Plant Ecol (2019) 220:1009–1020
https://doi.org/10.1007/s11258-019-00970-9

Management effects on plant species composition and ecosystem processes and services in a nutrient-poor wet grassland

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Received: 22 March 2019 / Accepted: 4 September 2019 / Published online: 12 September 2019

Abstract The effect of changing management practices, from a more intensive to a less intensive cutting regime with partial abandonment, on plant species composition, frequency, and abundance was determined for an oligotrophic wet grassland in the south Bohemia region of the Czech Republic using data from vegetation surveys conducted in 1965 (2–3 cuts per year) and 2013 (parts cut once per year, other portions abandoned). These data, coupled with nutrient data from a nearby wet grassland with similar species composition as well as data from the literature, were used to predict the possible effect of these vegetation changes on ecosystem processes and services. The former, more diverse *Molinia caerulea*-dominated state has been replaced by a less-diverse grassland dominated by clonal hemicryptophytes, such as *Carex acuta*. Partial restoration has been accomplished where mowing has been resumed. Using Ellenberg indicator values for moisture and nutrients, the present species composition indicates that the area has become wetter over time, likely due to management decisions made at the regional scale. Carbon and nutrient sequestration has likely been enhanced in the current state, while services linked to greater species diversity have likely suffered. Such tradeoffs in ecosystem services must be considered when deciding whether to restore the more diverse *Molinia caerulea*-dominated state. Decisions at the regional scale will also influence the ability of achieving a desired structure.

Keywords Plant species diversity · *Carex acuta* · *Molinia caerulea* · Ellenberg indicator values · Ecosystem services

Introduction

Wetlands are important habitats that provide numerous ecosystem services, including water retention, improving water quality, sequestering carbon and other nutrients, providing habitat as well as cultural and educational opportunities (Russi et al. 2013; McInnes and Everard 2017). However, the area of wetlands in Europe as well as worldwide has been decreasing for many decades due to drainage and conversion to agricultural land uses so that now these

Communicated by Marjan Jongen.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11258-019-00970-9) contains supplementary material, which is available to authorized users.

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habitats are considered to be some of the most threatened in Europe (EEA 2012; Feranec et al. 2016).

Wet grasslands can be highly productive wetlands dominated vegetationally by graminoid species which can have either low or high species diversity, depending on the heterogeneity of the plant community mosaic (Ružička 1994; Prach and Straškrabová 1996; Joyce and Wade 1998; Veen et al. 2009). In Europe, wet grasslands are artificial systems, which are maintained through human actions, especially mowing for hay production (Tallowin and Jefferson 1999). As with wetlands in general, the area of wet grasslands in Europe has been declining as a result of agricultural intensification, drainage, and conversion to arable land, or abandonment (Joyce and Wade 1998; Tallowin and Jefferson 1999; Prach 2008; Joyce 2014). These changes in land use and management can result in less-diverse wet grassland habitats with changed soil microbial processes (Galatowitsch et al. 2000; Picek et al. 2000; Bollens et al. 2001; Šantrůčková et al. 2001; Brinson and Malvarez 2002). Thus, management regime can greatly affect the structure and functioning of wet grasslands, thereby determining the ecosystem services provided by these systems.

Molinia caerulea-dominated wet grasslands occur in nutrient-poorer conditions and tend to have high species richness and diversity (Kącki and Michalska-Hejduk 2010). Extensive management techniques, consisting of late season mowing without any nutrient additions, are the usual methods employed by agricultural and natural resource managers for maintaining such habitats (Kulik 2014). As like other wetland habitats, the area of *M. caerulea*-dominated wet grasslands has decreased greatly over the last few decades due to agricultural intensification and/or land abandonment, so that now these wet grasslands are considered to be rare and even threatened habitats in Central Europe (Zelnik 2005; Havlová 2006; Hájek and Poláková 2010; Bölöni et al. 2011). In the south Bohemian region of the Czech Republic, for instance, this type of wet grassland is now only found in the upland belts of pond littorals bordering on forests (Hroudová et al. 1988).

However, *M. caerulea* can also be an aggressive invasive species of nutrient-enriched habitats especially in western Europe resulting in decreased species diversity (Bobbink et al. 1998; Milligan et al. 2004; Franzaring et al. 2008; Mälson et al. 2008). A more extensive management regime, similar to that for *M. caerulea*-dominated wet grasslands on nutrient-poorer sites (one late season cut, no added nutrients), is the preferred method used by natural resource managers for controlling and reducing these expansive *M. caerulea* populations (Taylor et al. 2001; Boucníková and Kučera 2006; Čop et al. 2009) although success has occurred in some cases with more intensive management of several cuts in a growing season (Hájková et al. 2009).

Past studies investigating the impact of abandonment on *M. caerulea*-dominated wet grasslands have often used a phytosociological approach with much less emphasis on possible consequences for ecosystem processes and functions (for example, Havlová 2006; Kącki and Michalska-Hejduk 2010; Kulik 2014). Here, we also used data from phytosociological surveys, but incorporate data from a manipulative field experiment to gain insight on possible impacts of changing management regimes on ecosystem processes and functions. Both the plant community data as well as that from the manipulative experiment can be used to predict possible effects of management type on the ecosystem services provided by the wet grassland, including estimations of possible tradeoffs. Therefore, the aims of our study were to (1) describe the impact of changing management practices, a switch from a more intensive cutting regime of 2–3 cuts per growing season to a less-intensive regime of only one cut per year or even abandonment (areas left unmown), on plant species composition in an oligotrophic wet grassland and whether resuming mowing can restore the previous more diverse vegetation state; and (2) determine how changes in plant species composition can impact ecosystem processes, thereby influencing the provision of possible ecosystem services, using data from a manipulative field experiment as well as literature sources.

