











Potentially peat-forming biomass of fen sedges increases with increasing nutrient levels

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Abstract

1. Peat formation is a key carbon sequestration process in the terrestrial biosphere. In temperate fens, peat is mainly formed by below-ground biomass of vascular plants. Nutrient availability in temperate fens is naturally variable, and nowadays increasing due to atmospheric deposition, runoff from agriculture and mineralization of peat caused by drainage. To maintain or restore peat formation, it is important to understand how increased nutrient availability influences the main controls of peat formation, that is, below-ground biomass production and decomposition.
2. We investigated above- and below-ground biomass production and decomposition of five fen sedges (*Carex* spp.) grown under 12 different nutrient levels (realized with nitrogen amounts increasing exponentially across levels, with addition of phosphorus and potassium to ensure nitrogen limitation in each nutrient level) in a mesocosm experiment, designed to resemble a gradient of very low to very high nutrient availabilities in temperate fens. In addition, we measured nutrient stoichiometry in the biomass and related this to possible growth limitations and to root decomposition.
3. Our results indicate that higher biomass production at higher nutrient levels was not offset by an increase in decomposition. Increase of above- and below-ground biomass with higher nutrient levels was species-specific. Decomposition of standardized plant material in mesocosms was not dependent on the species growing in the mesocosms and showed only slight, if any, variation with differing nutrient levels. Decomposition of roots grown under different nutrient levels was mainly correlated with species identity and root lignin:cellulose ratio.
4. Our study suggests that the *Carex* spp. potentially peat-forming root biomass, here defined as the root biomass which is not decomposed during one growing season, increases with increasing nutrient levels: higher root biomass production is not

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counteracted by increasing decomposition during the growing season. Based on this pattern of positive mass balance in five common sedge species with differing growth characteristics, we propose that sedge communities establishing after rewetting have the potential for renewed peat formation regardless of the prevailing trophic level.

KEYWORDS

Carex, decomposition, eutrophication, Gompertz growth model, gradient design, mesocosm, root recalcitrance, wetland

1 | INTRODUCTION

Peat formation is a key process contributing to carbon sequestration in the terrestrial biosphere: Peatlands in the boreal and subarctic zone store c. 500 Gt of carbon (Yu et al., 2019), which is about the same amount as that stored in all forest biomass on earth (Pan et al., 2011). Rates of peat formation depend on the balance between peatland net primary production (NPP) and organic matter decomposition (i.e. peat formation only takes place if NPP exceeds decomposition), which are both impacted, among other factors, by nutrient availability (Frolking et al., 2010). A peatland with comparatively low productivity (e.g. a *Sphagnum* bog) can have a high long-term peat accumulation rate because its litter decomposes slowly (Rydin & Jeglum, 2013).

Most research on peat formation and carbon cycling has focused on rainwater-fed *Sphagnum* bogs (Gorham, 1991; Limpens et al., 2008; van Breemen, 1995), where upward-growing peat mosses form peat. However, in more continental areas in the temperate and boreal zone of the northern hemisphere, groundwater- and surface water-fed peatlands (fens) prevail. In Europe, they cover more than half of the total area of peatland (c. 1,000,000 km²; incl. shallow peatlands in European Russia, Joosten et al., 2017).

These fens are frequently dominated by sedges (*Carex* spp.). Fen peat is often formed predominantly by vascular plant roots and rhizomes growing into the existing peat body ('displacement peat', Joosten, 2016; Michaelis et al., 2020). That means that for fen peat formation, primarily below-ground biomass is of importance.

In fens, marked gradients in nutrient availability exist (Bernard et al., 1988; Kotowski & van Diggelen, 2004; Wassen et al., 1990; Wheeler & Proctor, 2000). These nutrient availability gradients can be caused naturally, for example, in river valleys, or can be caused by anthropogenic eutrophication (Kotowski & van Diggelen, 2004; Kotowski et al., 2006; Navrátilová et al., 2017; Wassen et al., 1990, 2002). Nutrient availability gradients have been shown to control biodiversity patterns and displacement of dominant species (Kotowski et al., 2006; Navrátilová et al., 2017). However, while a number of studies have elucidated the impact of increased nutrient input on bogs (e.g. Bragazza et al., 2012; Gerdol et al., 2007; Jutinen et al., 2010; Wang et al., 2014), the effects of differing nutrient availability on peat formation and carbon storage in sedge-dominated fens are as yet unclear. Elucidating these effects is crucial to better define the role of fens in terrestrial carbon budgets and their response to global and

regional environmental changes. Additionally, understanding how nutrient availability impacts peat formation is fundamental to plan restoration of fens for not only reducing greenhouse gas emissions but also for renewing carbon sequestration, and for predicting the outcome of these restoration efforts (Kotowski et al., 2016). Drainage increases peat mineralization, releasing mostly nitrogen (N) and phosphorous (P, Olde Venterink et al., 2009). P can however precipitate during drainage conditions and become re-mobilized during rewetting (Emsens et al., 2017; Zak et al., 2010). Rewetted fens can thus be much more nutrient-rich than pristine ones.

Whether such fertile systems can effectively accumulate peat depends, among other factors like hydrological (Chimner & Cooper, 2003), biogeochemical (Limpens et al., 2008) or microbiological (Artz, 2009) constraints, on how much of their NPP occurs below-ground, and on how biomass decomposability, especially of below-ground biomass, changes with variations in nutrient levels. The impact of nutrient levels on peat formation may vary due to changes in biomass production, allocation ratios of above- to below-ground biomass, and changes in litter quality for particular species (intraspecific differences), as well as due to a shift of species differing in their biomass production and litter quality along environmental gradients (interspecific differences, Aerts et al., 1992; Emsens, Aggenbach, Grootjans, et al., 2016).

General changes of peatland vegetation composition and above-ground biomass production in response to varying nutrient levels have been addressed in several studies. N-, P- and/or potassium (K)-limited wetland sites differ in species richness and total above-ground biomass (Olde Venterink et al., 2003; Wassen et al., 2005). High N fertilization (200 kg N/ha) is potentially toxic for roots (El-Kahloun et al., 2003). However, how below-ground biomass, which is most relevant for fen peat formation, is affected by nutrient availability, remains largely to be elucidated.

Above- and below-ground biomass production of different *Carex* species increases species-specifically with N fertilization, concomitant with an increasing shoot:root ratio (Aerts et al., 1992). Increased P levels lead to increased shoot biomass in different *Carex* species (Veerkamp et al., 1980), while the exact allocation pattern is species-specific (Pérez-Corona & Verhoeven, 1996). A higher ratio of above- to below-ground biomass under elevated nutrient levels would impact rates of peat formation, as below-ground biomass is the primary peat-forming biomass in fens (Michaelis et al., 2020; Sjörs, 1991). That is, increases in rates of peat formation would then be lower than increases of total biomass under increasing nutrient levels.

Litter quality, and thereby decomposition, are affected by variation in nutrient levels as well. On the one side, increased nutrient availability in a system apparently either inhibits or does not impact litter decomposition (Agethen & Knorr, 2018; Bridgman & Richardson, 2003; Emsens, Aggenbach, Grootjans, et al., 2016). On the other side, increased nutrient availability during plant growth can increase decomposability of the resulting litter (Aerts & de Caluwe, 1997; Emsens, Aggenbach, Grootjans, et al., 2016). At the same time, *Carex* tissue decomposition is highly dependent on tissue type, with roots decomposing slowest (Graf & Rochefort, 2009; Scheffer & Aerts, 2000; Thormann et al., 2001). However, comparisons of root decomposition rates of *Carex* spp. under different nutrient availabilities appear to be scarce.

In this study, we therefore aimed to elucidate how a gradient of nutrient levels, realized with exponentially increasing amounts of N across levels, and addition of P and K to create N limitation, affects above-ground and below-ground biomass production and decomposition in sedges. We studied sedge species with ecological optima at different parts of the nutrient availability gradient, and which represent different growth heights as well as growth forms. We hypothesized that (a) overall biomass production would increase with increasing nutrient levels, but this increase would mainly occur above-ground, resulting in an increased above:below-ground biomass ratio with increasing nutrient levels. Additionally, we assumed that (b) direct effects of nutrient level on decomposition would be small, that is, we expected decomposition of the same plant material to vary little between different nutrient levels. At the same time, we assumed an indirect positive effect of nutrient level on decomposition, with growth at higher nutrient levels leading to increased decomposability of the resulting *Carex* plant material. Following this, we hypothesized that (c) increase in root biomass would be smaller than increase in root decomposability, meaning that the potentially peat-forming root biomass of the investigated sedges would decrease with higher nutrient levels.

