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Nutrient patches are transient and unpredictable in an unproductive mountain grassland

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Abstract While plant roots respond consistently to nutrient availability under experimental conditions, our understanding of the role of such response in the field is hindered by poor knowledge of size and duration of nutrient patches there. In particular, knowledge of patch duration is critically important for understanding types of root response. We determined spatial and temporal variations in phosphate-P, nitrate-N and ammonium-N concentrations, and pH in an unproductive mountain meadow for which extensive data on fine-scale root distribution exist. We sampled soil solution weekly over 2.5 growing seasons using suction cups to in a hierarchical spatial design with the smallest grain of 3.3 cm. Overall concentrations of all studied nutrients were fairly low with occasional and short-term, but large-in-magnitude peaks, with no pronounced spatial or temporal structure at any scale. Temporal variation was much stronger than spatial variation, with both interannual differences and within-season differences playing a role. Phosphate-P was consistently highest in spring, whereas ammonium-N increased during summers. The ammonium-N, the major nitrogen source at the site, was negatively correlated with phosphate-P. Our data suggest that repeated sampling of soil solution in fixed positions is necessary to cover the entire extent of nutrient variation in the field. It shows that there are no stable nutrient patches at the fine scale, and the duration and size of nutrient patches are smaller than usual growth responses of roots. This implies that under such conditions, the best rooting strategy is homogeneous space occupation linked with fast

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physiological response to varying nutrient concentrations.

Introduction

Physical, chemical and biological parameters of soils are extremely heterogeneous over a number of scales (Stark 1994). This heterogeneity plays a key role in determining the spatial structure and physiological activity of roots. Plant roots proliferate at sites enriched by nutrients, change their morphology or topology and/or increase their uptake capacity (Robinson 1994; Hodge 2004). This foraging behaviour can be adaptive if it enables plants to efficiently use soil resources even from enrichments smaller than the size or shorter than the life-time of the root systems of single plant individuals (Kesser et al. 2016). However, proper understanding of the potential of such adaptive responses requires knowledge of the fine-scale distribution of soil resources in the environment where the foraging occurs (Hodge 2006, 2009; Cahill and McNickle 2011).

Conceptually, the costs and benefits of foraging are determined by size, duration and intensity of resource patches in the soil (Fitter 1994; Stuefer 1996; Hutchings et al. 2003; Hodge 2006; McNickle et al. 2009; McNickle and Cahill 2009). In particular, the benefits of root proliferation in resource patches increase with their duration (Kembel and Cahill 2005), because the growth response is rather slow compared to the rapid changes in root's physiology (Van Vuuren et al. 1996). Significance of these patch attributes has been examined experimentally (Lamb et al. 2012; Zhou et al. 2012; García-Palacios et al. 2013; Li et al. 2014, see also Hutchings et al. 2003 and Hodge 2004 for partial reviews of earlier research) showing, for example, that the change in duration of an artificially created nutrient pulse can reverse the growth rates of two grasses (Campbell and Grime 1989). Similar differences affect the performance of plants in competitive environments (Novoplansky and Goldberg 2001; Gebauer et al. 2002; Parepa et al. 2013; Mommer et al. 2012).

Assessing the ecological relevance of root responses critically depends on the knowledge of the distribution of soil resources in the field. Fairly extensive data exist on spatial variation in soil nutrients (Jackson and Caldwell 1993; Gross et al. 1995; Gallardo and Paramá 2007; Hirobe et al. 2013; Inoue et al. 2017; Kreuzeder et al. 2018), which is often finer than the extent of the root system of single plants (Farley and Fitter 1999; Gallardo and Paramá 2007; Zhou et al. 2008; Kreuzeder et al. 2018).