Methods

Study site

The study wet grassland is located in the Záblatské Louky Nature Reserve (49°06′N, 14°39′E) in the Třeboň Basin Biosphere Reserve (TBBR, South Bohemia, Czech Republic). The site, approximately 100 ha in size, is a marginal wetland located in the inundation area of a large fishpond, i.e., a human-made lake aimed at commercial fish production. Carbon accumulation is typical of such poorly flushed marginal wetlands in the TBBR (Prach 2002). Currently, the site is a sedge meadow dominated by non-tussock forms of *C. acuta* and *C. vesicaria*, with other common species including *Phalaris arundinacea*, *Lythrum salicaria*, and *Galium palustre*, as well as the moss *Calliergonella cuspidata*. A large portion of this site is mown once a year in mid-July, except for the area nearest the edge of the fishpond which has become overgrown by shrubs, mostly *Frangula alnus* and *Salix* spp. A nearby hollow produced by peat extraction indicates a longer period of wetland presence. The former, *M. caerulea*-dominated structure of Záblatské Louky was formed as a result of the traditional management regime of low fertilization with 2−3 cuts per growing season (Blažková 1973).

Comparison of plant species composition

Phytosociological surveys were conducted in 1965 (seven relevés taken from Blažková (1973) and hereafter referred to as the B survey) and 2013. For the latter sampling, 19 relevés (hereafter referred to as the K survey) were sampled in stands with similar vegetation units as those described by Blažková (1973), because the exact locations of the earlier B relevés could not be determined. Relevé plot size was 25 m^2 for both samplings. Species cover in all relevés was determined using the 9° Domin–Hadač abundance scale (Kent 2012). Species names follow Kubat (2002).

To determine the effect of management changes on the plant species composition, we first determined the frequency distribution of the species identified in each survey by calculating the variance-to-means ratio (V/m) as well as testing whether the distributions differed from a Poisson distribution using a X^2 test (Ludwig and Reynolds 1988). For this, the nine points of the Domin–Hadač scale were converted to percent cover by using the mid-point of the percent cover ranges for each point. Therefore, a scale value of 1 = 0.1%, 2 = 0.5%; 3 = 2%; 4 = 5%; 5 = 10%; 6 = 20%; 7 = 38%; 8 = 62%; 9 = 88%. The non-parametric sign test was used to analyze between-survey differences in relative frequencies and abundances due to the non-normality of the data. Sign tests were conducted using SYSTAT v. 11.

A multivariate analysis was used to describe the potential relations between individual plant species and their correlation to temporal factors (Legendre and Legendre 2012). We expected a linear response of species to the environment; therefore, we selected a constrained ordination (RDA) method, which was computed using Canoco for Windows v. 5 (ter Braak and Šmilauer 2012; Šmilauer and Lepš 2014). The explanatory effects of particular environmental variables were evaluated using the Monte Carlo permutation test (MCPT) with 999 permutations.

Effect of mowing

Aerial photographs of the Zablátské Louky area from 2003, 2006, 2009, and 2013 showed that part of the studied grassland had been mown in some or all of these years. Therefore, portions of the grassland in which were located the K survey plots were subjected to the resumption of different mowing regimes (all 4 years, partial mowing—years 2003 and 2006 only, unmown). The effect of mowing regime on plant species composition in the K survey plots was determined by RDA in Canoco v. 5 (ter Braak and Šmilauer 2012). The effect of mowing intensity on species diversity, measured as mean species number per plot, in the relevant K survey plots and how these plots compare to the B survey plots was determined by oneway ANOVA in SYSTAT v. 11. Non-metric multidimensional scaling (NMS) in PcOrd v. 6 (McCune and Mefford 2011) was used to determine how closely the species composition in the relevant K survey plots subject to different mowing intensities resembled that in the earlier B survey.

Ellenberg indicator values

Ellenberg indicator values (EIV) for nutrient (EIV N) and moisture (EIV M) were used to determine whether important environmental conditions of the wet grassland, namely trophic status and hydrology, changed over time. Indicator values for each species were taken from the check list for the Czech Republic (Chytrý et al. 2018). A relative measure of each indicator value was calculated for each species by multiplying the Ellenberg value by the mean cover proportion of a species in each relevé. Thus, the proportion acted as a weighting factor. Between-survey differences in the relative indicator values for the species were calculated using the Wilcoxon Sign test in SYSTAT v. 11.

Plant nutrient contents

Nutrient contents (C, N, P percentages) and their stoichiometric ratios were determined for aboveground and belowground structures of the dominant species in a manipulative nutrient-enrichment experiment conducted in a nearby part of the wet grassland. These data, as well as a description of the experimental design, have been published elsewhere (Picek et al. 2008; Edwards et al. 2015; Edwards 2015). Data from the unfertilized control treatment are used here.