2 | MATERIALS AND METHODS

2.1 | Studied sedge species and experimental design

2.1.1 | Sedge species

We selected five *Carex* species with differing affinities to the nutrient availability gradient as expressed by their Ellenberg N values, and which represent both tussock and rhizomatous growth forms (Table 1).

2.1.2 | Mesocosm experiment

General setup

We conducted a 4-month mesocosm experiment (May to September 2018) to study biomass production and decomposition of five

TABLE 1 Sedge species used in the study characterized by their Ellenberg indicative value for nitrogen ($N_{\text{Ellenberg}}$; Ecoflora database, Fitter & Peat, 1994), minimum (min) to maximum (max) canopy height (LEDA database, Kleyer et al., 2008), and clonal growth type

Species	$N_{\text{Ellenberg}}$	Min to max canopy height [m]	Clonal growth
<i>Carex acutiformis</i> EHRH	5	0.3–1.2	Rhizomes
<i>Carex appropinquata</i> SCHUHMACH	4	0.25–0.45	Tussocks
<i>Carex elata</i> ALL	5	0.6–1.2	Tussocks
<i>Carex lasiocarpa</i> EHRH	2	0.3–1.0	Rhizomes
<i>Carex rostrata</i> STOKES EX WITH	2	0.3–0.7	Rhizomes

different *Carex* species (Table 1) in response to varying nutrient levels. Mesocosms allow to study effects of single parameters in a highly controlled and reproducible manner. Mesocosm studies have been used to, for example, investigate effects of water table level on peatland carbon fluxes (Blodau et al., 2004), nitrogen uptake in oligotrophic wetlands (Wozniak et al., 2008), and the impact of atmospheric CO₂ and pore water nitrogen concentrations on mangroves and salt marshes (McKee & Rooth, 2008). We employed a gradient design with a high resolution of nutrient levels ($n = 12$) and no replication to characterize nonlinear responses (Kreyling et al., 2018). Sedge specimens were collected in November 2017 from fens of Biebrza and Rospuda valleys in Poland ($n = 9$ per species) in different locations to avoid repeated sampling within clones (Supporting Information Table S1). Plants were split into single nodes with one shoot and a few roots, which were planted in peat in small pots and kept in a sand bed over winter.

Mesocosms were set up in 125 L pots (see Supporting Information Figure S1 for setup of the mesocosms). Each pot was filled with 6.3 kg of expanded clay (10–20-mm diameter, 3NRG GmbH Bischofswerda), which was covered with fleece. Above that, 28.5 kg of *Sphagnum* peat (Torfwerk Moorkultur Ramsloh) was added. The peat was a mixture of peat from Germany and Baltic states and had a degree of decomposition of 2–3 (von Post scale, von Post, 1922) and a pH of 5.5 (adjusted with carbonated chalk). We used *Sphagnum* peat instead of fen peat in order to realize lower minimum nutrient levels (undecomposed oligotrophic fen peat is restricted to well-preserved sites and was therefore not available). Each pot was connected via a tap at the bottom and an upward-bent drainage tube to one 20-L water canister. This way, the maximum water table was defined for each pot and kept constant within a few centimetres below the peat surface. Overflow water was directed to the canisters. Water collected in the canisters was used to water the same pots again, so that no solute nutrients were lost from the system. In each pot, nine individuals of one *Carex* species were planted after roots were washed free of the former soil substrate and leaves were cut to similar lengths in May 2018 (14.–18.05.2018). Our study design resulted in a total of 60 mesocosms (five *Carex* species, each at 12 nutrient levels).

Pots were placed in a completely randomized design. The peat surface was covered with straw to prevent algal growth. A net installed app. 2 m above the mesocosm pots was used for protection against birds. Pots were initially watered twice a week and then, during the hottest period of the summer, daily to keep water levels close to the surface. Initially, each pot received 35 L of groundwater (0.14 mg N/L). Subsequently, tap water was used for irrigation (0.53 mg N/L), and a mixture of tap and rain water, if the latter was available during the very dry summer. N added through irrigation water was accounted for; for total N values, see Supporting Information Table S2 and below. Total N and total P in peat and, for N, in water used for irrigation were determined with simultaneous oxidation according to Grasshoff et al. (1999), using potassium peroxodisulfate as oxidant. Total P as phosphate was measured colorimetrically at 880 nm, total N as nitrate using ion chromatography (Sykam, Eresing, Germany) at a wavelength of 220 nm (Grasshoff et al., 1999; Köster et al., 2005).

Fertilization took place every 2 weeks for a total of six times, after an initial acclimatization period of two weeks. $(\text{NH}_4)_2\text{HPO}_4$ was used in different amounts to create 12 nutrient levels (factor 1.54 increase for $(\text{NH}_4)_2\text{HPO}_4$ for consecutive nutrient levels).

The lowest fertilization N level in our design corresponds to $3.56 \text{ kg N ha}^{-1} \text{ a}^{-1}$ ($6.13 \text{ kg N ha}^{-1} \text{ a}^{-1}$ if N by irrigation is added) and is about four (two) times lower than the annual N budget of a Polish mesotrophic fen (Biebrza valley), which was estimated by Wassen and Olde Venterink (2006) as $13.4 \text{ kg N ha}^{-1} \text{ a}^{-1}$. When anthropogenic sources (atmospheric deposition and groundwater influx) are excluded, mineralization adds app. $4 \text{ kg N ha}^{-1} \text{ a}^{-1}$, which is close to our fertilization starting level. We quantified N in peat pore water before the start of the experiment, but not mineralization of N in our study. The highest fertilization N level used in our study is equivalent to $418 \text{ kg N ha}^{-1} \text{ a}^{-1}$ ($422 \text{ kg N ha}^{-1} \text{ a}^{-1}$ when taking into account N added by irrigation) which corresponds to yearly N input in agricultural West-European grasslands ($>304 \text{ kg N ha}^{-1} \text{ a}^{-1}$, Olde Venterink et al., 2006), and to the N budget in Dutch floodplains (exceeding $183.6 \text{ kg N ha}^{-1} \text{ a}^{-1}$, Wassen & Olde Venterink, 2006). It is still lower than the highest total N loads recorded for degraded fens rewetted with nutrient-enriched surface water ($>2,500 \text{ kg N ha}^{-1} \text{ a}^{-1}$, Audet et al., 2020). P and K levels were adjusted to make sure that they were non-limiting, that is, we defined nutrient levels by the amount of N given and added corresponding amounts of P and K to create an N-limited system. In a dataset of pore water samples from fens in NE Poland, medium mass-based N:P ratio was 0.9 (own data, unpublished) and this level was ensured by adding $0.45 \text{ g KH}_2\text{PO}_4$ during the first fertilization. Additionally, $8.17 \text{ g K}_2\text{CO}_3$ was added per fertilization round to amend the low K content of the water used. For the resulting total amounts of N, P and K see Supporting Information Table S2.

In September 2018 (01.-11.09.2018; mean duration of the experiment: 113 days), plants were removed from the pots, washed and dried (above-ground biomass: 70°C , below-ground biomass: 35°C) to determine the weight of shoots, roots and rhizomes. A total of eight pots, four of *C. lasiocarpa* and four of *C. appropinquata*, contained contaminations with other sedge or, in one case, a rush

species. The contaminating plants were removed before weighing. Individual rhizomes were counted (each branch-off was included as new rhizome) and measured using a standard office ruler.