Temporal heterogeneity of nutrient availability is known for much larger scales (see e.g. Cain et al. 1999; Guo et al. 2004), but longitudinal data at fine scales are essentially lacking (but see e.g. Ryel et al. 1996; Farley and Fitter 1999), which makes assessment of ecological relevance of spatial heterogeneity difficult. However, we do know that the amount of macro-nutrients in artificially created nutrient patches in controlled experiments usually drops to background values within several weeks (Lamb et al. 2004) or even days (Van Vuuren et al. 1996; Fransen et al. 1999) after their establishment. This indicates that nutrient turnover in the field may be also quite rapid. Surprisingly, only a very few studies have so far assessed realistic nutrient dynamics at a comparably fine temporal scale (Ball and Williams 1968; Vincent 1970; Farley and Fitter 1999). In addition, to the best of our knowledge, only one study observed both spatial and temporal fine-scale heterogenities of soil resources in the field at one place for more than one season (Farley and Fitter 1999) and thus gave a complex overview of distribution of soil resources "from the plant's eye". Such data are necessary to understand root responses to nutrient heterogeneity existing under field conditions (Hinsinger et al. 2005; Felderer et al. 2013).

The aim of the present study was therefore to identify and analyse the availability of phosphorus and nitrogen in a mountain temperate grassland at spatial and temporal scales perceivable by root systems of single plant individuals. We chose unproductive grasslands as systems where competition for nutrients is likely to be intense and therefore their heterogeneity in the soil to be highly important. We also made use of the fact that this and nearby meadows had been extensively studied and we possessed good knowledge of root fine-scale distribution, including species-specific data (Pecháčková et al. 1999, 2003; Herben et al. 2018). Our specific aim was to determine the

amount and spatial/temporal pattern of variation in the availability of nutrients at several scales to determine size, duration and intensity of nutrient patches in the soil. This will permit comparison of these parameters to scale of root responses known from the literature, and to spatial structure of root systems known from the site. It will also make possible to assess relevance of artificially created heterogeneity of nutrient concentrations in ecological experiments.

We sampled soil solution for 2.5 growing seasons in spatially hierarchical design with spatial and temporal grains of 3.3 cm and 1 week, respectively, by means of suction cups. Each sample of the soil solution was analysed for pH, nitrate-N, ammonium-N and phosphate-P concentrations. For each of these nutrients, we separated spatial and temporal sources of variation and linked them to the changes in the soil solution volume. Three years of observations allowed us to separate the within-year and between-year temporal variations and examine the predictability of the temporal variation within a season.

Methods

Study site

The study site was located in a mountain grassland in the Krkonoše Mts., in the northern part of the Czech Republic (Braunovy louky, ca. 4 km ESE of Pec pod Sněžkou, latitude 50°41′28″N, longitude 15°47′35″E, 895 m a.s.l.). The mean temperature of the study area in the warmest and coldest months (July and January) is 15.0 °C and − 4.0 °C (2002–2012) at the nearby meteorological station (Pec pod Sněžkou, ca. 816 m a.s.l.). Mean annual precipitation is 1289 mm. The growing season is from mid-April after snow-melt until November; the total number of days with snow per year in the study period ranged from 137 to 182. The soil at the site is a Cambisol, and the bedrock is composed of phyllites and mica schists. There is a gradual increase in the frequency of stones up to a depth of 20 cm. Root density decreases with depth, with most roots not extending deeper than 12 cm (Pecháčková, unpubl. data).

The studied grassland has been maintained by summer mowing; the last major manuring episode was around 1955. The average vegetation height is 15–20 cm, and its productivity is low, not exceeding

800 kg ha^{-1} (dry matter) (Hadincová et al. 1997). The vegetation of the site is species poor, homogeneously covering the whole area of the studied grassland. The dominant plant species—*Nardus stricta* L. (cca 80% of cover)—indicates low productivity of a site. The dominant species is accompanied by three other principal species: *Anthoxanthum alpinum* Á. Löve and D. Löve, *Avenella flexuosa* (L.) Drejer and *Festuca rubra* L. The vegetation can be assigned to the Sileno vulgaris-Nardetum strictae (*Nardo-Agrostion*) type (Chytrý [ed.] 2007).

