



Nutrient Inputs and Hydrology Interact with Plant Functional Type in Affecting Plant Production and Nutrient Contents in a Wet Grassland

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Abstract

We studied the effect of nutrient additions and hydrology on the above-ground production and shoot nutrient contents of representative species of the conservative (*Carex acuta*) and competitive (*Glyceria maxima*) plant functional types in a minerotrophic wet grassland. Above-ground samples were collected in May, late June (time of maximum biomass) and August (re-growth following cutting) from plots subjected to nutrient addition treatments in years with differing hydrology, ranging from drought to prolonged flooding. Net above-ground primary production (NAPP) and shoot nutrient contents (C, N, P) were determined separately for *C. acuta* and *G. maxima*. Between-year and species differences were analyzed by repeated measures ANOVA and generalized linear mixed models (GLMM). NAPP decreased with hydrologic stress with the proportion due to *C. acuta* increasing with flooding, while *G. maxima* responded positively to nutrient additions. As expected, C% was greater, but N and P% were lower, in *C. acuta* shoots compared to *G. maxima*. Hydrology affected above-ground production and shoot nutrient contents more than nutrients, but both interacted with plant functional type, with likely impacts on ecosystem processes. Future studies must consider multiple factors to predict the effect of climate and management changes on wetlands.

Keywords *Carex* · *Glyceria* · Hydrology · Nutrient addition · Plant functional type

Introduction

Climate change is expected to affect hydrologic regimes through changes in precipitation amounts and seasonal patterns. This is especially relevant for Central Europe, which is predicted to have drier conditions with changed precipitation patterns as a result of climate change (IPCC 2014). Such changed hydrologic patterns are expected to affect plant species composition with subsequent repercussions on ecosystem

functions (Garssen et al. 2017). Other human actions, including increased nutrient inputs resulting from agricultural intensification (Vitousek et al. 1997), can interact with site hydrology resulting in changed plant species composition and diversity (Wisheu and Keddy 1992; McJannet et al. 1995; Bollens et al. 2001; Brinson and Malvarez 2002) as well as affecting plant biomass and nutrient allocation patterns (Saggar et al. 1997; Detenbeck et al. 1999; Gough et al. 2000; Pezeshki 2001) with such changes ultimately impacting ecosystem processes and functions (Grigulis et al. 2013; Kaštovská et al. 2015).

Changing environmental conditions affect ecosystem processes through impacts on plant species traits, as well as influencing the dominance of various functional types (Diaz et al. 2004; Minden and Kleyer 2015). The conservative and competitive plant functional types represent end points of a growth-survival gradient predicted by life history theory (Grime 1988; Metcalf et al. 2006; White et al. 2016; De Deyn 2017). Compared to conservative species, competitive species tend to grow in nutrient-richer habitats, have greater photosynthesis and nutrient uptake rates, leading to faster

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growth of tissues with higher N contents, which results in faster decomposition and nutrient turnover rates (Orwin et al. 2010; de Vries et al. 2012; Baxendale et al. 2014).

Although it is well-known that both internal (e.g., primary production, biomass and nutrient allocation patterns) and external conditions and processes affect plant growth and development (Wardlaw 1990; De Deyn 2017), most of the studies conducted on this topic have focused on the impacts of single factors. However, ecological systems, including wetlands, are influenced by multiple, co-occurring factors, which may interact in a non-additive manner (Dieleman et al. 2012; Sierra et al. 2015). Multifactorial studies may therefore provide greater and more realistic insights into how ecosystems respond to changing conditions brought about by various human activities including climate change (Reese et al. 2018).

Manipulative field experiments offer one means for investigating the effect of multiple, interacting factors on plant growth and ecosystem processes. Such an experiment was established in two wet grasslands in the South Bohemia region of the Czech Republic to study the effect of long-term (seven years, from 2006 to 2013) nutrient inputs on plant-soil interactions (Picek et al. 2008; Edwards et al. 2015). Wet grasslands are graminoid-dominated wetlands (Joyce and Wade 1998; Joyce 2014) that, in Europe, are maintained by human activities. Therefore, the composition of these habitats is vulnerable to any change in management practices (Joyce and Wade 1998; Tallowin and Jefferson 1999; Prach 2008), which can then cascade to affect ecosystem processes and functions (Kaštovská et al. 2015, 2017).

In addition to the nutrient addition treatments, there were uncontrolled changes in the hydrologic conditions over the seven years of the study, with the first three years being drier while the wet grasslands were flooded for long periods in the later years (Edwards et al. 2015). Here, we present results from one of the grasslands in which representative species of the conservative and competitive plant functional types, specifically *Carex acuta* and *Glyceria maxima*, respectively, were co-dominants. *Carex acuta* and *G. maxima* are tall emergent macrophytes forming stands on flat or gently sloping parts of wetlands on gleyed clays or seasonally shallowly flooded or waterlogged organogenic sediments (Hejný and Husák 1978; Hroudová and Zákavský 2002). Both species have mean Ellenberg moisture indicator values of 8 (Chytrý et al. 2018), but differ in their mean Ellenberg indicator values for nutrients, being 4 and 9 for *C. acuta* and *G. maxima*, respectively. *Carex acuta* replaces short sedges such as *C. nigra* in formerly oligotrophic wetlands subject to nutrient additions (Prach 1993, 2008), but it tends to be outcompeted by reeds including *G. maxima* under eutrophic conditions. Data are from three years (2007, 2008 and 2012) differing in their hydrologic conditions. Site hydrologic conditions were quite dry in the 2007 and 2008 growing seasons with minimum water levels being far below the rooting zone (Fig. 1). These

two seasons differed in that 2007 followed a wetter year while the year preceding 2008 was also dry. These years differed from the 2012 growing season, in which the water level rarely fell below the rooting zone with periods of prolonged flooding (Fig. 1).

The aim of the study was to determine how nutrient additions and site hydrology interact in affecting above-ground plant production and shoot nutrient contents in representative species of the conservative and competitive plant functional types and to provide insight into how these two species seemingly can co-exist (Baxendale et al. 2014; Cortois et al. 2016). We hypothesized that nutrient supply and site hydrology interact to affect above-ground plant production and shoot nutrient contents, but that the effect is specific to the functional type. Therefore, the conservative species *C. acuta* is expected to be favored under more stressful conditions of low nutrients and less-than optimal water level conditions (including both drought and prolonged flooding), but that increased nutrient supplies coinciding with less stressful hydrologic conditions will favor the more competitive species *G. maxima*.