Litter decomposition in mesocosms (decomposition experiment 1)

To compare decomposition of similar biomass under different nutrient levels, and thus to assess how decomposition rates are impacted by nutrient levels in the surrounding peat, extra material from *Carex* specimens of the study species was used, that is, the same (standardized) *Carex* mixture was used in all mesocosms. Shoot and root biomass of plants not transferred to the mesocosms was mixed and used to prepare litter bags, resulting in a mixture of about one-third of *C. rostrata* and two-thirds of *C. acutiformis*, with minor portions of *C. elata* and *C. appropinquata*. To study how senescence impacts decomposability, fresh and senescent leaves were oven-dried (70°C) and placed in separate litter bags above-ground (hereafter termed horizon 'X') in the mesocosms. Management of sites by mowing for nature conservation purposes also leads to fresh as well as senescent leftover shoot biomass. Root material (oven-dried, 70°C) was placed in the intermittently wet topsoil at a depth of up to 5 cm below the surface (hereafter termed horizon 'H1'). Between 0.14 and 0.64 g of the mixed *Carex* material were filled into nylon bags (mesh size 0.14 mm, size $7.0 \times 5.5 \text{ cm}$), which were dried (70°C) and weighed before filling. Additionally, to be able to distinguish the effect of peat horizon on decomposition, green and rooibos tea (Lipton tea bags, Unilever, London, UK; 5.5 cm edge length standard triangular pyramid bags) were placed in all three horizons, that is, above-ground (X), as well as in intermittently wet topsoil (H1), and in the permanently wet peat (20–25 cm below surface, referred to as horizon 'H2'). Before the experiment, whole tea bags were weighed, and bags for *Carex* material were weighed empty and with the plant material added. One bag per material was added per mesocosm.

Litter and tea bags were collected at the end of the experiment, cleaned and roots growing on or inside the wet bags were removed with forceps. The bags were then dried (70°C). For *Carex* litter bags, the whole bags were weighed at the end of the experiment, and for tea bags, the whole bags as well as the bags with contents removed were weighed to calculate mass loss as % of initial mass. The total incubation time was 75 days.

2.1.3 | Decomposition of roots grown in mesocosms in incubations (decomposition experiment 2)

Root samples (20 g) were taken as intact dry roots from five different places per mesocosm (from the root biomass collected and dried after the end of the mesocosm experiment). For analysing root decomposition, washed roots were dried at 60°C . After cutting into c. 1-cm-long pieces and mixing, three replicates (~1 g) were prepared from each root sample. Root samples were then placed in nylon litter bags in 0.75-L jars filled with fen peat (collected from a depth of 0 to 1 m from the moderately drained Calowanie fen in Poland, 52.00 N , 21.35 E , Klimkowska et al., 2010). We collected peat in the

field for this experiment so as to have a typical fen microbial community, which is potentially already adapted to sedge root decomposition. The peat was saturated and topped with fen water from the same location until the jar lid, and incubated without opening (thus presumably under anoxic conditions) for 100 days at 18°C. Roots were then dried again at 60°C and weighed to calculate mass loss as percent of initial root mass.

2.2 | Nutrient content of the biomass

For mass-based total carbon to total nitrogen (C:N) ratio determination and for determination of further elemental ratios by X-ray fluorescence (XRF) analysis (see below), one representative subsample of the washed and dried *Carex* plant material per pot was taken, separately for shoot and root biomass as a mixed sample of whole stems or roots (for XRF and shoot C:N analysis), or of root samples from a depth of c. 5 cm (root C:N analysis), including material of all nine individuals in the respective pot.

Biomass was ground and dried again in paper bags at 75°C (60°C for C:N analysis of root biomass) until it reached a constant weight. The subsamples were stored in an exsiccator until weighing for C:N and XRF analysis.

Some 10–12 mg of dry mass of the ground shoot biomass per pot was used to determine shoot C:N ratios using a CHNS elemental analyser (Vario ELIII, Elementar). Results were multiplied with a correction factor that was obtained from calibration with standard material (Orchard Leaves Standard, Elemental Microanalysis).

For C:N ratio determination of root biomass, subsamples of c. 2 g dried roots were ground under liquid nitrogen. C:N ratios were determined using c. 10 mg of ground sample and a CHNS/O analyser (Flash2000 CHNS/O Analyzer, Thermo Scientific). A calibration curve obtained with standard material (aspartic acid (Elemental Microanalysis), NCS DC 73349 (National Analysis Center for Iron & Steel [NACIS], China)) was used for correction.

For XRF analysis, 500 mg of the dried and ground root or shoot biomass per pot sample was used and pressed to a pellet of 13-mm diameter (7 to load, Specac pellet die) without addition of further pelleting aids. The pellets were placed into sample holders with 10 mm masks and measured by wavelength-dispersive X-ray fluorescence spectroscopy (WD-XRF; ZSX Primus II, Rigaku). We analysed Mg, Si, P and Ca for subsequent data evaluation, as calibrated by a set of 15 certified reference materials (biomass of vascular plants and mosses, peat, organic sediment) and five own working standards (peat).

2.3 | Biomass quality: Root lignin to cellulose ratios

For determining lignin:cellulose ratios, dried *Carex* root biomass was cut into fragments and ground with a mortar under liquid nitrogen. Samples were sieved (0.2 mm mesh size). Determination of the root lignin:cellulose ratio was based on the determination of acid-detergent lignin and acid-detergent cellulose, as described in

Gessner (2005), with minor modifications. About 0.5 g of ground sample was placed in an extraction tube. Some 20 ml of acid-detergent solution (20 g/L cetrimonium bromide (CTAB) in 0.5 M sulphuric acid) and eight drops of decahydronaphtalene were added. Tubes were heated in a water bath and boiled for 1 hr. Samples were then filtered using Gooch crucibles with known weight set on filter manifolds. Filtered contents were broken up and washed with boiling water. Washing was repeated with acetone until the liquid appeared colourless. Subsequently, acetone was removed from acid-detergent fibre using a vacuum and the remaining sample dried at 105°C for 3 hr. Oven-dried crucibles were placed into a desiccator for 1 hr and weighed to the nearest 0.1 mg. Contents of crucibles were then covered with 72% H₂SO₄ (app. 15°C) at room temperature and stirred with a glass rod. Crucibles were hourly re-filled with 72% H₂SO₄ and contents stirred. After 3 hr, acid was removed by vacuum filtration. Residual acid was removed by washing with hot water. Crucibles were then dried overnight at 105°C, placed in a desiccator for 1 hr, and weighed. Subsequently, crucibles were ignited in a muffle furnace at 550°C for 3 hr and cooled to 105°C. After placing them in a desiccator for 1 hr, crucibles were weighted again. For calculations of acid-detergent lignin and cellulose, see Equations (1) and (2). Two replicates were measured for all but seven mesocosm pot samples, for which not enough material was available, and the mean values were used for further analysis.

$$\text{ADC} = \left(\frac{W_o - W_H}{W_s} \right) \times 100 \quad (1)$$

$$\text{ADL} = \left(\frac{W_H - W_i}{W_s} \right) \times 100 \quad (2)$$

ADC, acid-detergent cellulose; ADL, acid-detergent lignin; W_o , weight before treatment with 72% H₂SO₄; W_H , weight after treatment with 72% H₂SO₄; W_i , weight after ignition following 72% H₂SO₄ treatment; W_s , weight of the oven-dried sample.

2.4 | Statistical data evaluation

We used R version 3.6.1 (R Core Team, 2019) with the packages AICCMODAVG 2.2-2 (Mazerolle, 2019), BOOT 1.3-24 (Canty & Ripley, 2019), BROOM 0.5.5 (Robinson & Hayes, 2020), DPLYR 0.8.5 (Wickham, François, et al., 2020), GGLOT2 3.3.0 (Wickham, 2016), NLTSTOOLS 1.0-2 (Baty et al., 2015), TIDYR 1.0.2 (Wickham & Henry, 2020), EGG 0.4.5 (Auguie, 2019), GLMNET 3.0-2 (Friedmann et al., 2010), GLMNETUTILS 1.1.5 (Microsoft & Ooi, 2020) and SVGLITE 1.2.3 (Wickham, Henry, et al., 2020).

2.4.1 | Biomass production

Data of biomass (total, as well as shoot, root and rhizome separately, and ratio of above-:below-ground biomass) harvested at the end of the mesocosm experiment were evaluated using a hierarchical

regression procedure, starting with linear models (of transformed data, if necessary) of the predictors 'species identity' and 'total N' (representing the nutrient level, please see above), and, for teabag data only, 'peat horizon'. For analyses, we used the sum of N given by fertilization and mean N added by irrigation (calculated with the N concentration of tap water for mixtures of rain and tap water, Supporting Information Table S2). The total N amount thus presents an upper estimate of N present. Calculations using fertilization N only, that is, a more conservative approach, led to qualitatively identical results (data not shown).