Data collection and treatment

Soil solution was collected using suction cups composed of two parts—a ceramic tube (5 mm long, 1 mm diameter) for soil solution extraction that was glued to polyetheretherketone (PEEK) tubing using two-component cement. The ceramic tube was made of Al_2O_3 with a porosity of 48% and maximum pore dimensions of 1 μm (KPM, Berlin). Its tip was sealed by melting with glass over a Bunsen burner (in accordance with instructions in Göttlein et al. 1996 and Göttlein pers. comm.). The tubing was 4 or 10 cm long (depending on the depth of installation of the ceramic tube) and 2 mm in diameter. Each suction cup was connected by means of additional silicone tubing to a collecting bottle with a vacuum maintained at approx. 50 kPa.

The suction cups were inserted into six parallel transects. The transects were 1 m apart with the two most distant transects 5 m from each other (Fig. 1). Each transect was composed of 10 suction cups 3.3 cm apart (60 suction cups in total). The distance was sufficiently small to show nutrient variation within the spatial range of the root system of individual plants at the site (see Pecháčková et al. 1999, 2003) and at the same time it allowed independent activity of the suction cups (tested in a pilot study by measuring sulphates in soil solution sampled by suction cups at various distances from the point of artificial injection). The cups were inserted into two soil depths: 4–5 cm and 10–12 cm. These depths reflect zones with considerably different root densities (Pecháčková, unpubl. data). All the suction cups in one transect were inserted into one soil depth; transects with suction cups at different depths were located in an alternated fashion.

The collections were carried out in one-week intervals. The cups were set immediately after the
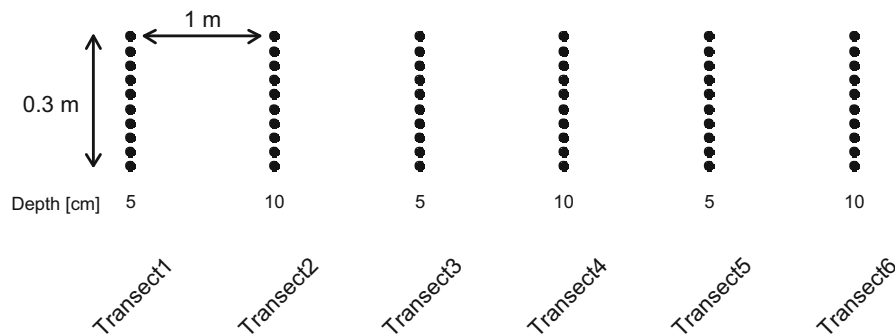
Fig. 1 Scheme of spatial arrangement of the suction cups (black points) at the study site. Suction cups in transects 1, 3 and 5 were installed into 4–5 cm depth, and suction cups in transects 2, 4 and 6 were installed into 10–12 cm depth. Note that horizontal and vertical distances are not drawn to scale (see the arrow labels)

snow melted in 2002 (beginning of May), 2003 (mid April) and 2004 (end of April) and kept until the first snowfalls of 2002 (end of October) and 2003 (end of September), and until summer of 2004 (beginning of July) resulting in a total of 53 collection weeks.

The sampling period covered the major part of the growing season with characteristic courses of temperature, covering both the spring increase and decline in the autumn. Spring 2002 was warmer compared to the other 2 years, but with more abundant precipitation (Electronic Supplemental Material S1). In 2003, there was a pronounced decline in precipitation in May and June with an increase in temperature, resulting in a pronounced drought associated with the decline of total water volume collected (Electronic Supplemental Material S2), returning to higher values only at the very end of the measurement period in that year. In contrast, there was only a slow decline in the collected soil solution during the 2002 and 2004 seasons.

After each sampling, we poured the solution from the collection bottles into transfer boxes. We then washed out the collecting bottles with distilled water and dropped a small amount of methanol into each bottle to conserve the subsequently collected solution. Finally, we re-established the under-pressure in each of the collecting bottles. The bottles were inserted into aluminium foil to minimize the effect of heating on the collected solution. The samples were frozen within a few hours after collection. Then, the samples were transported to the analytical laboratory of the Institute of Botany AS CR in Třeboň where chemical analyses were performed. First, total volume and pH were determined in each sample. Then, nitrate-N, ammonium-N and phosphate-P concentrations were measured using flow injection analysis (FIA STAR, Foss Tecator A/S). Limits of detection of the analyses (hereafter LODs) were calculated as 0.168 mg/l, 0.095 mg/l and 0.013 mg/l for nitrate-N, ammonium-N and phosphate-P, respectively, in accordance with the methodological approach suggested by Hibbert and Gooding (2006).