Methods

Study Site

Nutrient addition experiments were conducted in a wet grassland with mineral soil in the Třeboň Basin Biosphere Reserve (TBBR: 49° 10'N, 14° 46'E), Czech Republic. A complete description of the study site is given in Picek et al. (2008) and Edwards et al. (2015). The wet grassland is located in the floodplain of a small river (Nežárka) and is frequently flushed. Floodplain wetlands with mineral soil tend to predominate on frequently flushed sites (Hejný and Segal 1998). The site has a silt-sand alluvial substrate and is dominated by *G. maxima* and *C. acuta* with few other species present (L. Rektoris, pers. comm.). This particular wet grassland is managed as an active agricultural area used for hay production and contains no rare, threatened nor endangered plant species. It was chosen as our study site because of the apparent co-existence of two dominant species belonging to different plant functional types. As an actively managed agricultural field, the site is mown two times during the growing season, in early-mid June and August, which correspond to the mowing times of the neighboring fields. Altitude of the study site is 410 masl.

Experimental Design

A field experiment was established in Spring 2006 and ran until the end of 2013. See Picek et al. (2008) for a full description of the experimental design. Briefly, four blocks were established in the site, with three treatment plots (12.25 m²)

per block. Fertilization treatments (0, 65 and 300 kg NPK $\text{ha}^{-1} \text{yr}^{-1}$, corresponding to an unfertilized control, and Low and High fertilization treatments, respectively) were administered to randomly selected plots using a commercial NPK fertilizer (Lovofert 15:15:15 NPK, Lovochemie, a.s.). The fertilizer was added in two half doses during the growing season (mid-May and July) to simulate normal agricultural practices. Adjacent plots were separated by at least 1.5–2 m wide buffer strips. Nutrient addition occurred when there was no standing water in the sites and when weather forecasts predicted that at least the following two days would be without precipitation. Laboratory analyses of the soil from the sites showed that the added nutrients were immobilized into the plants and microbes within 48 h. Thus, the manner of nutrient addition and buffer width were deemed to be sufficient to prevent the spread of the applied fertilizer to neighboring plots.

Continuous water level measurements were taken from a well established in the center of the site. Water levels were taken at 15 s intervals using the STELA system, which consisted of a field datalogger (M4516) with a GSM/GPRS modem (MG40) and water level sensor (Fiedler-Magr, Electronics for Ecology, Czech Republic). For this study, daily water level means were calculated from the continuous water level readings using MOST (Monitoring Station) version 2.3 (Fiedler-Magr, Electronics for Ecology, Czech Republic).

As noted by Edwards et al. (2015), 2007 and 2008 were dry years (Fig. 1) with mean water levels during the respective growing seasons being below the root zone, which was visually estimated to be the top 20 cm of the soil profile. This sharply differed in 2012 when the sites had standing water for most of the growing season (Fig. 1). Therefore, the plants growing in the wet grassland were subjected to drier

conditions in the first two years of the study, but then had to contend with periods of prolonged flooding in 2012.

Data Collection

Above-ground plant samples were collected from randomly selected quadrats (two 25 * 25 cm quadrats) in 2007, 2008 and 2012, representing 2, 3 and 7 years of nutrient additions (see Picek et al. 2008; Zemanová et al. 2008 and Edwards et al. 2015 for fuller descriptions). Quadrats were separated by at least 10 cm in a plot and were never re-sampled during the study. Sampling occurred at approximately monthly intervals during the 2007 and 2008 growing seasons (early May to October), but only three times during the 2012 sampling period (beginning of the growing season (late April), time of maximum above-ground biomass (early July) prior to the first cutting, and in August following re-growth but before the second cutting). In all years, the harvested above-ground matter was separated into live, standing dead and litter components, with the live material further divided by species. The number of live shoots were counted per quadrat as a measure of shoot density. These harvested materials were dried at 70° C for 48 h in a forced air oven (Memmert, Germany) and weighed. The dry weights (DW) and shoot density counts were then extrapolated to a meter square basis (e.g., g DW m^{-2}).

Data Analyses

Plant Density, Size and Production

Shoot density (shoot number m^{-2}) and average shoot weight (above-ground biomass divided by shoot number in a

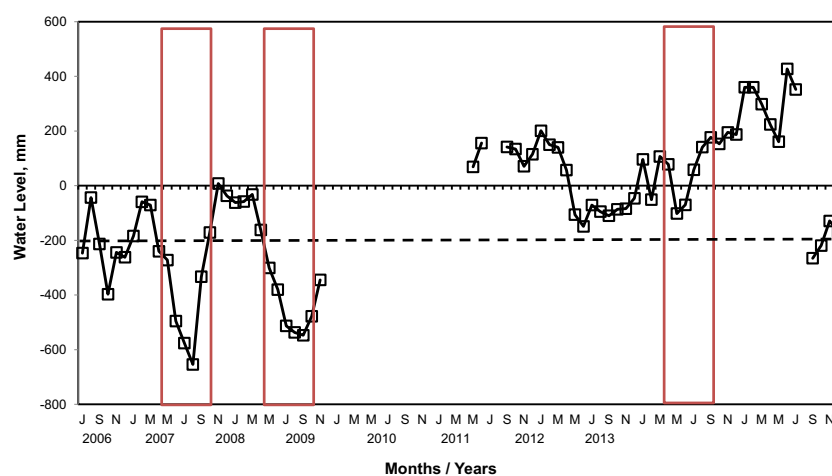


Fig. 1 Monthly mean water levels in the study wet grassland from the start of long-term nutrient additions in 2006 to the end of the experiment in 2013. Water levels were measured at 15 s intervals by a water level sensor (Fiedler-Magr, Czech Republic) in a well located in the center of the site. Daily means were calculated from these data and then these were

used to calculate the monthly means. Blocks indicate the 2007, 2008 and 2012 growing seasons analyzed in this study. The solid line at zero represents the soil surface while the dashed line at 200 mm below the soil surface represents the lower boundary of the root zone. Gaps in the water level data are when the water level sensor was malfunctioning

particular plot) were calculated for *C. acuta* and *G. maxima* for all harvests in the three growing seasons.