Nitrogen resorption efficiency (RE_N) was determined in the experimental plots by collecting aboveground leaf samples of the dominant plant species *Carex acuta* at two times in the 2012 growing season. The first collection occurred at the time of maximum aboveground biomass (early September) following mowing of the grassland in early July of that year. A second set of leaves was collected at the time of leaf senescence in early November 2012. At both sampling times, full, undamaged leaves were collected from four randomly selected areas in each control plot, with the samples from an area consisting of one leaf from three randomly chosen shoots, and thus there were three leaves collected per area. The three leaves collected in each area were combined for analyses making a total of four replicate samples per plot. The leaves from each sampling time were transported to the laboratory where they were first scanned on an Epson V700 Photo Scanner for later determination of leaf area, and then dried at 65 °C in a forced air oven (Memmert, Germany) and weighed.

C, N, and P percentages were determined from the dried plant biomass samples. 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). Stoichiometric ratios (C:N, C:P, N:P) were determined from these data (Sterner and Elser 2002). Differences in the percentages of leaf C and N between the mature and senesced leaves were tested by *t* tests using SYSTAT v. 11 following natural logarithm transformation when necessary to attain normality and homogeneity of variances.

Results

Comparison of plant species composition

The frequency distributions indicated that species had clumped distributions for both surveys (V/m = 25.33 and 38.08 for the K and B surveys, respectively). Seven of the 54 species were found in all relevé plots in the B survey (*Carex nigra*, *C. panicea*, *Deschampsia caespitosa*, *Galium uliginosum*, *Ranunculus acris*, *R. auricomus*, and *Rumex acetosa*), while no species were found in all K survey plots. At the other extreme, several species were found in only one relevé in each survey (B: *Carex hirta*, *Phalaris arundinacea*, *Phragmites australis,* and *Taraxacum* sect. *Ruderalia*; K: *Filipendula ulmaria*, *Glyceria maxima*, *Nardus stricta,* and *Phragmites australis*).

Species percent cover in a relevé ranged from 0 to 88% with there being 15 and 12 common species, defined as those having cover > 20% (Domin–Hadač scale values of 6 or greater) in at least one relevé plot, in the K and B surveys, respectively. Only six of these species met this criterion for being a common species in both surveys (*Alopecurus pratensis*, *Carex nigra*, *Deschampsia caespitosa*, *Juncus filiformis*, *Molinia caerulea*, and *R. repens*), while the cover of the other species either greatly increased or decreased (see Supplemental Table 1). Although meeting the criterion for being considered as a common species in both surveys, the percent cover of *Molinia caerulea* decreased from a mean of 14.6 to 7.5% per plot in the B and K surveys, respectively.

The difference in species composition between the two surveys is seen in the RDA diagram (Fig. 1a). The first RDA axis, which explained 17.2% of the variance ($F = 4.98$; $p < 0.001$), was related to the changes in species composition and abundances between the two surveys, and thus reflects temporal changes. The changing management regime over time resulted in the reduction or even absence especially of grassland and fen species (*Cardamine pratensis*, *Cirsium palustre*, *Galium uliginosum*, *Mentha arvensis*, *Myosotis nemorosa*, *Ranunculus acris* and *R. auricomus*, *Rumex acetosa*, *Senecio aquaticus*, *Succisa pratensis*, and *Valeriana dioica*). Meanwhile, the cover of clonal hemicryptophytes (*Carex acuta* and *Phalaris arundinacea*) increased while several other species (*Glyceria maxima, Iris pseudacorus* and *Calamagrostis canescens*) were not reported in the earlier B survey

(Fig. 1). Changing moisture conditions appeared to be the main factor correlated to the second axis ($F = 1.56$; $p = 0.081$), but explained only 5.3% of the data variance. The effect of moisture is seen in the species composition of two groups at opposite ends of this axis. The first group, situated at the lower end of the axis, consists of species favoring wetter soils (*Hydrocotyle vulgaris*, *Molinia caerulea*, *Lycopus europaeus*, *Lythrum salicaria*). The second group, located at the upper end of the axis, is composed of species more typical of alternately drier, but in spring regularly flooded meadows, including *Alopecurus pratensis*, *Cerastrium holosteoides*, *Lychnis flos-cuculi,* and *Poa trivialis*. The average Ellenberg indicator values for moisture (EIV M) significantly differed between the two groups ($\chi^2 = 13.53$; $p = 0.001$).

Still, the relative abundance (measured as percent cover averaged over all relevés in a survey) of the identified species did not differ between the two surveys (sign test, $p = 0.078$), with 39 species being more abundant in the B survey, while the abundance of 24 species was greater in the later K survey (see Supplemental Table 1). Differences in relative frequencies were also not significant (sign test, $p = 0.314$).

However, while the total number of species was similar in the B and K surveys (54 and 55, respectively; Supplemental Table 1), these were found in a smaller area in the B survey (7 plots vs. 19 plots in the K survey), indicating decreased species diversity over time. The average number of species per plot decreased from 32.43 ± 4.58 in the B survey to 14.68 ± 5.99 in the K survey (Fig. 1b), giving further support for the possible loss of diversity over time.