Subsequently, more complex models were kept if they improved the corrected Akaike information criterion (AICc; Supporting Information Table S3). In addition to this hierarchical regression approach, diagnostic plots were used to evaluate model fits. Nonlinear models were used where appropriate, that is, where backed up by theoretical considerations and where they improved model diagnostics and data fit (see Supporting Information Table S3 for models tested). For nonlinear models, bootstrapping of residuals (10,000 bootstrap samples) was used to estimate 95% confidence bands. Non-overlap of 95% confidence bands was interpreted as significant difference in the respective responses.

2.4.2 | Root decomposability (decomposition experiment 2)

To evaluate the impact of nutrient level (represented by total N) and of litter quality on root decomposability, we employed elastic net regression (Zou & Hastie, 2005). This allowed us to mitigate the effect of multicollinearity of the total of seven predictors used while simultaneously excluding non-informative predictors: Coefficients of covariates with little contribution to the response are shrunken towards zero, and groups of collinear covariates are shrunken together. Elastic net regression bridges two other penalized regression techniques, ridge and lasso regression. Ridge regression allows for coefficient shrinkage, but not for variable selection. Lasso regression, on the other hand, does remove predictors, but has some unwanted properties, like selecting one variable at random from a group of highly correlated predictors and removing the other predictors of this group (Zou & Hastie, 2005). We used GLMNET (Friedmann et al., 2010) in R for calculation. Two hyper-parameters need to be tuned: hyper-parameter α controls the relative strength of lasso and ridge penalty, while λ controls overall model complexity penalization. For cross-validation of the elastic net penalty α , cross-validation as implemented in GLMNETUTILS (Microsoft & Ooi, 2020) was used (Supporting Information Table S3). The mean cross-validated error for a range of α values, with λ set to lambda.1se (so that the error of the model is within one standard error of the minimum) was evaluated over 1,000 iterations to find the optimum α . Regression coefficients were then calculated over 1,000 iterations with the selected α and λ set to lambda.1se. For regression, the predictors 'species identity', 'total N', 'root C:N ratio' and 'lignin:cellulose ratio', as well as 'calcium

(Ca) content', 'magnesium (Mg) content' and 'silicon (Si) content' were used, as were the two-way interactions of species with the other predictors. Cross-validation over the hyper-parameter α indicated lower mean cross validation errors for higher values of α . For numerical stability, α was set to the largest evaluated value <1 (1 would translate to lasso regression), that is, 0.729. Model coefficients of 'total N', 'lignin:cellulose ratio', 'C:N ratio', 'Mg content', 'Si content' and 'Ca content' were evaluated with $\alpha = 0.729$ over 1,000 cross-validations for the hyper-parameter λ with λ set to lambda.1se.

2.4.3 | Calculation of potentially peat-forming root biomass

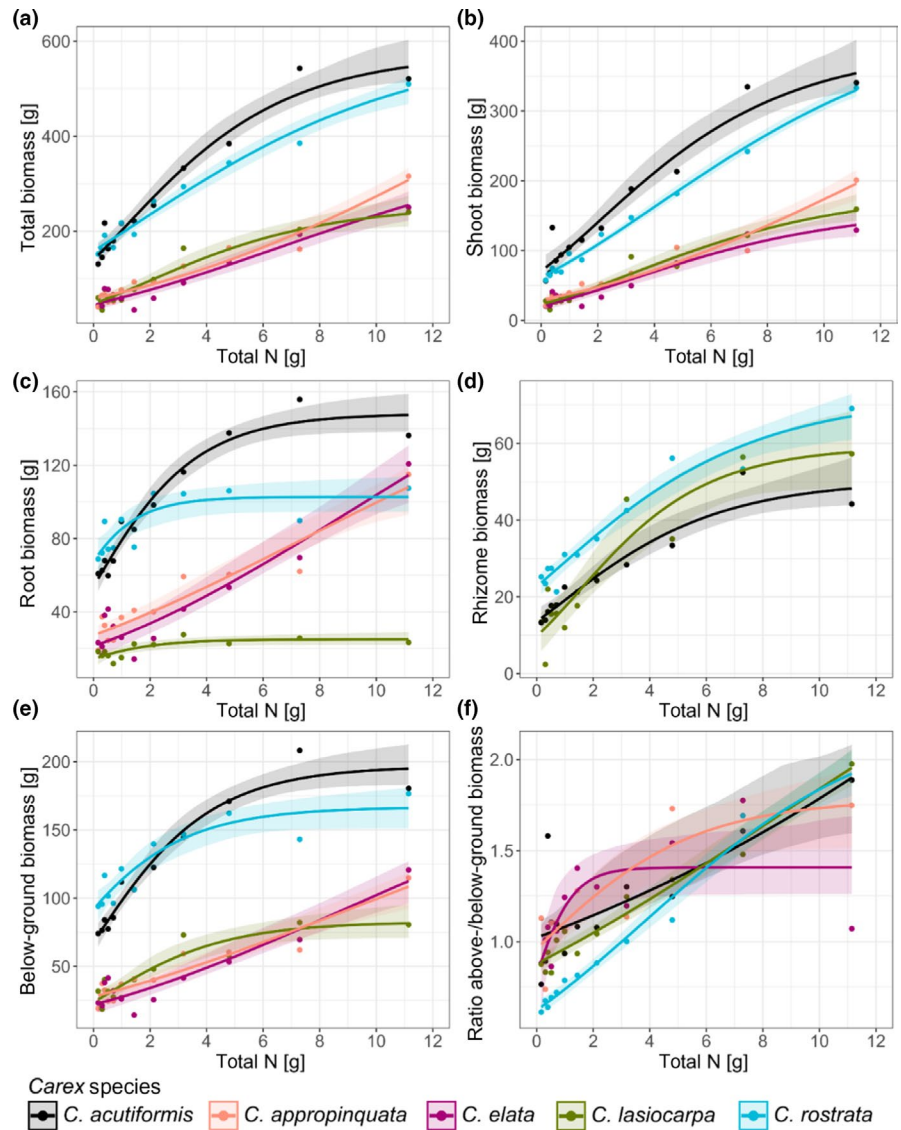
We also calculated the theoretically remaining total root biomass after 113 days of decomposition. For that, we used the total root biomass as modelled by a Gompertz growth model (Results, Supporting Information Table S3) at the end of the mesocosm experiment, and the root biomass loss rate during the root incubation experiment (decomposition experiment 2). As durations of the mesocosm experiment (113 days on average) and the root decomposition experiment (100 days incubation) differed, we calculated the root mass loss for 113 days, assuming that decomposition would remain constant on average per day over 100 and 113 days. To obtain uncertainty estimates for the remaining root biomass, we used the modelled upper and lower 95% confidence interval margins of the modelled root biomass, and the 95% confidence interval of the root biomass loss during the incubation experiment: the upper 95% confidence interval margin of the modelled root biomass and the lower 95% confidence interval margin of the root biomass weight loss give an upper estimate for the remaining root biomass. Likewise, the lower 95% confidence interval margin of the modelled root biomass and the upper 95% confidence interval margin of the root biomass loss result in a lower estimate of the remaining root biomass.

3 | RESULTS

3.1 | Biomass production

Total biomass production (above-ground and below-ground) of all species increased with increasing nutrient level (represented by total N, please note that our nutrient treatment also included P and K, to create N-limitation) by 340%–780%. At the same time, total biomass production patterns differed across species, as suggested by partially non-overlapping 95% confidence bands (Figure 1a). The Gompertz growth model fit (see Supporting Information Table S3 for model selection) suggested that total biomass production of *C. acutiformis*, *C. lasiocarpa* and *C. rostrata* levelled off at higher nutrient levels, whereas no saturation was observed for *C. elata* and *C. appropinquata*. Based on

FIGURE 1 Biomass production and nonlinear model fit for the five *Carex* species grown under different nutrient levels (represented by total N) in mesocosms. (a) Total biomass, (b) shoot biomass, (c) root biomass, (d) rhizome biomass, (e) below-ground biomass (i.e. root + rhizome biomass), (f) ratio between above-ground and below-ground biomass. All biomass production data were fit using Gompertz growth models, above-:below-ground ratio was fit using a logistic growth model. Shown are mean estimates (solid lines) and 95% confidence bands (semitransparent ribbons) based on bootstrapping of residuals



95% confidence bands, both *C. acutiformis* and *C. rostrata* had higher total biomass production than the other three species, regardless of the nutrient level. Contaminating plants (i.e. plants of other species) in pots with *C. lasiocarpa* and *C. appropinquata* should have only little, if any, influence on the overall pattern: contaminations in *C. lasiocarpa* pots were only found in lower nutrient levels (up to level 8; note the exponential increase of N amount over levels). In *C. appropinquata* pots, another sedge grew in two lower levels as well as in the pots with nutrient levels 10 and 11. In the latter, the contaminating sedge had a low root and shoot biomass production in level 10 as compared to *C. appropinquata* (3.5% of *C. appropinquata* root and 5.1% of *C. appropinquata* shoot), and a somewhat higher biomass production in level 11 (14% of *C. appropinquata* root and shoot). Thus, without the contaminating sedge, some saturation of *C. appropinquata* biomass production at the highest nutrient levels might have been observed.

