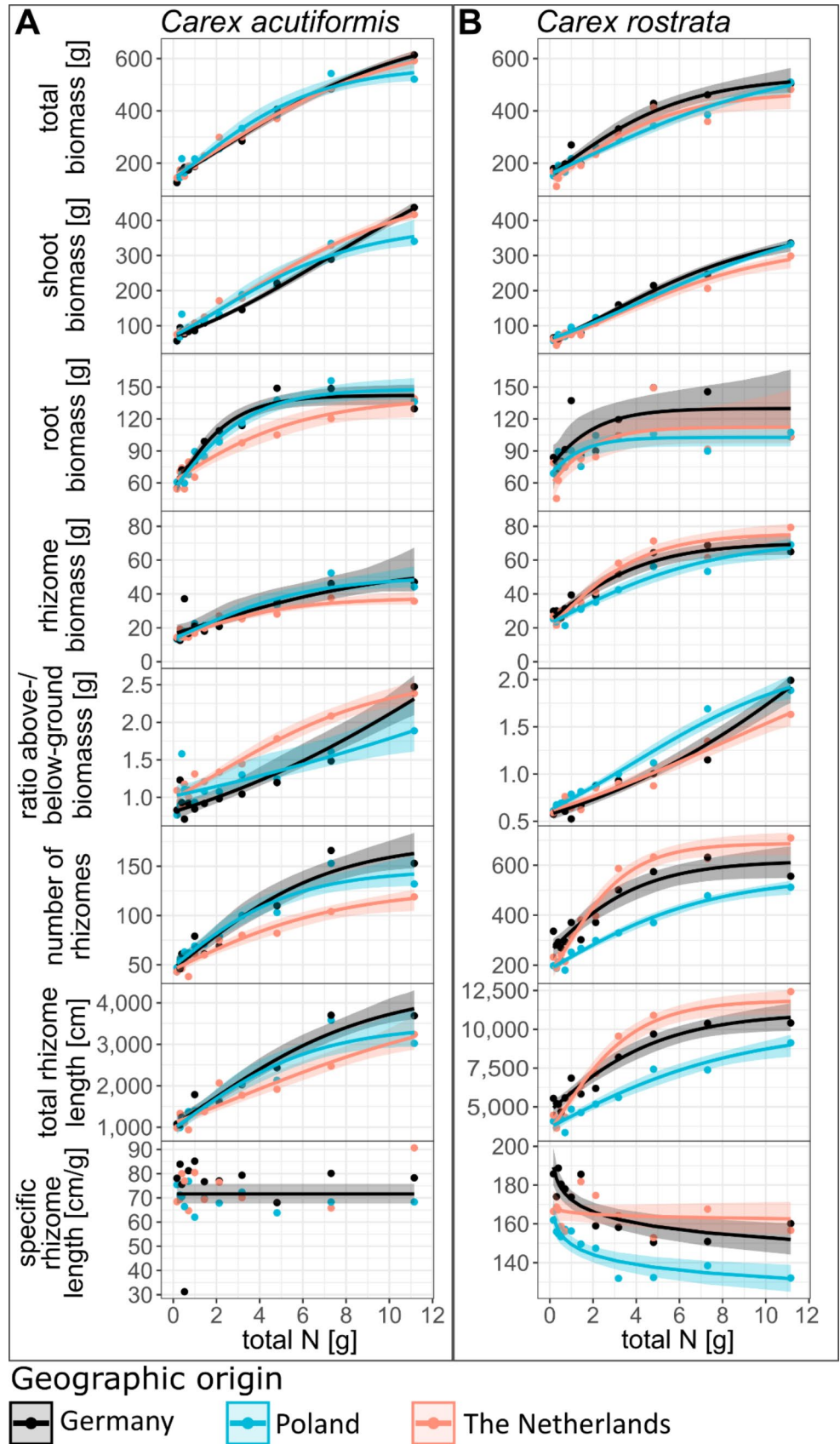
Discussion

Our study indicates genetic differentiation of *Carex* species due to geographically differing environmental conditions in fen peatlands, in accordance with our hypothesis (i): we found significant differences in plant biomass production of *Carex* from different origins in our common garden experiment. This genetic differentiation hints towards local genetic adaptations. At the same time, both *Carex* species from all origins exhibited high phenotypic plasticity. In contrast to our hypothesis (ii), both species showed similar total biomass production profiles across the whole nutrient gradient, despite their differences in natural nutrient availability preferences.

Genetic differentiation of *Carex* from different origins was suggested by notably fewer rhizomes with a lower total length and lower specific rhizome length in *C. rostrata* from Poland as compared to the other origins. Simultaneously, the Polish sampling sites for this species had mostly lower indicator values for nutrients than the sampling sites in Germany and The Netherlands. At the same time, the differences in *C. acutiformis* root biomass and number of rhizomes between origins do not seem to be correlated to site-specific ecological indicator values. In the following, we propose two, potentially synergistic, explanations for the origin-specific differences observed in *C. rostrata* rhizome growth.

(A) *C. rostrata* from different origins differ in their clonal spread or foraging behavior, with more efficient local resource use – i.e., less length increase per unit biomass investment – in Poland and a more explorative rhizome growth in the other origins. Causes for origin-specific clonal spread differences might be higher competition pressure or pressure of other stressors at the Polish than at the other two sites, or a lack of resources at the other sites. Such patterns of differential clonal growth behavior depending on local environmental conditions also occur in the sedges *Scirpus planiculmis* (Ning et al. 2014), *Scirpus olneyi* (Ikegami et al. 2007) and *Carex brevicuspis* (Deng et al. 2013).