Due to the many cases of limited sample volumes, the concentrations of all three nutrients were measured only in a subset of samples (1820 out of the theoretical total of 3180); measurements for at least one nutrient were available for an additional 47 samples. If the volume of the sampled liquid was too low, samples were diluted by distilled water (in 1085 out of 1867 measured samples). Dilution factors were chosen as the minimum dilution that yielded the volume required for the analysis; the most common dilution factors were 2, 3, 5 and 10.

All concentration values detected in undiluted samples, including values between 0 and the respective LOD were retained in the analyses. However, measured concentrations sometimes fell below the LOD values as a consequence of dilution. In these cases, we retained values that remained below the LOD after recalculation to undiluted concentrations. In contrast, values that were lower than the LOD when measured in the diluted samples, but upon recalculation to undiluted concentrations yielded values higher than the LOD, were excluded as unreliable. The excluded values represented 5, 184 and 202 values for nitrate-N, ammonium-N and phosphate-P, respectively (i.e. 0.3, 9.9 and 10.9% of the available measurements of each nutrient). Values above LOD measured in diluted samples were retained (after

recalculation) in all cases. This yielded a dataset with 1510 complete measurements of all three nutrients and 1866 cases in which at least one nutrient was measured.

Data analysis

Data on the chemical parameters were analysed using mixed linear models. All chemical parameters except pH were log-transformed before analysis. First, we assessed the relative contributions to overall variation in the dataset by fitting a full mixed model with year, week, transect, depth (nested in transect) and position (nested in each transect) as random factors. As depth was consistently noninformative using Akaike information criterion (AIC), we excluded it from all subsequent analyses. The model was fit using restricted maximum likelihood by the function lmer in the package lme4 version 1.1-11 (Bates et al. 2015) as we needed to estimate variation due to crossed random factors (time and space). The components of variation (with depth excluded) were assessed using variances of individual random effects.

Further, we examined the systematic effects of year, week, and their interaction by taking the third-order polynomial of week as a quantitative (fixed) predictor, and year as a fixed factor, with volume and depth as additional fixed covariates, and with spatial components (transect and position within it) as random factors. The third order polynomial of week was used to account for potential nonlinearity and asymmetry of the time course of individual chemical parameters throughout the seasons; pilot analyses showed increased predictive power (assessed by AIC) compared to second-order polynomials. The model was fitted using the function lme from the package nlme (Pinheiro et al. 2016) and the minimum adequate model was identified using a stepwise procedure with AIC from the function stepAIC. Significance of individual fixed terms of the resulting model was assessed by comparing models fitted by ML with and without that term included. The final model was fitted using REML and its predictive power (of fixed factors only, i.e. using marginal R^2) was assessed following Johnson (2014). We also used the final model to calculate the time course of the predicted values of all four chemical parameters during the season. These were calculated for each year separately, but averaged over values of depth, volume, and the random factors

(transect and position). These values were backtransformed to their original scale by taking antilogarithms for nitrate-N, ammonium-N and phosphate-P. For term selection and testing, the models were fitted using maximum likelihood (ML); restricted maximum likelihood (REML) was used for the final fit and calculation of the predicted values.

Spatial and temporal autocorrelations were calculated using the function acf (R Core Team 2014). Temporal correlations were calculated for each position and within each year separately. Mean and lower and upper 95% quantiles of these data were reported. Similarly, spatial correlations were calculated separately for each observation date for each set of 10 positions within each transect, and the mean and 95% quantiles were calculated from them.

We further explored interrelationships among the chemical parameters using multivariate techniques. First, we used PCA on standardized log-transformed variables to display relationships among the chemical parameters. We used redundancy analysis (RDA) to show the effect of volume and week on how these relationships change through time. Only complete cases (1281 samples out of 3180) were used in the multivariate analyses. All multivariate analyses were performed using package vegan ver. 2.3-3 (Oksanen et al. 2016).