Mean NAPP ($\text{g DW m}^{-2} \text{ yr}^{-1}$) for the three growing seasons was calculated from the total dried living, standing dead and litter material for each treatment type in each year (see Picek et al. 2008 and Káplová et al. 2011). Since the site was mown twice during the growing season, live production was calculated as the difference between the mean live stem DW in the sampling period just before the site was mown minus the mean initial DW ($\text{LIVE}_{\text{Pre-cut}} - \text{LIVE}_{\text{Initial}}$). To this value was added the difference between the post-mowing sampling period with the maximum mean live DW minus the mean live DW immediately following the mowing, which was assumed to be similar to the initial live DW value. Therefore, total mean live production (LIVEPROD) for each treatment per site was calculated as $\text{LIVEPROD} = [(\text{LIVE}_{\text{Pre-cut}} - \text{LIVE}_{\text{Initial}}) + (\text{LIVE}_{\text{Post-cut}} - \text{LIVE}_{\text{Initial}})]$. The production of dead material was determined by adding the standing dead and litter DWs collected in each quadrat and calculating the mean dead DW for each nutrient treatment. Differences in mean dead DW per treatment were calculated between subsequent sampling dates with positive differences included in estimating NAPP. NAPP for each treatment type was calculated by adding together the total live production (LIVEPROD) with those positive differences in dead matter ($\text{NAPP} = \text{LIVEPROD} + \text{DEAD}_{\text{Positive}}$).

Nutrient contents (percentages of C, N, P) were determined for the harvested above-ground biomass samples, with the exception of the June 2007 sampling which was omitted from the nutrient analyses (see below). C and N were analyzed using a CN analyzer (ThermoQuest, Italy) while P was determined using a flow injection analyzer (FIA, Lachat QC8500, Lachat Instruments, USA). The molar contents of C, N and P were then used to determine the respective stoichiometric ratios (C:N, C:P, N:P; Sterner and Elser 2002). The standing stocks for C, N and P were calculated by multiplying the CNP percentages with the above-ground live biomass at each harvest.

Repeated measures ANOVAs were conducted in SYSTAT v. 11 to determine whether the individual calculated parameters (shoot density and average shoot weight, above-ground biomass, NAPP, nutrient percentages, their stoichiometric ratios and nutrient standing stocks) changed over the years. In addition, repeated measures ANOVAs were run to determine whether the proportion of total above-ground production contributed by *C. acuta* and *G. maxima* differed over time. When needed, the ANOVAs were run following natural logarithm or square root data transformations to achieve normality and variance homogeneity. Scheffé's comparison of means test was used in the case of significant nutrient treatment effects while Bonferroni corrections were used for determining the significance of the temporal effect (Sokal and Rohlf 1995).

Environmental Effects

In addition to the nutrient treatments, several water level parameters were determined from the daily mean water level measurements. From the water level data we were able to determine the mean, minimum and maximum water levels during a particular period of the growing season preceding the harvesting of plant biomass in any particular year, as well as the amplitude of water level fluctuation within any particular period (= maximum – minimum). Similar to Edwards et al. (2015), we also calculated two relative water level indicators, the number and proportion of days in a particular period preceding the selected harvesting of plant biomass in which the water level was below the root zone (the top 20 cm of the soil layer). These relative parameters were included due to their greater ecological relevancy than the basic water level parameters.

The influence of the nutrient treatments and water levels, as well as their possible interaction, on the collected above-ground plant production, shoot density and shoot nutrient content data in each site, were determined using generalized linear mixed models (GLMM) in R v. 3.3.0 (R Core Team 2016) with the nlme package (Pinheiro et al. 2016). Appropriate hydrologic measures to be included in the models for each site were determined by calculating variance inflation factors (vif) in the car package (Fox and Weisberg 2011) to remove highly correlated variables ($\text{vif} > 3$). For NAPP, water level factors were determined for the entire growing season in a particular year, running from April 1 to the date of that year's last harvest. Shoot biomass and nutrient contents were analyzed for each selected harvest (May, June and August). For the first period, water level data were obtained from the start of the growing season (April 1) to the date of the first harvest. Subsequent periods were from the date of the previous harvest to the day of the selected harvest. Hydrologic measures for the full growing season analyses (NAPP, species proportion of site NAPP) were highly correlated to each other ($r > 0.97$), therefore the mean water level for the growing season was selected as the hydrologic measure for these analyses. For the shoot biomass and nutrient content analyses, water level amplitude and the number of days in which the water level was below the root zone (a measure of drought) were chosen by the vif analysis for those models.

Mixed models were then run separately on each dependent variable (NAPP, proportional NAPP, above-ground biomass of the dominant species as well as their CNP percentages, the resulting C:N, C:P, and N:P ratios and the CNP standing stocks). Species, the nutrient addition treatments and selected hydrologic measures were used as the explanatory (fixed) variables. Year and block were random variables tested to determine the possible influence of within-site temporal and/or spatial differences on the dependent variables. The block effect was never significant and thus was omitted from the

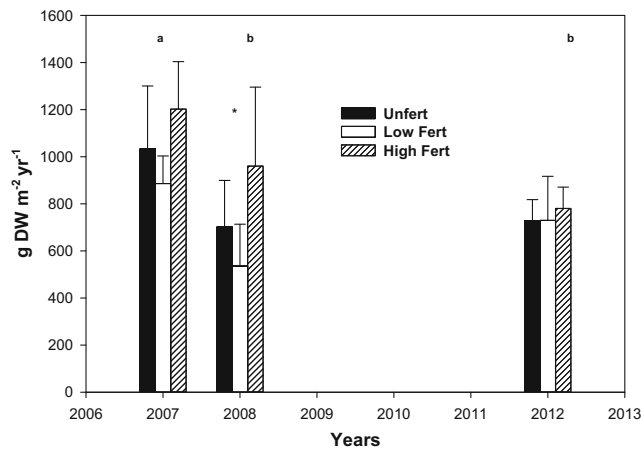


Fig. 2 Average (mean ± 1 SD) net above-ground primary production (NAPP; g dry weight * m⁻² * yr.⁻¹) as affected by nutrient addition treatments for a wet grassland with mineral soil. NAPP was calculated at the time of maximum biomass in the 2007, 2008 and 2012 growing seasons. Nutrient treatments: Unfert = unfertilized control (0 kg NPK m⁻² yr.⁻¹); Low Fert = low fertilization (65 kg NPK m⁻² yr.⁻¹); High Fert = high fertilization (300 kg NPK m⁻² yr.⁻¹). Significant differences between treatments in a growing season: * - p < 0.05. Different letters represent significant differences (α = 0.05) between years

analyses. All of the mixed effect models were run following the procedure outlined in Zuur et al. (2009). The best model for each tested dependent variable was chosen based on comparison of Akaike information criteria (AIC) scores (Akaike 1987).