Effect of mowing

Resumption of mowing led to a significant change in plant species composition. Areas that were not mown (= abandoned) were dominated by hemicryptophytic species (*Carex acuta*), species that had greater cover in the K survey compared to the B survey (*Phragmites australis*) or were absent in the earlier B survey (*Calamagrostis canescens*, *Glyceria maxima*, *Iris pseudacorus*). These species form a group on the right side of the first RDA axis (Fig. 2). Another group of species was connected to areas mown in all four years. This group is in the upper center of the RDA diagram (Fig. 2) and includes several species that were common in the B survey, including *Alopecurus pratensis*, *Lychnis flos-cuculi*, *Poa pratensis*, *P. trivialis,* and *Trifolium repens*.

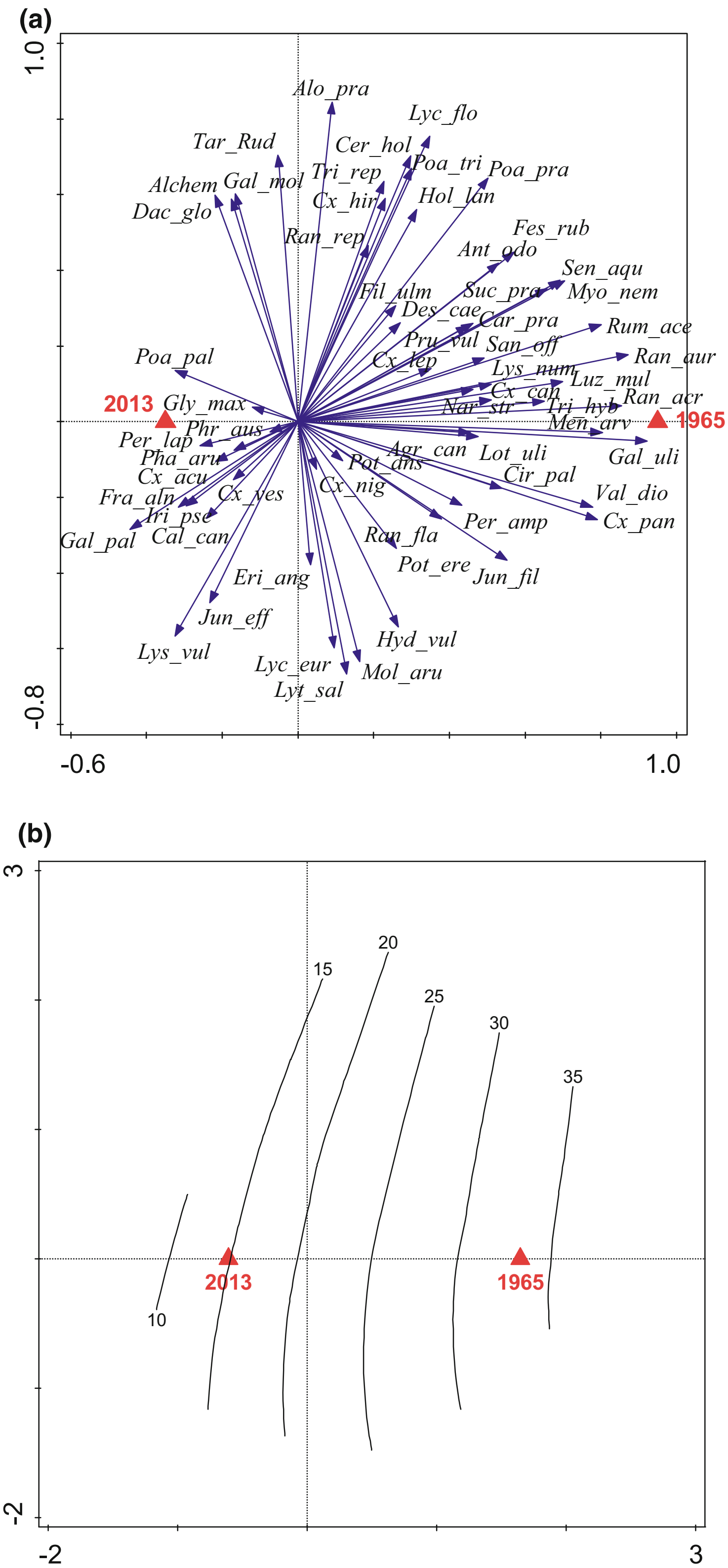
The average number of species per plot significantly increased with mowing frequency (oneway ANOVA; $F = 46.92$; $p < 0.001$), from 7.50 ± 3.32 in unmown plots to 32.43 ± 4.58 in the B survey plots (Fig. 3). The species number in the K survey plots mown in all four years was significantly greater than in the unmown and less-frequently mown plots, but was still significantly less than in the B survey. More frequent mowing seemed to result in a species composition approaching, although not equivalent to, that of the B survey plots, as shown by the NMS analysis (Fig. 4). The K survey plots were separated by increasing mowing frequency along axis 1, which explained 18.3% of the variance. The higher covers of *Alchemilla* sp., *Alopecurus pratensis*, and *Dactylis glomerata* led to the separation of the B survey plots from the K survey plots mown in all four years along axis 2 (explained variation = 13.1%).

Indicator valuation

The species from the B and K surveys ranged from those associated with moist and low-nutrient conditions to those usually found in aquatic and eutrophic conditions (Table 1). Overall, the relative moisture (EIV M) and nutrient (EIV N) values were similar for the B and K surveys. However, more detailed analyses indicated that the wet grassland had greater moisture and nutrient levels in 2013 compared to 1965. There was a significant decrease in the proportion of species indicative of moist habitats (EIV M of 5–7), while there was no change for species indicative of aquatic habitats (EIV $M > 8$). Likewise, the proportion of plant species indicating low N levels (EIV N of 2–3) decreased, although this was a weak relationship (Table 1). Species which grow in nutrient-rich conditions (EIV N of 7–9) had greater cover in 2013 than in 1965, although again the relationship was weak at best ($p = 0.099$).