Above-ground biomass production increased with increasing nutrient levels by 570%–940%, whereas below-ground biomass

production increased by 190%–600%. Shoot (Figure 1b) and root (Figure 1c) models showed significantly higher shoot and root biomass production (i.e. 95% confidence bands did not overlap) of *C. acutiformis*, and, for shoot biomass only, of *C. rostrata*, than of the other three species. Rhizome weights of all three rhizomatous species (*C. acutiformis*, *C. lasiocarpa* and *C. rostrata*) showed saturation with higher nutrient levels as indicated by the Gompertz growth model (Figure 1d). Rhizome lengths and numbers, however, were more divergent between species (Supporting Information Results and Figure S2). Overall, below-ground biomass production showed a similar pattern as that for total and above-ground biomass (Figure 1e).

Ratios of above-ground (shoots) to below-ground (roots + rhizomes) biomass production increased with increasing nutrient levels, that is, shoots accumulated an increasing share of total biomass production with increasing nutrient levels (Figure 1f). A nonlinear logistic model suggested levelling off of the above-:below-ground biomass production ratio for *C. appropinquata* and *C. rostrata*, as well as for *C. elata*.

3.2 | Nutrient stoichiometry in shoot and root biomass

Mass-based C:N ratios of all *Carex* shoots and roots decreased with increasing nutrient levels (Figure 2). While species differed in shoot C:N ratios, with *C. acutiformis* showing highest and *C. appropinquata* lowest C:N, all followed the same pattern with increasing nutrient level. Root C:N was less affected by species identity, and, again, all species followed the same trend to lower C:N ratios with increasing nutrient levels. N:P, N:K and K:P ratios (Supporting Information Figure S3) were rather divergent between species as compared to C:N ratios, especially in roots (Supporting Information Figure S3d–f). Additionally, ratio patterns differed between shoots (Supporting Information Figure S3a–c) and roots of the same species.

3.3 | Litter and tea decomposition in mesocosms (decomposition experiment 1)

Fresh and senescent mixed *Carex* shoot material at the surface showed a slight increase in decomposition (as mass loss) over the lower nutrient levels (Figure 3a–c). Fit of a beta growth function suggested maximum decomposition at medium nutrient levels. *Carex* root decomposition in the intermittently wet peat horizon (H1, up to 5 cm below the surface) did not change significantly with nutrient levels (comparison between a model including species and total N and a total N-only model was not significant). On average, significantly more fresh shoot material than senescent shoot material decomposed at the surface (73.9 vs. 63.9%, Kruskal–Wallis test with Dunn post hoc test, p adjusted using Benjamini–Hochberg (BH) correction: $p < 0.001$), and both showed higher decomposition than roots in the intermittently wet peat (39.4%; Kruskal–Wallis test with Dunn post hoc test, p adjusted using BH correction: $p < 0.001$ for both comparisons; Figure 3d).

Green tea decomposition was not correlated to nutrient level or species present in the mesocosms (Supporting Information Table S3). However, it did differ between peat horizons: green tea decomposition was lowest at the peat surface (75.2%;

Kruskal–Wallis test with Dunn post hoc test, p adjusted using BH correction: $p < 0.05$ for X-H1 and X-permanently wet peat, H2; Figure 3e). It was not significantly higher in intermittently wet peat (H1, 79.6%) as compared to permanently wet peat (H2, 78.3%; $p > 0.1$). Rooibos tea decomposition, on the other hand, was positively correlated with nutrient level, and also differed between species and peat horizons, and was overall higher at the surface than in both intermittently and permanently wet peat (Figure 3f). When pooling data for all nutrient levels and species, rooibos tea decomposition differences between the surface (40.6%) and both horizons in the peat (H1: 37.3%, H2: 37.8%) were significant ($p < 0.01$ for both comparisons), whereas the difference between H1 and H2 was not ($p > 0.5$). Decomposition of rooibos tea was significantly lower than that of green tea in all horizons ($p < 0.0001$ for all three comparisons).

3.4 | Decomposability of roots grown under different nutrient levels (decomposition experiment 2)

Carex root material loss was between 21% and 74% of the initial root material weight used for incubation experiments. Highest mass loss was observed for *C. elata* (62%–74%), regardless of the nutrient level the plants grew at, and lowest for *C. lasiocarpa* and *C. appropinquata* (21%–39% of initial root mass, Supporting Information Figure S4). Differences between species amounted up to over 30% of mass loss difference between *C. elata* and *C. appropinquata*, that is, while *C. elata* had a root mass loss up to over 70%, maximum mass loss of *C. appropinquata* roots was only about 40%. *Carex* root mass loss also increased slightly with increasing nutrient level the plants grew at (on average 4.5%–7.4% from lowest to highest level according to our model, which takes into account multicollinearity of the predictors), but decreased with increasing Mg and Ca content and increasing lignin:cellulose ratio (the latter for all but *C. elata*; Table 2, Supporting Information Table S4 and Supporting Information Figure S4): an increase from the lower to the upper quartile for all three parameters of the respective species decreased root biomass loss by app. 1%–4%. Si content and the C:N ratio did not impact root biomass loss according to our model.

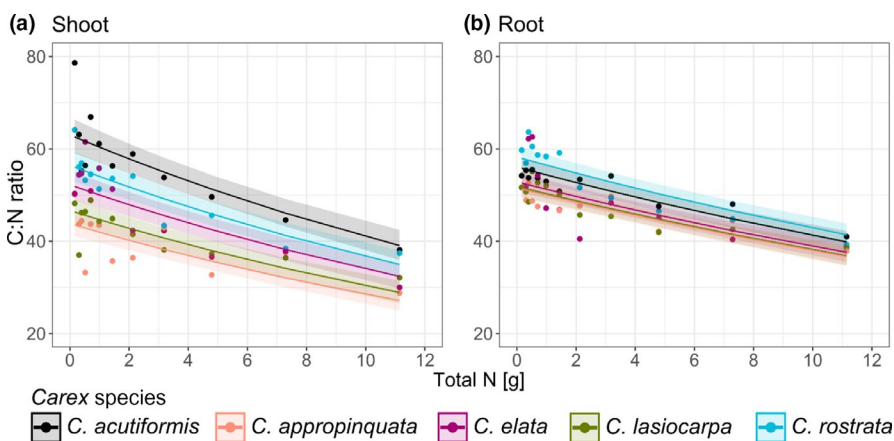


FIGURE 2 C:N ratios for (a) shoot and (b) root biomass of the five *Carex* species grown under different nutrient levels (represented by total N) in mesocosms. Shown are raw data points and results of a log-transformed linear model with mean estimates (solid lines) and 95% confidence bands (semitransparent ribbons)