Results

Above-Ground Production

Total site NAPP significantly decreased from 2007 to 2008 and then remained similar in the 2012 growing season (Fig. 2). Based on the mixed model analysis (GLMM), this significant between-year difference in NAPP was due solely to the nutrient treatments (Table 1), likely due to the greater production in the High fertilization treatment plots in 2008 (Fig. 2).

Table 1 Generalized linear mixed models (GLMM) of the effects of nutrient additions and site hydrology on site net above-ground plant production (NAPP), the proportion of NAPP attributed to the two co-dominant species in a wet grassland and shoot density (Shoot Dens = shoot number m⁻²) and average shoot size (g) for the two species.

Analyses	Spec	Nut	MWL	Spec*Nut	Spec*MWL	Year
NAPP		5.67 **				4.90 *
Prop NAPP	3.99 *	0.14	0.39	6.96 **	77.24 ***	4.29 *
Shoot Dens	38.08 ***		5.81 *		26.62 ***	
Shoot Size	12.48 ***	0.38	2.00	3.22 *	3.57 +	

The proportion of total NAPP attributable to the two co-dominant species in the wet grassland site (*C. acuta*, *G. maxima*) differed over time, with that of *C. acuta* increasing from 2007 to 2012 (from a minimum of 21% to a maximum of 78%) while it decreased for *G. maxima* (Fig. 3). Both species responded differently to the nutrient treatments and changes in site hydrology (significant species*nutrient and species*hydrology interactions; Table 1). For example, the proportion of total NAPP attributed to *C. acuta* increased with greater flooding (2012) while that for *G. maxima* decreased, but the species had opposite reactions to the nutrient treatments, which were more apparent in 2007 and 2012 (Fig. 3). Similarly, between-species differences were noted in the shoot densities of the respective species, with *C. acuta* density significantly increasing from 2007 to 2012 (p < 0.001) while *G. maxima* showed the opposite trend (Fig. 4), mostly in their response to site hydrology (significant species*mean water level interaction; GLMM analysis, Table 1). In addition, there was a weak nutrient effect on *G. maxima* shoot density (t = 2.560; p = 0.093), with the density significantly decreasing in 2012 in all nutrient treatments, but with maximum densities occurring in 2008 in the Low and High fertilization treatments (Fig. 4). The average shoot size did not change for either species over time (repeated measures ANOVA, p > 0.154), with *G. maxima* shoots always being significantly larger than that of the average *C. acuta* shoot (Table 1; Fig. 4). However, there was a significant increase in average *G. maxima* shoot size in the High fertilization treatment over the years, resulting in a weak significant species * nutrient interaction (Table 1).

Shoot Nutrient Contents

Season and changes in the relevant environmental conditions significantly affected the shoot nutrient contents (CNP percentages, stoichiometric ratios and CNP standing stocks; appendix S1). Shoot C% significantly increased, while N and P% decreased, from the beginning of the growing season to the time of maximum biomass before the first cutting in late June / early July. These then remained stable or slightly

Fixed effects = nutrient additions (Nut), hydrology (mean water level = MWL) and species (Spec; all except NAPP). Year and block were random effects; block was always not significant. T values only for factors included in each model. P values: + < 0.10; * < 0.05; ** < 0.01; *** < 0.001

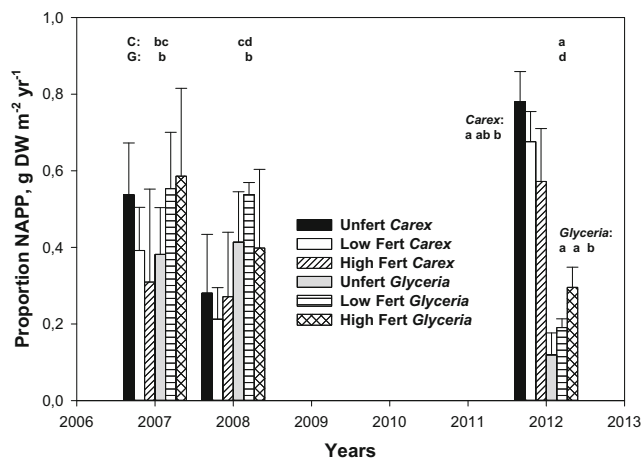


Fig. 3 The proportion of total net above-ground primary production (NAPP) represented by the dominant plant species (C = *Carex acuta*; G = *Glyceria maxima*) in a wet grassland with mineral soil subjected to nutrient addition treatments. NAPP was measured as the sum of sequential harvests; see text for details. Different letters represent significant between-year differences determined by repeated measures ANOVAs. Nutrient treatments: Unfert = unfertilized control (0 kg NPK m⁻² yr.⁻¹); Low Fert = low fertilization (65 kg NPK m⁻² yr.⁻¹); High Fert = high fertilization (300 kg NPK m⁻² yr.⁻¹). Between-treatment differences in 2012 are indicated by different letters for each species

increased to the second peak in biomass before the second cut in August (Fig. 5; appendix S1). C% was the lowest in 2008, the driest year, but the greatest in 2012 in young shoots at the beginning of the growing season. Early season N and P% increased over the years, indicating a positive effect of the nutrient treatments. Similar trends were seen at the time of the second biomass peak in August (Fig. 5). However, yearly changes in the CNP contents at the time of the first cutting in June/July differed from those of the other seasonal measures with C% also being greater in 2012 than 2008. However, N and P% showed species-specific changes, decreasing over the years in *C. acuta* while the opposite trend was observed for *G. maxima*.

Nutrient treatments significantly affected only the N% and the C:N ratio. For *G. maxima* shoots, these factors significantly differed between nutrient treatments early in the 2008 and 2012 growing seasons (May samples) and at the time of maximum biomass (June) but only in 2008. Early season N% was significantly greater in the unfertilized control treatment while the C:N ratio showed the opposite trend (Figs. 5 and 6; appendix S1) implying that plants in the fertilized treatments began to grow earlier than those that did not receive additional nutrients. However, shoot N% and the C:N ratio differed significantly in the Low fertilization treatment in the June 2008 sampling. Significant nutrient effects on the nutrient contents of *C. acuta* shoots were observed only late in the growing season (August sampling). As with *G. maxima*, N% and the C:N ratio were significantly different in the Low fertilization treatment in 2008 while all standing stocks

were significantly greater in the unfertilized control treatment in 2007 (appendix S1).