Plant nutrient content

There was little change in leaf C% between the mature and senescent leaves of *C. acuta* (44.62 and 44.72, respectively), while N% significantly decreased over time (2.33% and 0.68% for mature and senesced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Tri_rep
Alchem
Gal_mol
Cx_hir
Hol_lan
Dac_glo
Ran_rep
Fes_rub
Ant_odo
Sen_aqu
Fil_ulm
Suc_pra
Myo_nem
Des_cae
Car_pra
Rum_ace
Pru_vul
San_off
Poa_pal
Cx_lep
Ran_aur
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Cx_nig
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Cx_ves
Fra_aln
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Cx_pan
Gal_pal
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Jun_fil
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(b)
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-2
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25
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35
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2013
1965

◀**Fig. 1** **a** Ordination biplot of plant species centroids that were present in phytocenological releves from Záblatské Louky both in 1965 (Blažková 1973, 7 plots) and 2013 (19 plots). Direct gradient analysis (RDA) shows the position of the temporal variable (1965, 2013), which explained 17.2% of species variance (pseudo-$F = 5.0$, $p < 0.001$, 999 permutations). Species abbreviations: *Agrostis canina* Agr_can, *Alchemilla* sp. Alchem, *Alopecurus pratensis* Alo_pra, *Anthoxanthum odoratum* Ant_odo, *Calamagrostis canescens* Cal_can, *Cardamine pratensis* Car_pra, *Carex acuta* Cx_acu, *C. canescens* Cx_can, *C. hirta* Cx_hir, *C. leporina* Cx_lep, *C. nigra* Cx_nig, *C. panicea* Cx_pan, *C. vesicaria* Cx_ves, *Cerastium holosteoides* Cer_hol, *Cirsium palustre* Cir_pal, *Dactylis glomerata* Dac_glo, *Deschampsia caespitosa* Des_cae, *Eriophorum angustifolium* Eri_ang, *Festuca rubra* agg.Fes_rub, *Filipendula ulmaria* Fil_ulm, *Frangula alnus* juv.Fra_aln, *Galium mollugo* Gal_mol, *Galium palustre* Gal_pal, *Galium uliginosum* Gal_uli, *Glyceria maxima* Gly_max, *Holcus lanatus* Hol_lan, *Hydrocotyle vulgaris* Hyd_vul, *Iris pseudacorus* Iri_pse, *Juncus effusus* Jun_eff, *Juncus filiformis* Jun_fil, *Lotus pedunculatus* Lot_uli, *Luzula multiflora* Luz_mul, *Lychnis flos-cuculi* Lyc_flo, *Lycopus europaeus* Lyc_eur, *Lysimachia nummularia* Lys_num, *Lysimachia vulgaris* Lys_vul, *Lythrum salicaria* Lyt_sal, *Mentha arvensis* Men_arv, *Molinia caerulea* Mol_aru, *Myosotis nemorosa* Myo_nem, *Nardus stricta* Nar_str, *Persicaria amphibia* Per_amp, *Persicaria lapathifolia* Per_lap, *Phalaris arundinacea* Pha_aru, *Phragmites australis* Phr_aus, *Poa palustris* Poa_pal, *P. pratensis* Poa_pra, *P. trivialis* Poa_tri, *Potentilla anserina* Pot_ans, *P. erecta* Pot_ere, *Prunella vulgaris* Pru_vul, *Ranunculus acris* Ran_acr, *R. auricomus* agg. Ran_aur, *R. flammula* Ran_fla, *R. repens* Ran_rep, *Rumex acetosa* Rum_ace, *Sanguisorba officinalis* San_off, *Senecio aquaticus* Sen_aqu, *Succisa pratensis* Suc_pra, *Taraxacum* sect. *Ruderalia* Tar_Rud, *Trifolium hybridum* Tri_hyb, *T. repens* Tri_rep, *Valeriana dioica* Val_dio. **b** Species richness of relevés plotted in the RDA diagram. The contours indicate a smoothed estimation of the count of species within samples along the temporal gradient on the first axis

leaves, respectively). This represented a loss of 70.8% of leaf N with most of that being due to resorption (resorption efficiency, RE = 64.2%). The decrease in leaf N% led to a significant increase in the C:N ratio, from 19.37 to 66.84 (T test, $p < 0.001$) for mature and senesced leaves, respectively. There was also a high amount of phenolics (21.08%) in the leaf tissue.

Under the current situation found in this wet grassland, the belowground plant structures were also of low quality. The C% was similar to that found in the aboveground structures (41.80–44.62, respectively), but with low N and P percentages (0.79 and 0.10, respectively). These resulted in large stoichiometric ratios (C:N = 54.96; C:P = 430.12; N:P = 7.76) which are indicative of nutrient-poor conditions.