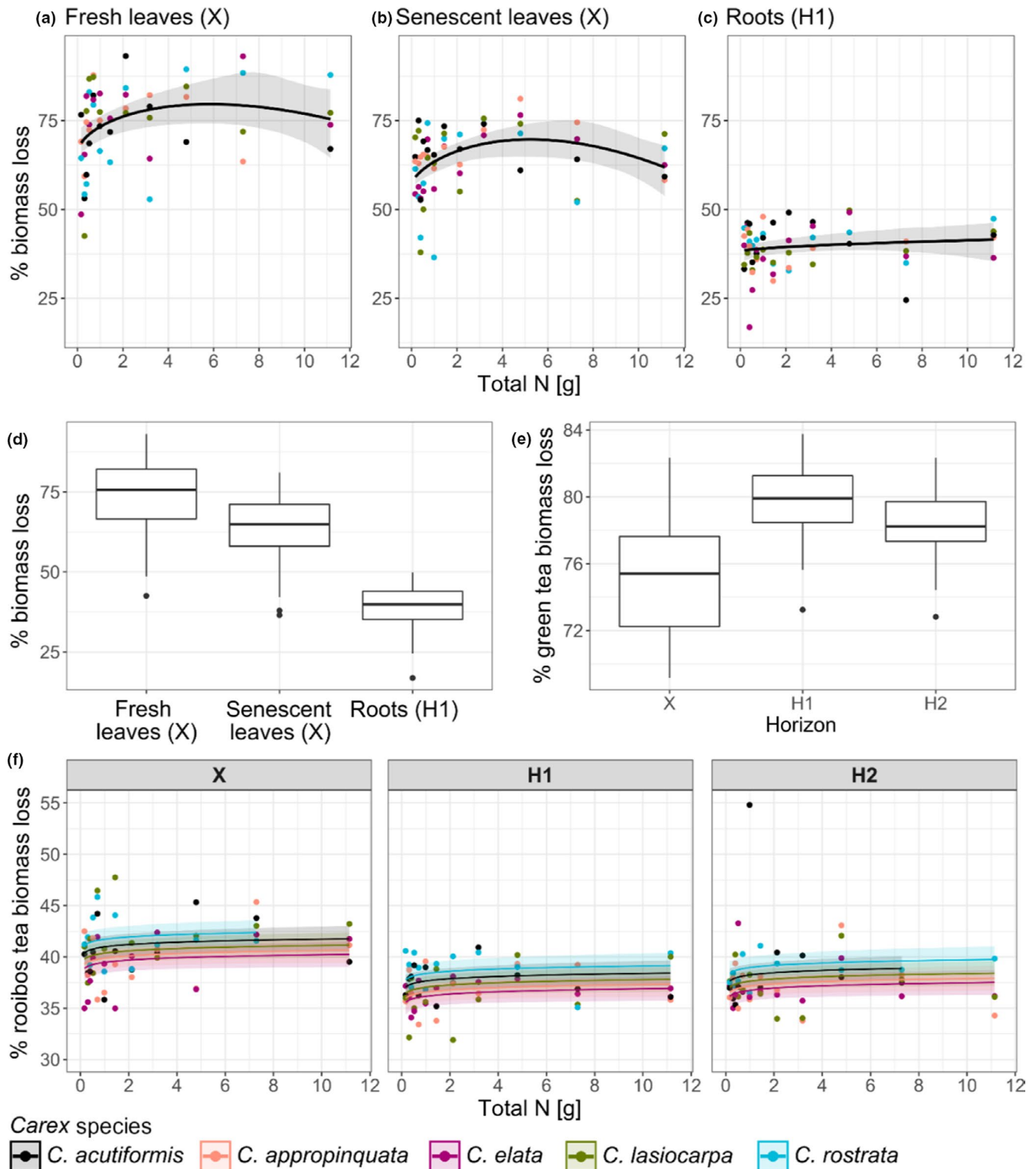


FIGURE 3 Decomposition data for mixed *Carex* plant material and green and rooibos tea under different nutrient levels (represented by total N) in mesocosms. (a) Fresh leaves placed at the surface (X), (b) senescent leaves placed at the surface, (c) roots placed in the intermittently wet peat horizon (H1, up to 5 cm below the surface), (d) boxplot of decomposition of *Carex* biomass (fresh leaves, senescent leaves, roots) pooled for all *Carex* mesocosm species and nutrient levels, (e) boxplot of decomposition of green tea pooled for all *Carex* mesocosm species and nutrient levels (H2: permanently wet peat, 20–25 cm below surface), (f) decomposition of rooibos tea separated for horizon and *Carex* species in the mesocosm plots. (a–c) show raw data points and results of a beta function model fit (mean: solid line, 95% confidence band based on bootstrapping of residuals: semitransparent ribbon). For fresh and senescent leaves, nutrient level, but not species, was relevant for decomposition according to our model selection, whereas for roots, neither species nor nutrient level was relevant (the beta growth model is shown for the sake of completeness). Sub-figure (f) shows raw data points and the result of a linear model fit with mean (solid line) and 95% confidence bands (semitransparent ribbons)

Calculated (theoretical) mass loss of roots after 113 days of decomposition increased with increasing fertilization level for all *Carex* species (Figure 4). The total mass loss was higher for species with initially larger root weight (*C. acutiformis*, *C. rostrata*) and smaller for species with initially lower root weight (*C. elata*, *C. lasiocarpa*, *C. appropinquata*).

TABLE 2 Main effects (mean \pm SE of the mean) of species, nutrient level (represented by total N) and root biomass quality on the loss rate of root biomass as evaluated using elastic net regression, that is, accounting for multicollinearity of the predictors. Coefficients are in the metric of the respective covariate. For coefficients of all effects including interactions between species and the other covariates, please refer to Supporting Information Table S4. For representative regression graphs, please refer to Supporting Information Figure S4

Covariate	Coefficient
(Intercept)	63.86 \pm 0.03
<i>Carex elata</i>	4.88 \pm 0.02
<i>Carex lasiocarpa</i>	-2.85 \pm 0.02
<i>Carex appropinquata</i>	-1.87 \pm 0.03
<i>Carex rostrata</i>	0.71 \pm 0.03
total N (g)	0.41 \pm 0.00
lignin:cellulose ratio	-31.49 \pm 0.06
Ca content (%)	-5.36 \pm 0.02
Mg content (%)	-20.43 \pm 0.11
Si content (%)	-0.01 \pm 0.00
C:N ratio	0.00 \pm 0.00

4 | DISCUSSION

4.1 | Nutrient levels impact foremost biomass production rather than decomposition

We here show different responses of *Carex* spp. biomass production and decomposition along a wide gradient of nutrient levels, created by different amounts of N in an N-limited system. In accordance with our hypothesis (a), total biomass production increased from the lowest to highest nutrient level. Also in accordance with hypothesis (a), the above-:below-ground biomass production ratio increased linearly or saturated, that is, biomass production above-ground increased relatively more than below-ground, at least at the lower part of the nutrient level gradient. However, below-ground biomass production increase was also substantial. Decomposition of *Carex* mixed shoot and root material (standardized material) placed in the mesocosms was only slightly impacted by the external nutrient level, in line with our hypothesis (b). While higher nutrient levels during growth also slightly increased decomposability of roots with increased nutrient contents, species identity was the main determinant for root mass loss.

The general trends observed were stable across species. Taken together, these results lead us to reject our hypothesis (c), that potentially peat-forming root biomass of *Carex* sedges will decrease with increasing nutrient levels—on the contrary, based on this study, *Carex* potentially peat-forming root biomass apparently increased with increasing nutrient levels. The results of our study obtained for fen sedges are thus in contrast to the situation observed in bogs, where fertilization leads to decreased C sequestration due to both

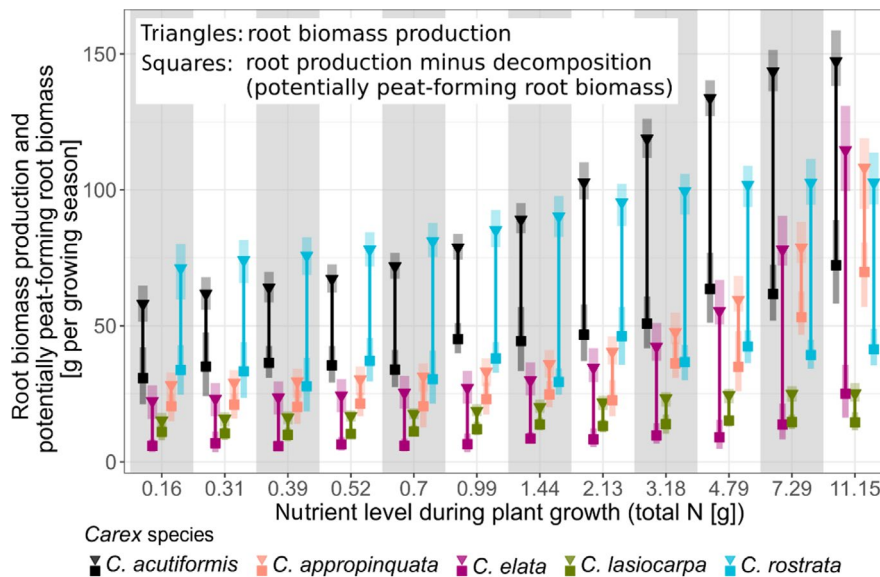


FIGURE 4 Root biomass production at the end of the mesocosm experiment (modeled by Gompertz growth model, top-down triangles) and potentially peat-forming root biomass after 113 days when assuming the same mass loss as in the anaerobic root decomposition experiment (squares, mean values; calculated for 113 days, assuming the same mean loss per day as during the 100 day incubation). Solid vertical lines indicate the respective mass loss. Semitransparent bands indicate 95% confidence intervals for the modelled initial root weights based on bootstrapping of residuals, and uncertainty estimates for the remaining root weight, calculated with the 95% confidence interval of the modelled initial root weight and the 95% confidence interval of root mass loss during the incubation experiment. Please note that the x axis is not to scale, but is separated in regular intervals, to ensure readability for lower nutrient levels (represented by total N)