All nutrient content parameters (CNP percentages, the stoichiometric ratios, standing stocks) were significantly affected by both the nutrient addition treatments and site hydrology (Table 2), both singly for most of the nutrient content parameters, with the exception of C standing stock, as well as there being significant species-specific responses (appendix S1). Compared to the competitive species *G. maxima*, *C. acuta*, the conservative species, had significantly greater shoot C%, but lower N and P%, with corresponding differences in the appropriate stoichiometric ratios (Figs. 5 and 6). The species also differed in the seasonality of maximum N and P stocks, with *G. maxima* stocks being the highest in June (time of maximum biomass) while *C. acuta* plants reached their maximum later in August (appendix S1). Only N% and the C:N ratio were significantly influenced by the nutrient addition * hydrology interactions (Table 2).

The species also differed in their responses to changing site hydrologic conditions. The changes in shoot nutrient contents were more strongly connected to the drought measure (number of days in a period the water level was below the root zone) than the amplitude of changing water levels. The stronger connection was especially notable for C and P%, and the C:N and N:P ratios (Table 2). However, changes in the CNP standing stocks were more connected to water level fluctuations (amplitude), due to the stronger effect on shoot biomass.

Discussion

Plant growth, production and allocation patterns are important parameters that influence how plants affect ecosystem functioning (Ehrenfeld et al. 2005; Orwin et al. 2010; Baxendale et al. 2014). These plant parameters are in turn influenced by external environmental factors as well as internal factors such as the functional type of the given species, which is linked to life history strategies (Grime 1988; Metcalf et al. 2006; De Deyn 2017). In agreement with our original hypothesis, we noted significant interactions between these internal and external variables, but not always in the ways that were initially predicted.

Environmental Effects

In our study, both the nutrient addition treatments and changes in site hydrology significantly affected NAPP and shoot nutrient contents. However, our results indicate that changes in site hydrology can outweigh the effects of nutrient additions, as noted in other wetlands (Güsewell et al. 2003; Hefting et al. 2004).

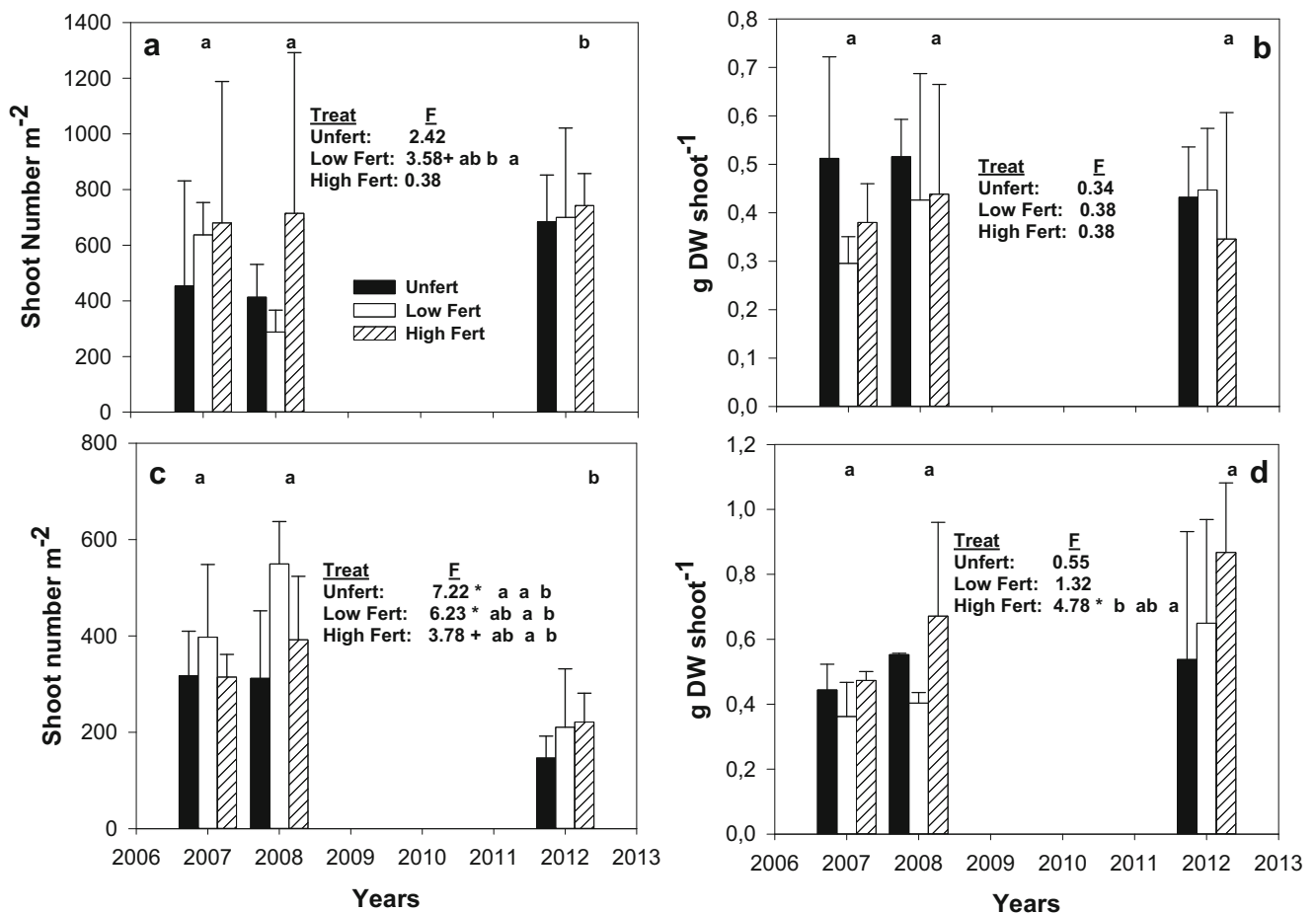


Fig. 4 The effect of nutrient treatments and time on shoot density (a, c) and average shoot size (b, d) of the two dominant species in a wet grassland at the time of maximum aboveground biomass in the 2007, 2008 and 2012 growing seasons. Species: *Carex acuta* (a, b); *Glyceria maxima* (c, d). Nutrient treatments: Unfert = unfertilized control (0 kg

NPK m⁻² yr⁻¹); Low Fert = low fertilization (65 kg NPK m⁻² yr⁻¹); High Fert = high fertilization (300 kg NPK m⁻² yr⁻¹). Different letters at top of each graph represent significant differences ($\alpha = 0.05$) between years. Between-treatment differences between years were calculated using repeated measures ANOVA

As expected, site NAPP was significantly greater in the High fertilization treatment compared to the unfertilized control. The significant increase in N and P% in young shoots at the beginning of the 2008 and 2012 growing seasons further show the positive effect of the nutrient treatments.