Discussion

Wet grassland structure and functions are greatly affected by the type of management applied. In our site, the formerly *Molinia caerulea*-dominated, more diverse wet grassland has been replaced by a less-diverse system with a greater cover of clonal hemicryptophytes (Klimeš and Klimešová 2002; Kulik 2014). Similar changes to *M. caerulea*-dominated wet grasslands have been seen in other parts of central Europe, including the Czech Republic (Hájek and Poláková 2010) as well as Poland (Kącki and Michalska-Hejduk 2010; Kulik 2014) and Slovenia (Zelnik 2005).

The noted changes in species abundances in general coincided with the application of a more extensive management regime of no nutrient additions and only one cut per growing season. This is contrary to what would be expected with the use of more traditional management methods. Traditional management regimes in grasslands tend to result in habitats with greater plant species diversity compared to areas that have been subjected to changed management regimes, either agricultural intensification or land abandonment (Hájek and Poláková 2010). That is why extensive management is the recommended treatment for either maintaining more diverse *M. caerulea*-dominated wet grasslands in oligotrophic habitats or controlling expansive populations of *M. caerulea* in nutrient-enriched sites (Taylor et al. 2001; Hejcman et al. 2010). However, a return to a more intensive cutting regime, as recommended by Hájková et al. (2009), may aid in beginning to restore a more diverse wet grassland on our site. This recommendation is supported by the results of the mowing experiment in that the species composition has become more similar to that of the previously more diverse *Molinia caerulea*-dominated grassland with increased mowing frequency. Such a rapid return to a desired pre-existing state is similar to that found in other wet grassland restoration studies (see Table 4 in Joyce 2014). However, complete equivalency has not yet occurred, similar to other wet grassland restorations that have been limited or restricted in attaining complete restoration (Berg et al. 2012; Joyce 2014). In our site, the presence of *Carex acuta*, for example, may hinder complete attainment of the previous state since this species allocates a large proportion of its total biomass to belowground structures and thus could readily re-

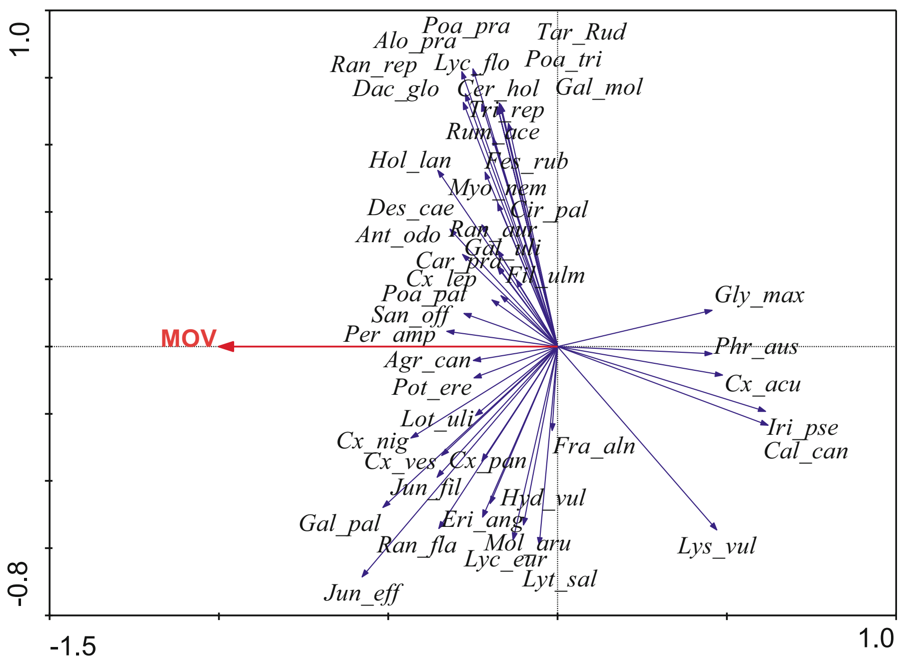

Fig. 2 Ordination biplot (RDA) of plant species present in phytocenological relevés from Záblatské Louky subject to different mowing regimes. Mowing occurred in 2003, 2006, 2009, and 2013. Information from aerial photographs allowed for determining whether specific quadrats in the K survey were never mown or mown in two of the years or in all four years. Axis 1, which accounted for 13.4% of the explained variation in the data (pseudo-F = 2.62; $p = 0.025$), shows the effect of mowing intensity (MOV) on percent cover. See Fig. 1 and Supplemental Table 1 for species names and abbreviations

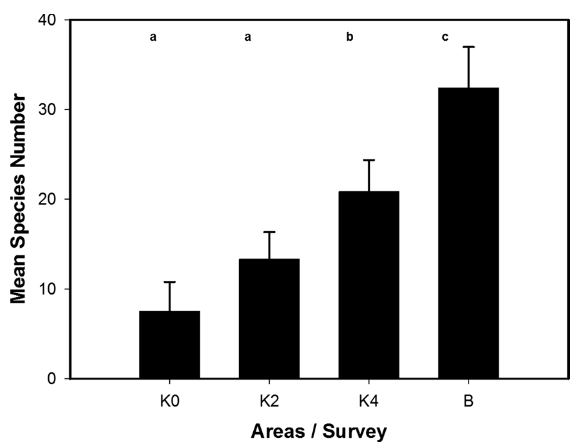

Fig. 3 Species number (mean ± 1 SD) for plots from the 2013 (K) vegetation survey included in a mowing experiment and the earlier 1965 (B) survey for comparison. Based on aerial photographs, portions of the Záblatské Louky wet grassland were mown in 2003, 2006, 2009, and 2013. Particular plots in the K survey were either unmown (K0, $n = 4$), mown only in 2003 and 2006 (K2, $n = 6$), or mown in all four years (K4, $n = 6$). Different letters for the K mowing treatment and the B survey plots ($n = 7$) represent significant differences in mean species number ($\alpha = 0.05$) based on results from a oneway ANOVA test

sprout after cutting due to large carbon storage reserves (Edwards et al. 2015). In that case, some sort of soil disturbance, such as sod cutting, may be necessary to reduce *C. acuta* cover (Gaertner et al. 2010; Berg et al. 2012). Further studies are needed to determine under what conditions mowing alone can reduce the cover of hemicryptophyte species in attempting to restore more diverse wet grasslands.