Fig. 2 Total biomass production, as well as biomass production of shoots, roots, and rhizomes, ratio of above- to below-ground biomass, number of rhizomes, total rhizome length, and specific rhizome length of (A) *Carex acutiformis* and (B) *C. rostrata*, sampled from different geographic origins, in mesocosms. Total N [g]: total nitrogen per mesocosm. Dots: Raw values, lines: regression curves, semitransparent ribbons: 95% confidence bands



(B) Gas exchange efficiency of *C. rostrata* differs between sites, potentially due to site-specific differences in long-term drainage history. While the Ellenberg indicator values for moisture did not differ between origins of *C. rostrata*, sampling sites in Poland were mostly undrained, in contrast to the long-term drained sites in Germany and The Netherlands (see Methods). Potentially thicker rhizomes (i.e., same total biomass, but more aerenchymes) in the Polish *C. rostrata* might allow for a more efficient gas exchange in water-logged soils (Sharma et al. 2008). Similarly, in the sedge *Scirpus planiculmis* rhizome, its morphology, but not biomass, is soil moisture-dependent (Ning et al. 2014). In Germany and The Netherlands, a lower specific rhizome length (i.e., longer rhizome per weight unit) might have also aided re-colonization after rewetting.

The differences in rhizomatous growth are probably not related to nutrient storage per se, as total rhizome weight and thus total investment into storage tissues did not differ between *C. rostrata* of all three origins. However, the lower shoot C:N ratio and higher %N in shoots of *C. rostrata* from The Netherlands, where sampling locations were associated with high nutrient indicator values, might point to local variations in nutrient uptake efficiency.

High phenotypic plasticity was visible in almost all measured traits in both species. Phenotypic plasticity enables plants to deal with changing environmental conditions (Valladares et al. 2007). Phenotypic plasticity might therefore be especially advantageous in heterogeneous habitats, such as peatlands. More generally, considerable phenotypic plasticity occurs in different *Carex* species (Więclaw 2017; Więclaw et al. 2021, 2022), including alpine *Carex* species, i.e., in species which also live in rather heterogeneous habitats (Schmidt et al. 2018). An advantage of increased biomass at higher nutrient levels, as observed in our study, could be higher ability to deal with competition, e.g., for light (Kotowski et al. 2006). In accordance with this, boreal peatland vascular plants exhibit a plastic response to N addition, with plant height being especially important at higher N levels (Lin et al. 2020). A notable exception from the general pattern of high phenotypic plasticity was the specific rhizome length, where *C. acutiformis* showed no response to increasing nutrient levels, whereas *C. rostrata* specific rhizome length decreased. In general, rhizome morphology responses to nutrients and competition are highly species-specific (reviewed in de Kroon and Hutchings 1995; Hutchings and de Kroon 1994). The reasons for this lack of phenotypic plasticity, and whether it is due to plasticity costs outweighing advantages, or whether it might even impact the performance of *C. acutiformis*, warrant further research.

Overall, maximum biomass trait differences of *Carex* for the same species and nutrient level encompassed of up to two thirds of that between species in our study. This means that specimens of the same *Carex* species can behave almost as different as two different species. Such high intra-specific reaction magnitudes impact how plant species respond to environmental changes (see also Malyshev et al. 2016; Münzbergová et al. 2017). Therefore, a species' reaction magnitude to environmental changes needs to be taken into account for example for restoration measures involving re-introduction or assisted colonization of plants: For choosing suitable species, not only a species' general ecological preferences are important, but also local adaptations of specific populations (van Andel 1998), and the ability of these populations to deal with current and future environmental changes.

It remains to be elucidated whether the intra-specific differences in *Carex* from different origins have an adaptive value. Intra-specific, genetically fixed clonal growth differences might lead to niche partitioning, as proposed for clonal growth differences between *Carex* species (Tammaru et al. 2021). This could then lead to formation of ecotypes, i.e., genetically fixed geographic varieties, which occur in other *Carex* species (Chapin and Chapin 1981; Chapin III and Oechel, 1983; Choler and Michalet 2002; Hájková et al. 2008). Intriguingly, root anatomical traits of *Carex* can be used to predict their Ellenberg indicator values for different ecological gradients (Hoffmann et al. 2021). It would be interesting to see whether there is a similar relationship between rhizome traits and ecological optima, and whether such a relationship can also be found on the level of intra-specific variation.

In summary, we found indications for below-ground genetic adaptation and high phenotypic plasticity above- and below-ground for two common and widely distributed *Carex* species of temperate fen peatlands. The data presented here underline that within-species differences in trait responses to environmental gradients can be in the same order of magnitude as those between species, and that these differences might not be visible when only taking into account the more easily accessible above-ground biomass traits. Our study prompts further research into local intra-specific adaptations of *Carex* species with regard to clonal spread and nutrient uptake, e.g., considering rhizome C:N ratios, as well as into below-ground biomass traits, in particular of potentially peat-forming plant species.

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Author Contributions ES, FT, JK, and WK designed and coordinated experiments; CA and LK contributed to the experimental design; collection of the sedges and vegetation relevés were conducted by CA, DM, ES as well as LK and EP in The Netherlands, Germany and Poland, respectively; SD, GL, ES, FT, EP, JK, WK ran the experiment and sampled the data; TH analyzed the data and wrote the manuscript with input from all authors; JL coordinated C:N and XRF analyses of biomass samples; K-HK provided XRF analyses of biomass samples; MB and MS performed specific literature research and were involved in data interpretation and discussion. All authors gave input and approved the final manuscript.

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Data Availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests All authors declare that there is no conflict of interest.

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