The significant decrease in total site NAPP, with the continued dry conditions in 2008 and the prolonged flooding in the 2012 growing season, shows the importance of site hydrology on plant growth and production. While both the 2007 and 2008 growing seasons were characterized by dry conditions with water levels far below the root zone, 2007 was preceded by a year (2006) with wetter conditions in the growing season (Fig. 1) while 2008 represented a second successive growing season with dry conditions. Thus, the prolonged dry conditions of 2008 may have resulted in decreased photosynthesis and growth, as found for several tree species (Sala et al. 2012; Klein et al. 2014; Wu et al. 2018; Dietrich et al. 2019). Future studies should focus on the influence of past hydrologic conditions on the growth and production of non-woody wetland plant

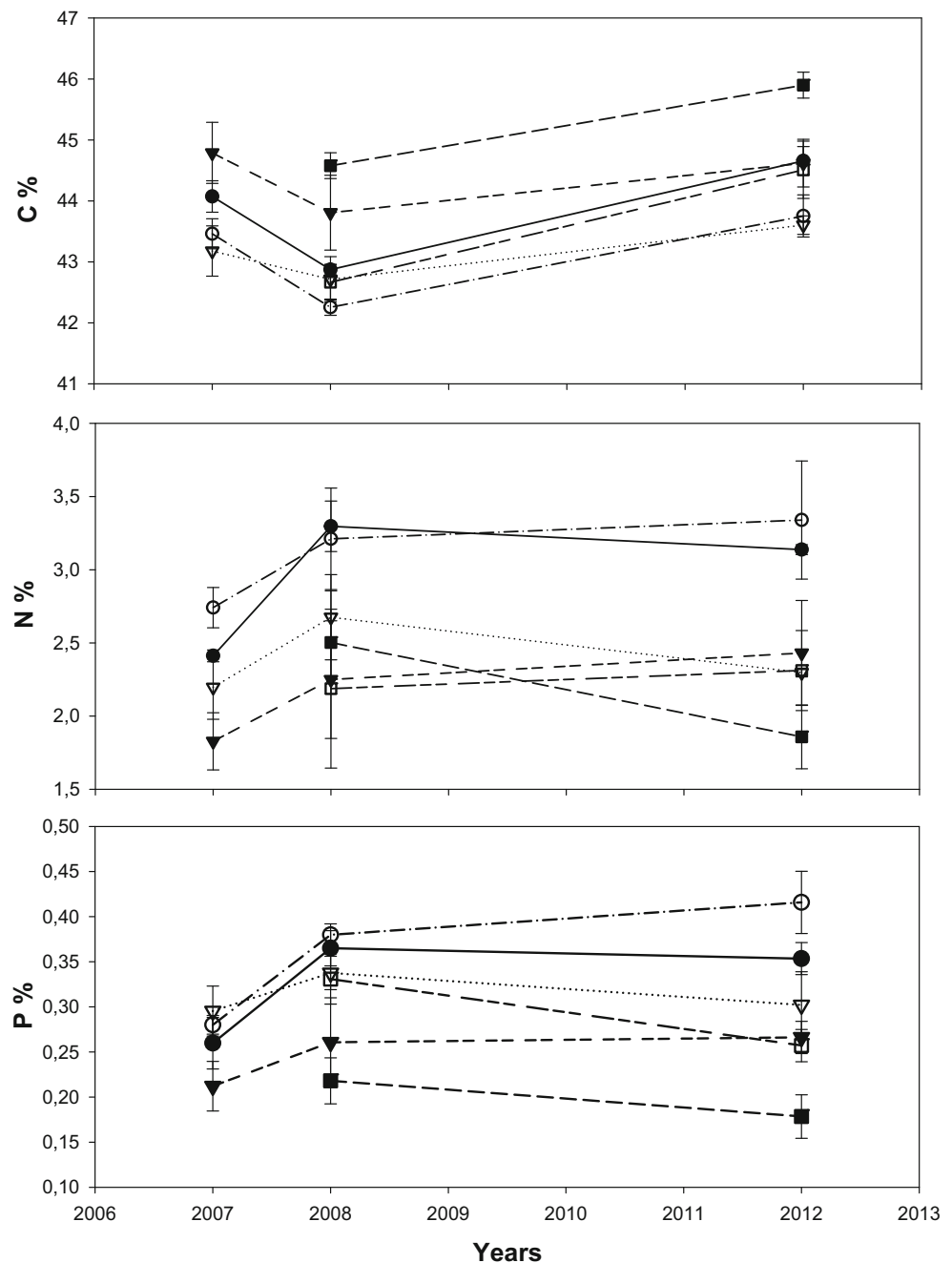
species and how the strength of this effect may change through interactions with other environmental factors.

The decrease in total site NAPP with increased hydrologic stress and the observed changes in shoot nutrient contents during the growing season related to plant development (Dykyjová and Úlehlová 1998) are very common and expected results. What is more interesting was the response of the two plant species, representative of different plant functional types, to changing environmental conditions and how these species seemingly co-exist in the study site.