The reduced cover of moist species (EIV M = 5–7) and increased cover of species associated more with wetter, aquatic habitats (EIV $M > 8$), especially *C. acuta* and *C. vesicaria*, whose growth strategy could result in changed nutrient turnover rates as well as affecting other ecosystem processes (Kaštovská et al. 2015). Unfortunately, nutrient contents were not measured for this site in neither the 1965 nor 2013 samplings. We therefore used data from published studies on *M. caerulea* growing in nutrient-poor habitats similar to our site, as well as results on the nutrient content of *C. acuta* plants growing in a nearby site (see Edwards et al. 2015; Edwards 2015) to show the possible impacts of changing plant nutrient contents on ecosystem processes.

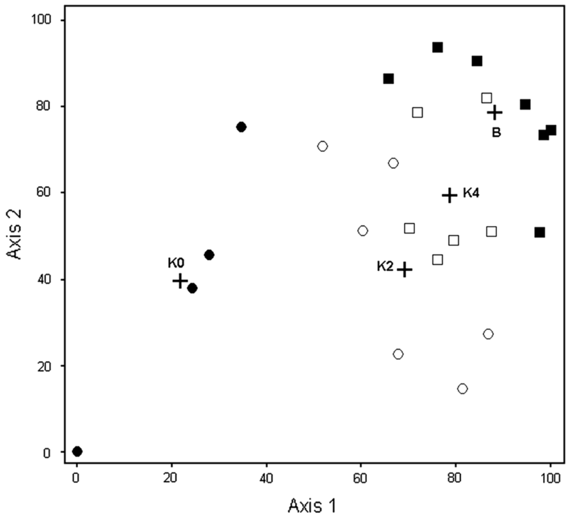

Fig. 4 Non-metric multidimensional scaling (NMS) biplot of the species composition from the 2013 (K) survey showing the centroids and plots which were subject to different mowing regimes. Based on aerial photographs, portions of the Záblatské Louky wet grassland were mown in 2003, 2006, 2009, and 2013. Particular plots in the K survey were either unmown (K0—closed circles), mown only in 2003 and 2006 (K2—open circles), or mown in all four years (K4—open squares). The species composition of these plots were compared to that of the earlier 1965 vegetation survey of Blažková (1973; B—closed squares). Axis 1 accounted for 18.3% of the variation in the data while axis 2 explained 13.1% of data variation. Final stress = 11.09

Table 1 Comparison of Ellenberg indicator values for moisture (M) and nutrient (N) analyzed using the Wilcoxon sign test for the plant species found in the Blažková (B) and Kučera (K) relevés in the same area of the Záblatské Louky wet grassland

	B	K	*z*	*p*
M All	37	26	− 1.068	0.286
5–7	22	11	− 2.260	0.024
8–10	15	15	0.607	0.544
N All	37	26	− 1.006	0.314
2–3	14	5	− 1.730	0.084
4–6	21	11	− 1.365	0.172
7–9	2	10	1.647	0.099

Numbers for each relevé indicate the number of species which had larger relative indicator values compared to the other relevé. See text for explanation of how the relative indicator values were calculated. Indicator values: M: 5–7 = moist to wet/8–10 = wet to aquatic; N: 2–3 = low N/4–6 = medium N/7–9 = high N

Our site is a wet grassland growing on nutrient-poor peat soil. Under similar habitat conditions in the Netherlands, the N content of *M. caerulea* leaf litter was 0.87% (van Vuuren et al. 1993), which is larger than that found in senesced leaves of the *C. acuta* plants growing in our site (N content = 0.68%). Both species had similar C% resulting in the C:N ratio being smaller for the *M. caerulea* plants compared to the *C. acuta* plants from our site (53.9 to 66.8, respectively). Additionally, in a greenhouse study, Thornton et al (1999) found leaf N% to be about 1% in senesced leaves of *M. caerulea* grown under low-N conditions.

Likewise, *M. caerulea* root litter growing in a nutrient-poor wet heathland had a N content of 1.7% (Aerts 1993), which is double that for dead roots of *C. acuta* from our site (*N* = 0.85%). Phosphorus levels were similar for both species, being 0.033 and 0.048% for *M. caerulea* and *C. acuta*, respectively. The greater N content found in *M. caerulea* root litter is at least partly due to the greater resorption efficiency (RE) of this species, which can be up to 85% of foliar N (van Heerwaarden et al. 2005), compared to an RE_N of about 64% for the *C. acuta* plants from our site. It is therefore likely that *M. caerulea* root litter in our site had a lower C:N ratio compared to the roots of *C. acuta*. The lower C:N ratios indicate that the *M. caerulea* plants had better quality litter, which would decompose faster with higher nutrient release rates compared to *C. acuta*.