Results

Mean and median concentrations of ammonium-N were almost one order of magnitude higher than concentrations of nitrate-N (Table 1). Concentrations of phosphate-P were lower than nitrate-N. Mean pH in the soil solution was 5.2 (Table 1). All measured parameters except pH showed highly skewed distributions (Table 1, Fig. S3 in the Electronic supplemental material).

The analysis of variance components showed the dominant effect of year in the variation of all four chemical parameters (Fig. 2). The additive effect of year explained more than 50% of all explained variation for ammonium-N, phosphate-P and pH. Moreover, its interaction with week (i.e. differences in seasonal course of chemical parameters among years) explained an additional 20% of the explained variation in ammonium-N and pH, about 35% in phosphate-P and about 60% in nitrate-N. The net

Table 1 Descriptive statistics of volume and chemical parameters

	Mean	Quantiles					Maximum
		5%	25%	50%	75%	95%	
Volume (ml)	5.01	0.3	1.3	3.2	6.7	17.4	30
Nitrate-N (mg/l)	0.034	0.007	0.013	0.021	0.034	0.082	1.257
Ammonium-N (mg/l)	0.506	0.018	0.057	0.193	0.677	1.965	6.32
Phosphate-P (µg/l)	26.97	0.39	2.9	9.8	19.5	64.7	3200
pH	5.189	3.93	4.77	5.32	5.67	6.11	6.97
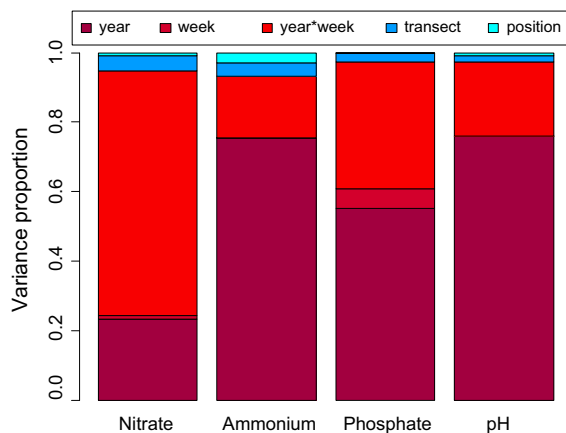
Fig. 2 Components of the variance of the soil solution chemical parameters (normalized to sum to one). Red hues indicate temporal components, blue hues spatial components. For additional details, see the "Methods"

effect of week (i.e. the systematic effect of season independent of year) was negligible except for phosphate-P, where it accounted for 10% of the explained variance.

The role of the spatial components of variation (transect and position) relative to the temporal components was minor, never accounting for more than 5% of the total explained variation (20% if the effect of year was not taken into account, with the exception of nitrate-N where the spatial component reached 30%). However, the role of fine-scale variation at the scale of centimetres (position) was comparable to the large-scale variation at the scale of metres (transect) explaining up to 40% of the spatial component of variation (lowest in phosphorus-P, and highest in pH and ammonium-N; Fig. 2, lower pane).

Overall fit of the model was high for ammonium-N and pH, lower for phosphate-P, and very poor for nitrate-N (Table 2). Fitting models with week as a quantitative predictor showed highly significant effects of higher order terms, indicating strong

nonlinearity in the seasonal change of all four chemical parameters (Table 2). Further, the time course of all four chemical parameters differed among individual years; the interaction of year with the second power term of week was significant in three chemical parameters (except pH), while interaction with the third power was significant in all parameters (Table 2, Fig. 3; see also Fig. S4 in the Electronic supplemental material). The effect of depth was negligible (Table 2). The effect of volume was significant for nitrate-N and ammonium-N (negative), but only marginally significant for phosphate-P (positive).