Role of Plant Functional Type

We predicted that the conservative species *C. acuta* would be better able to handle adverse, stressful conditions, but this was only partially supported by our results. Contrary to expectations, the significant decrease in total site NAPP in the 2008 growing season was due largely to the negative response of *C. acuta* to the continued dry conditions, most likely related to

Fig. 5 Seasonal shoot CNP percentages (mean \pm SE) for the two dominant graminoid species in the wet grassland, the conservative species *Carex acuta* (filled symbols) and the competitive species *Glyceria maxima* (open symbols). Seasons: May (early) = circle; June (time of maximum biomass) = square; August (late) = inverted triangle. Means were calculated by combining data from the three nutrient treatments for any sampling period in a particular growing season since most of the nutrient data did not significantly differ. See appendix S1 for all of the data

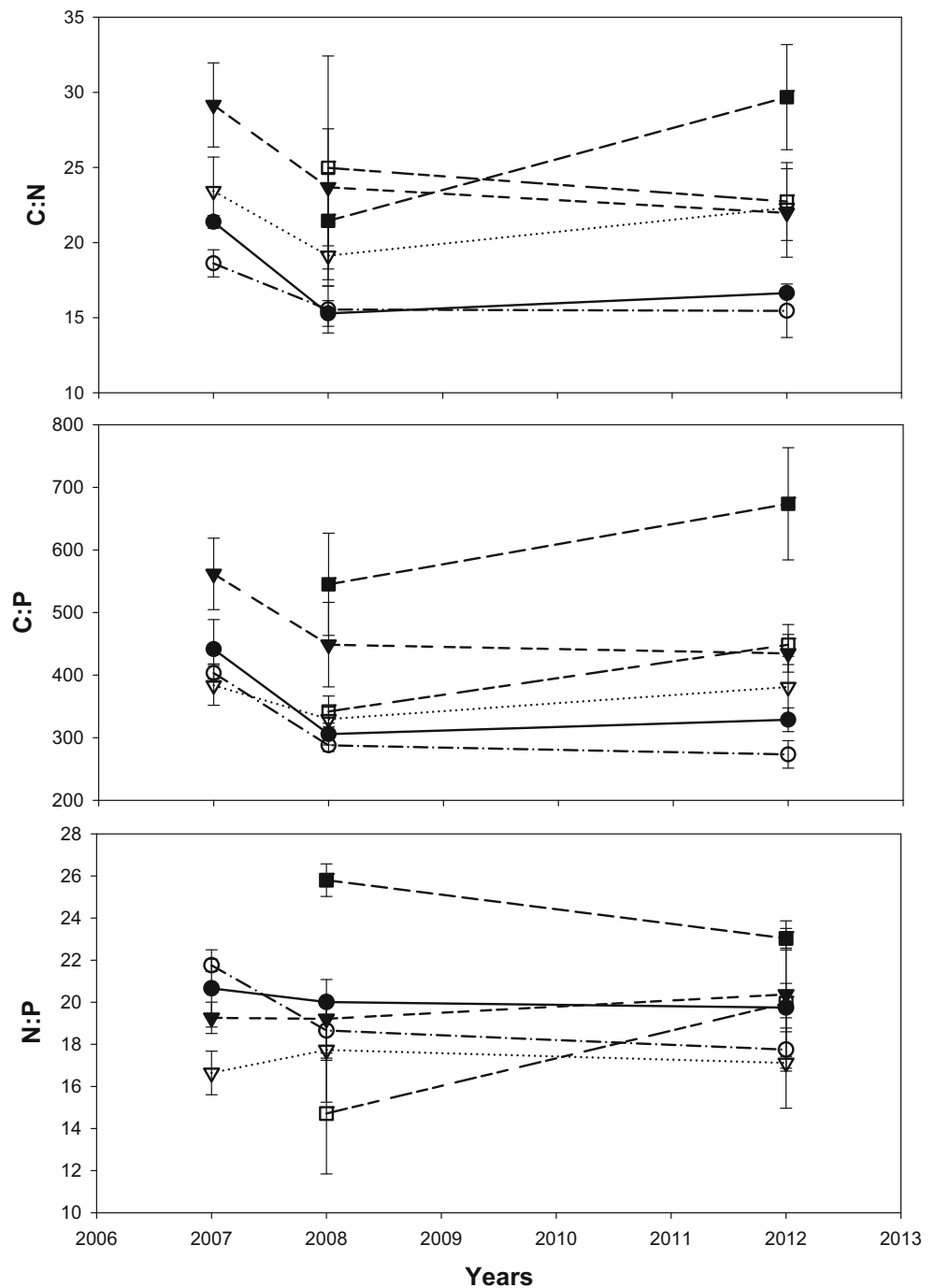


reduced plant nutrient uptake leading to decreased photosynthetic rates and growth brought about by the more stressful hydrologic conditions (Dykyjová and Úlehlová 1998; Lambers et al. 1998). This negative response was seen particularly in plants subjected to the Low fertilization treatment, which produced significantly fewer shoots and contributed significantly less to total site NAPP than plants in the other nutrient treatments (Figs. 3 and 4), while also having lower shoot N and P percentages at the time of maximum biomass in 2008. The different response of the *C. acuta* plants in the Low fertilization treatment plots was a surprise given that the treatment plots were randomly located within blocks spread across

the wet grassland site and with no significant block effect for any of the tested parameters.

The situation was reversed under the prolonged flooding conditions in 2012, in which *G. maxima* growth and production were significantly negatively affected while that of *C. acuta* rebounded to levels similar to those of the 2007 growing season. This result agrees with the findings of Menges and Waller (1983) who classified *Carex* species as stress-tolerators especially in terms of their ability to survive prolonged flooding in riparian areas. Several *Carex* species, including *C. acuta*, have developed adaptations that allow them to tolerate flooded conditions, including the capacity to

Fig. 6 Seasonal stoichiometric ratios (mol mol^{-1} ; mean \pm SE) in shoots of the two dominant graminoid species in the wet grassland, the conservative species *Carex acuta* (filled symbols) and the competitive species *Glyceria maxima* (open symbols). Seasons: May (early) = circle; June (time of maximum biomass) = square; August (late) = inverted triangle. Means were calculated by combining data from the three nutrient treatments for any sampling period in a particular growing season since most of the nutrient data did not significantly differ. See appendix S1 for all of the data



switch growth form and produce tussocks (Perelman et al. 2003; Crain and Bertness 2006), as well as being able to release large amounts of oxygen from their roots to the rhizosphere (Mainiero and Kazda 2005). This results in the formation of an aerobic zone in the rhizosphere that leads to increased nutrient availability and uptake rates (Končalová 1990; Visser et al. 2000; Colmer 2003).