Such differences due to changes in species composition were noted by van Vuuren et al (1993) when comparing the decomposition rates of *M. caerulea* and *Erica tetralix* in a nutrient-poor wet heathland. In that case, the shoot litter decomposition rate of *M. caerulea* was double that of *E. tetralix*, while the roots of *M. caerulea* decomposed ten times faster than for *E. tetralix*. As with *C. acuta* in our site, the *E. tetralix* litter in the study of van Vuuren et al (1993) had lower N and P, but higher lignin concentrations than *M. caerulea*. Under such conditions, *M. caerulea* produces more aboveground litter, but a comparative amount of belowground litter, than *C. acuta* in our site (see Aerts 1993 for *M. caerulea* and Picek et al 2008; Edwards et al. 2015 for *C. acuta*); thus, the expected faster decomposition rates of the *M. caerulea* structures will result in a larger nutrient input to the soil from litter decomposition. Such an increased soil priming effect would lead to faster soil mineralization rates and lower soil organic matter (SOM) content in areas dominated by *M. caerulea* (Kaštovská et al. 2015).

Ecosystem services

The application of a less-intensive management regime in our site likely led to a change in the ecosystem services provided by the wet grassland. The cover of *C. acuta* and other such species have increased in the current state of the wet grassland. Such species are representative of the conservative plant functional type in that they tend to grow in nutrient-poor habitats and have lower photosynthesis and nutrient uptake rates resulting in the slower growth of nutrient-poorer tissues compared to more competitive species (De Deyn 2017). The reduced tissue nutrient contents result in slower litter decomposition rates with concomitant slower nutrient turnover rates (Kaštovská et al. 2015). Thus, the value of supporting ecosystem services, such as C and nutrient sequestration, are enhanced in the present state of the wetland (Quin et al. 2014). However, resumption of the traditional management regime, with 2–3 cuts per year, could result in the restoration of a more diverse, *M. caerulea*-dominated state, with the likely reduction in that particular supporting service, with its attendant connected services, in favor of services accruing from greater diversity. There is growing agreement that increased species diversity has a positive effect on the provision of ecosystem services. For example, increased species richness in meadows had a positive impact on the number of pollinators (regulating service) as well as increasing cultural services such as aesthetics because of the greater diversity in flower color (Fontana et al. 2014). It is therefore a question for managers which services are to be made the priority (Sanon et al. 2012; Daw et al. 2015; Deng et al. 2016).

The possible presence of each state depends not only on the management regime applied locally to the particular wet grassland, but is affected by events occurring at the regional scale of the landscape (see for example Verhagen et al. 2018; Duarte et al. 2018; Rodriguez-Echeverry et al. 2018). The increase in the cover of plant species indicating wetter, more aquatic conditions implies that the site has become more moist over time. This could be due either to changed weather patterns, management decisions, or a combination of the two. Analysis of monthly precipitation data for the South Bohemian region of the Czech Republic (data acquired from the Czech Hydrometeorological Institute) using the Wilcoxon sign test showed that precipitation amounts during the growing season (April–September) did not differ ($z = -0.327$; $p = 0.744$) for the periods of the B (1963–1965) and K (2011–2013) surveys. Therefore, the wetter site conditions are likely due more to management actions occurring at both the local (maintenance of drainage ditches) and regional (manipulation of fishpond hydrology) scales than any changes in the precipitation patterns. Such regional-scale properties would then limit the number of possible states for this wet grassland, with the present *C. acuta*-dominated state favored over the alternate *M. caerulea*-dominated system. Restoration of a higher diversity system would then require changes at the regional scale first (Verhagen et al. 2018). Only then would a different management regime at the local scale have a greater chance of successfully producing the preferred state (Power 2010; Deng et al. 2016).

Conclusions

Here, we showed that changes in management regime resulted in the wet grassland changing from a species-rich complex of meadows, dominated by *M. caerulea*, to one dominated by more conservative species, such as *C. acuta* (see Kaštovská et al. 2015; Edwards et al. 2015). These changes likely led to ecosystem processes (litter decomposition, nutrient turnover) occurring at different rates than when the site was a more diverse system. These changes also likely affected the value of different ecosystem services, with some being enhanced while the importance of others decreased. Such tradeoffs in ecosystem services need to be taken into account when deciding whether to restore *M. caerulea*-dominated wet grasslands.

While our mowing experiment indicates that partial restoration of the former grassland condition may be possible, complete restoration may also require some sort of soil disturbance as well as the emergence of slightly drier conditions, due to changed hydrological manipulation at the regional scale. Future studies will be required to determine how these two factors, operating at different scales, interact in affecting the plant community composition as well as the provision of possible ecosystem services.

Acknowledgements This paper is dedicated to the memories of Dagmar Dykyjová and Stěpan Husak, both of whom did so much to further our knowledge and appreciation of wetlands. We thank Ville Närhi for his great help as well as members of the Třeboň Basin Biosphere Reserve. Nutrient analyses were conducted by Daniel Vaňek. The study was supported by Grants from the Grant Agency of the Czech Republic (GACR: 526/09/1545) and the Grant Agency of the University of South Bohemia (GAJU: 143/2010/P).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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