decreased *Sphagnum* litter production and increased decomposition (Bragazza et al., 2006, 2012; Moore et al., 2019). At the same time, it has to be kept in mind that our study was done under controlled experimental conditions over one growing season with root biomass of perennial species, and losses by decomposition were estimated based on a modelling approach.

4.2 | Species-specific biomass production and allocation in response to nutrient level

While biomass production of all studied *Carex* spp. increased with increasing nutrient levels especially above-ground, in line with our hypothesis (a), we observed different patterns of biomass production for different *Carex* species. *C. acutiformis* and *C. rostrata* always produced more total biomass than the other species (also above- and below-ground biomass production was highest for these two species), and their total, as well as above- and below-ground biomass production increased relatively more in response to increased nutrient levels than in the other species. Similar total dry weights of *C. acutiformis* and *C. rostrata* to our study were also observed by Aerts et al. (1992) under high N supply, whereas in that study much higher total weights of *C. lasiocarpa* with up to almost 2 kg per m² were noted. More generally, above-ground *Carex* biomass appears to vary widely within as well as between species (Bernard et al., 1988).

With increasing nutrient levels, we observed early saturation of root and total below-ground biomass production for the rhizomatous species (*C. acutiformis*, *C. lasiocarpa*, *C. rostrata*). In contrast, no saturation of root biomass production for the tussock-forming species (*C. appropinquata*, *C. elata*) was observed. We assume that rhizomatous species respond to the intraspecific competition, which can for example be caused by light limitation (see below), by investing in organs for clonal spread, a strategy not available for the tussock-forming species. Likewise, investing into organs for clonal spread was suggested as an adaptation mechanism to light competition in fen communities by Kotowski and Van Diggelen (2004). As *C. rostrata* produced more, but shorter rhizomes (see Supporting Information Results), while investing approximately the same amount of biomass in rhizomes as compared to the other two rhizomatous species (Figure 1d), this species could have a competitive advantage in terms of a higher potential to grow with a closed canopy as dominant species. This is in accordance with the relatively high abundance of *C. rostrata* in rewetted fens in Northern Europe (unpublished data).

We noted above-:below-ground biomass production ratios between 0.6 and 2.1. Ratios in the literature for *Carex* spp. during the vegetation period range from under 0.05 to over 5.5 (Aerts et al., 1992; Bernard et al., 1988; Konings et al., 1992; Kotowski et al., 2006; Sjörs, 1991). An increase in biomass allocation to shoots under elevated nutrient levels, as observed in our study, seems to be a common response in different plant species and plant communities, including *Carex* species (Aerts et al., 1992; Müller et al., 2000; Peng & Yang, 2016; Poorter et al., 2012; Yan et al., 2019). Possibly, under lower nutrient supply relatively more biomass is allocated

below-ground to increase nutrient uptake, whereas under higher nutrient supply, relatively more biomass is allocated above-ground to maximize photosynthetic yield (Aerts et al., 1992) and to compete for light (Kotowski et al., 2006). This can have important implications for the potential rates of peat formation along gradients of nutrient availability: as fen peat is primarily formed by below-ground biomass (Joosten, 2016; Michaelis et al., 2020), a relative shift of biomass allocation to above-ground parts as nutrients become more available could potentially counterbalance an increased total biomass production. Thus, an increase in total biomass would not necessarily be paralleled by an increase in peat formation. However, in our study, biomass production also increased below-ground with higher nutrient levels, even if at a lower rate than above-ground biomass production.

We observed some saturation of plant total as well as organ-specific biomass production with increasing nutrient levels. Possible factors limiting further plant growth could have been, for example, availability of light or of other than supplied macro- or of micro-nutrients, as well as species-specific constraints like maximum enzymatic activities. Plant growth could especially have been limited by light competition in the densely overgrown mesocosms, as relative light intensity (RLI) depends on standing crop biomass and height. We measured above-ground biomass dry weights of up to 1.29 kg/m² (*C. acutiformis* grown at the highest nutrient level), which is even higher than reported maximum above-ground *Carex* biomass values of up to 1.18 kg/m² (Aerts et al., 1992). Above-ground biomass production saturation already started to occur at 0.46 kg/m² (*C. lasiocarpa*) to 1.27 kg/m² (*C. acutiformis*). Indeed, in fen communities, calculated RLI at ground level reduces to zero already at standing crop dry weight below 0.4 kg/m² (Kotowski & van Diggelen, 2004). However, it should be noted that light competition in our study was limited to (quite symmetric) intraspecific competition, whereas in the field it is mainly the (asymmetric) interspecific competition that differently restricts species-specific performance at nutrient-rich sites (Kotowski et al., 2010; Kotowski & van Diggelen, 2004). Another limiting factor in our study could be K availability. K:P ratio of roots was below 4.8 at the highest nutrient level, which would be the optimum ratio according to Knecht and Göransson (2004).

4.3 | Decomposition in mesocosms is not driven by species nor nutrient level

Decomposition in the mesocosms, that is, of mixtures of *Carex* materials and of tea placed in mesocosms, did not show a clear increase with increasing nutrient levels, as only for fresh and dried leaves at the surface a nonlinear nutrient level effect with slightly elevated decomposition at medium nutrient levels was observed. This effect was not distinguishable by species. These results are in line with our hypothesis (b), assuming little effect of external nutrient levels on decomposition of standardized plant material. Apparently, high N and P amounts in the peat had no stimulating effect on decomposition, and neither did different plant species growing in the mesocosms

modulate the microbiota's decomposition capacity. This lack of a stimulating effect of external nutrient supply on decomposition in peat is in line with other studies (Agethen & Knorr, 2018; Bridgman & Richardson, 2003; Emsens, Aggenbach, Grootjans, et al., 2016).

We observed at least 20% less mass loss of roots in the intermittently wet upper peat layer than of fresh and senescent leaves at the surface. According to the tea decomposition data, plant material quality appears to be more important than oxygen availability for decomposition: relative mass loss differed largely between green (more labile) and red (more recalcitrant) tea, but less between peat horizons. This is in line with other studies, which conclude that *Carex* tissue decomposition is dependent on tissue type, with roots decomposing slower than other tissues (Graf & Rochefort, 2009; Scheffer & Aerts, 2000; Thormann et al., 2001).

4.4 | Root decomposability is species-specific

Our investigation of decomposition of *Carex* roots produced under varying nutrient levels and incubated under standard conditions (decomposition experiment 2) indicated that *Carex* root biomass decomposability increased with higher nutrient levels, in accordance with our hypothesis (b). However, different root biomass traits modulated this pattern, and species identity had the greatest impact on root decomposability. This implies that some species-specific trait, or more likely a combination of traits, which we did not measure in our analysis, largely determines root decomposability. According to our model, root decomposability decreased for all species but *C. elata* with increasing lignin:cellulose ratio. The opposite trend observed for *C. elata* might be explained by the consistently lower lignin:cellulose ratios of *C. elata* as compared to the other species. On the other hand, our modelling results suggest that root biomass C:N ratio and Si content were not major drivers for *Carex* root decomposability. Reasons for the comparatively higher root decomposability of *C. elata*, aside from the lower lignin:cellulose ratio, remain to be elucidated.