The significantly larger average size of *G. maxima* shoots and the greater contribution of this species to total site NAPP

with increased nutrient supply under prolonged flooding conditions implies possible nutrient*hydrology interactions which, however, were not observed in the GLMM analyses. Such a possibility is supported by the opposite response of the *C. acuta* plants, which likely was due to the increased cost of maintaining a large belowground structure, which should put it at a competitive disadvantage under nutrient-richer conditions (Wedin and Tilman 1990; Kaštovská et al. 2017). Ecological theory predicts that more competitive species

Table 2 Generalized linear mixed models (GLMM) on shoot nutrient (C, N, P) percentages and their respective stoichiometric molar ratios, and CNP standing stocks (g m^{-2}) for the two co-dominant species (*Carex acuta*, *Glyceria maxima*) in the wet grassland site. Fixed effects = Nutrient additions (Nut), hydrology (amplitude of water level changes =

Amp; number of days in a period that water levels were below the root zone, visually estimated at 20 cm = Days) and species (Spec). Year and block were random effects but neither was significant. Only significant fixed effects and interactions are shown. P values: + < 0.10; * < 0.05; ** < 0.01; *** < 0.001

Factors	Spec	Nut	Amp	Days	Spec*Nut	Spec*Amp	Spec*Days	Nut*Amp	Nut*Days
CNP Percentages									
C%	240.0 ***	9.0 ***	57.0 ***	36.0 ***			5.0 ***		
N%	20.06 ***	33.11 ***	45.28 ***	44.58 ***		5.82 *	5.37 ***	1.73	2.81 ***
P%	194.56 ***	21.41 ***	35.34 ***	58.80 ***	4.24 *	0.62	8.75 ***		
Stoichiometry									
C:N	32.82 ***	30.24 ***	33.46 ***	50.19 ***		5.20 *	5.26 ***	1.15	2.63 **
C:P	220.20 ***	17.50 ***	23.30 ***	61.30 ***	4.00 *	0.50	9.60 ***		
N:P	57.32 ***	3.60 *		5.40 ***	2.58 +		8.65 ***		
Standing Stocks									
C	8.72 **	1.06	1.86	37.97 ***	6.34 **	79.06 ***	4.55 ***		
N	1.94	4.25 *	7.78 **	19.68 ***	4.96 **	83.17 ***	3.04 **		
P	0.49	3.60 *	6.56 *	24.63 ***	4.82 **	83.82 ***	5.69 ***		

should dominate under conditions of greater nutrient supply due to greater allocation to above-ground, photosynthesizing tissues and more efficient nutrient uptake resulting in faster growth compared to conservative species (van der Werf et al. 1993; Aerts and Chapin 2000). The apparent co-existence of these two species in our study site is likely due to interactions between multiple, co-occurring factors (Sierra et al. 2015). Based on the results of our study, the response of *C. acuta* and *G. maxima* to changing nutrient and water levels, resulting in either dominance of one of the species or co-existence, is shown in Fig. 7.

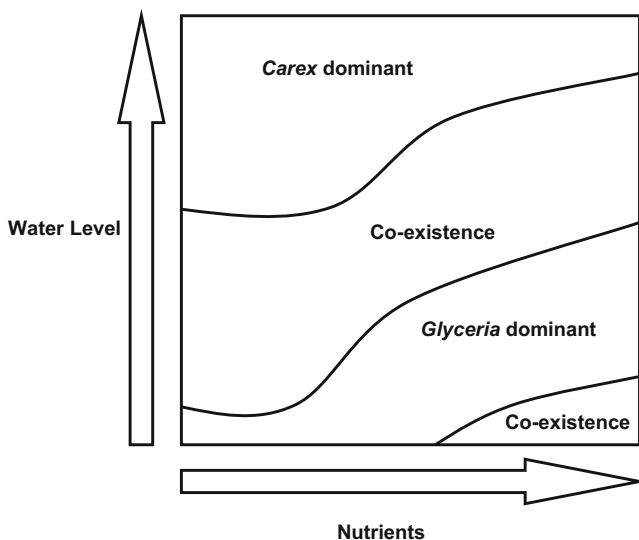


Fig. 7 Conceptual diagram showing the joint effect of nutrients and water level changes on the growth and production of the conservative *Carex acuta* and competitive *Glyceria maxima*, based on our study results (see Figs. 3 and 4)

Carex acuta would have the competitive advantage under wetter, especially flooded, conditions, because of its extensive root system with well-developed aerenchyma, many fine roots and large starch reserves (Končalová 1990; Vítková et al. 2017). However, the negative effect of flooding on *G. maxima* can be mitigated to a degree by increased nutrient supplies, which would result in the shoots of this species having significantly larger biomass (Fig. 4). Under drier conditions, increased nutrient levels would favor the competitive species *G. maxima*, because it can more efficiently use the higher nutrient supplies for growth (Westlake 1966; Hejny and Husák 1978; Hroudová and Zákavský 2002). However, *C. acuta* shoot density was greater in the High fertilization treatment even with low water levels. Since shoot density can be used as a proxy for fitness (Shipley et al. 2016), our results imply a possible increased competitive ability of *C. acuta* under conditions of low water, but high nutrient levels, which could result in species co-existence. Intermediate levels of both environmental factors would also favor co-existence.

Concluding Remarks

The effect of site hydrology and nutrient levels, in combination with plant functional type, interact to affect plant growth, production and nutrient content with the response of particular species being context and biologically dependent (Sorrell et al. 2002; Pennings et al. 2005). Species of different functional types can co-exist in wetland habitats such as our wet grassland because fluctuating environmental conditions are an inherent feature of many wetlands (Middleton 1999; Mitsch and Gosselink 2000) with multiple factors interacting to affect

plant species composition, community structure and eventually ecosystem functions. Which species is predominant at any point in time will then determine plant inputs to the soil, as seen by the significantly different shoot nutrient contents noted in this study, as well as similar nutrient differences in their belowground structures (Edwards 2015) and rhizodeposits (Kaštovská et al. 2017). Management actions that would increase water supply to the site, with increased flooding depth and duration, would favor the conservative *C. acuta* at the expense of the competitive *G. maxima* (Fischer et al. 2016). On the contrary, the expected drier conditions for Central Europe (IPCC 2014) would more likely negatively impact *C. acuta* than *G. maxima*, resulting in the predominance of the latter species at least over the short term. Such predominance of the competitive, faster growing species would be enhanced following re-wetting events, which are often followed by a pulse of available nutrients (Bloor and Bardgett 2012).

This illuminates the need for multivariable studies in the future. From such studies, we would be better able to predict the effects of changing climatic conditions and/or management actions on wet grasslands and other wetland systems.

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