In line with our results, *Carex* litter quality and decomposability have been shown to change primarily species-dependent with nutrient level changes, and increases in nutrient availability did not necessarily increase decomposability (Aerts & de Caluwe, 1997). Also in accordance with our study, root biomass C:N ratio appears not to be a decomposition driver of fen and perennial graminoids (Hartmann, 1999; Van der Krift et al., 2001). The role of lignin in biomass decomposition, however, appears to be ambiguous: While some studies found lignin contents to be significantly correlated with decomposition (Cai et al., 2015; Emsens, Aggenbach, Grootjans, et al., 2016; Moore et al., 2007), in another study no relationship between lignin and root decomposition was found (Scheffer & Aerts, 2000). While this discrepancy could, in theory, be due to oxic versus anoxic incubation conditions, as lignin is predominantly degraded aerobically (Thevenot et al., 2010), the studies of Moore et al. (2007) and Emsens, Aggenbach, Grootjans, et al. (2016) included surface (and thus oxic) incubations. Nevertheless, the lignin

content of biomass is likely especially important for decomposition in waterlogged soils.

Interestingly, in contrast to our results, Emsens, Aggenbach, Grootjans, et al. (2016) found no significant correlation between Ca and Mg contents and *Carex* litter decomposition over 116 days. Additionally, they did not observe a correlation between litter quality and decomposition rates under nutrient-rich conditions. Likewise, a correlation between Si content and decomposition of *Carex* litter was only found under nutrient-poor, but not under nutrient-rich conditions (Emsens, Schoelynck, et al., 2016). This indicates that incubation conditions, for example, chemical composition of the peat, and likely also microbiota present and plant species used, impact plant material decomposition substantially.

Similar to our results, where we observed a rather minor increase of *Carex* root decomposition with higher nutrient levels, fertilization of *Juncus effusus* did not significantly alter litter decomposition (Agethen & Knorr, 2018). Taken together, we suggest that fertilization plays a minor role for decomposition as compared to litter-inherent qualities.

4.5 | Effects of nutrient level on potentially peat-forming root biomass

Our investigation of potentially peat-forming root biomass of different *Carex* species was based on the amount of root biomass produced under varying nutrient levels in mesocosms (mean experiment duration of 113 days) and its decomposition rate under standard conditions, that is, an estimation of production and subsequent decomposition of the complete production within one growing season. We did not investigate here how an increase in nutrient level impacts decomposition of peat already present. However, as litter and tea decomposition varied only little with nutrient levels (Figure 3), this impact should be of minor importance (see also below). While our calculation of potentially peat-forming root biomass is certainly simplified, assuming that all root biomass produced is available for decomposition, that root biomass composition and thus decomposability do not change with plant age, and considering root decomposition only in the growing season, it nevertheless indicates that broadly two different peat formation routes exist: (a) low productivity and low decomposition with a concomitantly comparatively low peat accumulation rate, as seen, for example, in *C. lasiocarpa*, and (b) high productivity and high decomposition, together with a presumably comparatively high peat accumulation rate, as seen, for example, in *C. acutiformis*. At the same time, potentially peat-forming root biomass of a species is likely not only dependent on amount of root biomass generated, but can also change with nutrient level, as seen especially in *C. appropinquata*. Thus, species composition appears to be an important control for both productivity and decomposition and thus for resulting, potentially peat-forming, root biomass.

While our decomposition experiment went over 100 days at 18°C, decomposition in the field also takes place in the non-growing season. We here observed that increases in root mass loss with

increasing nutrient levels were much lower than the increases in root biomass production during the growing season, and would not expect mass loss to increase over-proportionally for some nutrient levels in the non-growing season. Rather, while we do expect some mass loss also during the non-growing season, we expect decomposition to decline substantially with decreases in temperature. Temperature at six different wet fen sites in northeastern Poland in a depth of 15–20 cm in October 2017 to September 2018 were on average 7.5–9.7°C over the whole year, 14.3–18.0°C from May to September, but only 2.9–3.8°C between October and April (unpublished data). A major influence of temperature on decomposition has been shown, for example, for pine needles (Domisch et al., 2006), and for litter decomposition in Canadian forests (Trofymow et al., 2002).

In addition to likely decreases of decomposition due to temperature decreases in the non-growth period, also changes in litter chemistry during decomposition will likely slow down further decomposition: During 15 weeks of incubation, cellulose content of litter from different species decreased significantly, whereas lignin content showed little change (Magill & Aber, 2000), indicating that the organic matter becomes more recalcitrant. Taken together, while we do expect root mass loss also during the non-growing season, we do not expect it to change the general pattern of our findings, that is, potentially more remaining root biomass with higher nutrient levels.

With time, the microbial community might also adapt to the nutrient level and the prevailing carbon source, with potential impacts on decomposition. For our analysis of root decomposability we collected peat in the field, to include a microbial community presumably adapted to decomposition of sedge roots. An adaptation to the prevailing leaf litter (the 'home-field advantage') has been shown to increase decomposition rates on average by 7.5% (Veen et al., 2015). However, for fine roots a home-field advantage seems to be less common, potentially because microbiota adapted to more recalcitrant biomass are less specialized on a certain chemical composition (Lin et al., 2020). Additionally, even a home-field disadvantage can occur (reviewed in Palozzi & Lindo, 2018). Moreover, changes in microbiota activity in peat soils in response to environmental changes have been shown to occur over time spans as short as 57 days (Juottonen, 2020). Thus, while a pre-adaptation of the microbial community to the prevailing nutrient level and litter input might influence decomposition rates, these effects certainly need to be studied in more detail in the future.

Another potential bias of our study is that we looked at 1-year-old root biomass, whereas sedges are perennials and their root production and root decomposability might change over time. While we studied and compared potentially peat-forming root biomass between different species, the actual peat accumulation rates in the field result from the species assemblages present, which themselves are determined by competitive abilities. For example, interspecific, asymmetric competition for light will likely restrict ranges of species occurrences in the field (Kotowski et al., 2006). This not only affects the species composition of vascular plants, but also the cover of mosses (which will likely be higher in nutrient-poor environments),

and thereby the contribution of moss biomass production to peat accumulation. We suggest that future investigations should look more carefully into these aspects. Moreover, while we studied a nutrient gradient under constant water levels, in nature these factors are usually interlinked: high nutrient supply is often combined with high water level fluctuations (Kotowski & van Diggelen, 2004; Wassen et al., 1990). As decomposition is impacted by the peat water content (Fenner & Freeman, 2011), by peat geochemistry (Emsens, Aggenbach, Schoutens, et al., 2016), as well as by the microbial community (Strickland et al., 2009), this interdependence of different environmental gradients should be taken into account for future ecosystem-level studies in fens.

5 | CONCLUSIONS

Our study points at an increase of the peat formation potential of *Carex* spp. with increasing nutrient levels: higher root biomass production at higher nutrient levels is not counterbalanced by higher potential decomposition. At the same time, according to our results, different *Carex* species differ in their potentially peat-forming root biomass by pronounced differences in root biomass production and root decomposability. When extrapolating from our mesocosm-based results to larger scales in natural and artificial settings, the peat formation potential of sedge-dominated fens thus appears to be strongly dependent on the dominant species, which itself is dependent on environmental factors, seed bank composition, as well as on competitive ability.

Rewetting leads to the establishment of peat-forming plants, including sedge communities, with some variation in community composition depending on the conditions before and after rewetting and the time since rewetting (Klimkowska et al., 2019; Timmermann et al., 2006; Zerbe et al., 2013). It remains to be investigated which factors promote this development. In the light of our study, aiming at favouring species like *C. acutiformis*, and also *C. rostrata* (due to its presumably comparatively high competitive ability via clonal spread) might be beneficial for peatland restoration measures. Taken together, we think that rewetted fens, even highly eutrophic ones, have the potential to quickly shift to a peat-forming state after restoration.

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AUTHORS' CONTRIBUTIONS

E.S., F.T., J.K., and W.K. designed and coordinated experiments; C.A. and Ł.K. contributed to the experimental design and collected the sedges in BeNeLux and Poland, respectively; E.S., F.T., G.L., J.K., W.K. ran the experiment and sampled the data; T.H. analyzed the data and wrote the manuscript with input from all authors; G.L. performed the root incubation experiments and lignin:cellulose ratio determination; J.L. coordinated C:N and XRF analyses of biomass samples and performed specific literature search; K.-H.K. provided XRF analyses of biomass samples. All authors gave input and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.x95x69ph6> (Hinzke et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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