Phosphate-P typically declined during the season in a nonlinear manner (convex—the coefficient of the second power term was positive), with an additional increase in late season of 2003. In contrast, ammonium-N tended to increase through the season, although the peak's increase occurred in different months in different years. There was an additional decline later in the 2002 season. The dynamics of nitrate-N were most strongly year dependent with essentially no clear trends common to all seasons and overall low predictive power of the model compared to the other chemical parameters of the soil solution (Fig. 3).

Temporal and spatial autocorrelations of all chemical parameters were weak (Fig. 4). pH and ammonium-N showed a significant mean correlation over one week, with a subsequent decline below zero; no positive correlation of subsequent samples was shown by nitrate-N and phosphate-P. Nitrate-N, ammonium-N and phosphate-P were negatively (albeit weakly) correlated over the lag of 2–3–4 weeks. Spatial correlations were also weak, with no indication of nutrient patches extending beyond the resolution of the study (3.3 cm). pH and ammonium-N were the only two parameters with positive spatial autocorrelation at this scale. Neither spatial nor temporal

Table 2 Tests of the effects of year, week, their interaction, depth and volume on the four chemical parameters

	Nitrate-N	Ammonium-N	Phosphorus-P	pH
Marginal R^2	0.171	0.632	0.317	0.578
P values				
Week	2.629 n.s.	1077.384***	392.02***	257.347***
Week, second power	40.404***	18.412***	21.506***	26.49***
Week, third power	0.12 n.s.	14.1***	11.032***	0.078 n.s.
Year	84.794***	734.225***	119.514***	477.388***
Depth		5.317		
Volume	2.059 n.s.	0.001 n.s.	12.762***	
Week:year	4.79**	48.007***		76.48***
Week 2:year	55.047***	132.024***	29.189***	5.414**
Week 3:year	17.777***	13.679***	8.474***	51.233***
d.f.	1774	1579	1576	1254
Standardized coefficients				
Week	− 0.533	0.359	− 0.278	0.289
Week, second power	− 0.178	− 0.289	0.143	− 0.170
Week, third power	0.220	0.036	− 0.054	0.060
Year 2003	− 0.736	− 1.923	0.488	− 1.332
Year 2004	− 1.182	− 1.469	0.529	− 0.400
Depth		− 0.104		
Volume	− 0.072	− 0.055	0.047	
Week:year 2003	0.655	− 0.752		0.862
Week:year 2004	1.442	1.526		− 0.278
Week 2:year 2003	0.728	0.699	0.330	
Week 2:year 2004	3.258	3.206	− 0.458	
Week 3:year 2003	− 0.414	0.219	0.195	− 0.776
Week 3:year 2004	1.277	1.267	− 0.097	− 0.406

Coefficients of the interactions of higher powers of week with year are not shown. Empty cells indicate effects not selected in the final model. Week 2—second power of week, Week 3—third power of week. *P < 0.05, **P < 0.01, ***P < 0.001, n.s. not significant. Empty cells indicate effects not included in the final model. All main effects have d.f. = 1, with the exception of year (d.f. = 3)

correlation differed between the two depths (data not shown).

There were a number of correlations among the soil variables (Table 3, Fig. 5). Both nitrogen forms were correlated; nitrate-N was weakly positively correlated with phosphate-P which was in turn strongly negatively correlated with ammonium-N. pH was positively correlated with ammonium-N and negatively with phosphate-P. Ammonium-N showed a negative relationship with volume. The first two axes of the PCA explained 72% of the total variation; the first axis separated phosphate-P-rich samples from those with high pH and high ammonium-N, which constitutes the main gradient in the data. Redundancy analysis with volume and week as predictor variables showed that this main gradient is linked to season; ammonium-N and pH increased through the season, whereas

phosphate-P (and partly nitrate-N) decreased (Fig. S5 in the Electronic supplemental material).

Discussion

Structure of spatiotemporal variation in nutrient concentrations

Scattered pattern of distribution of concentration peaks of all nutrients in the soil solution suggests rather low background values with infrequent, short-lived, but large-in-magnitude concentration peaks (see also Farley and Fitter 1999). Durations of these peaks though different among individual nutrients, typically did not exceed 1–2 weeks. Temporal component of variation was consistently much more important than the spatial component, indicating fast turnover of
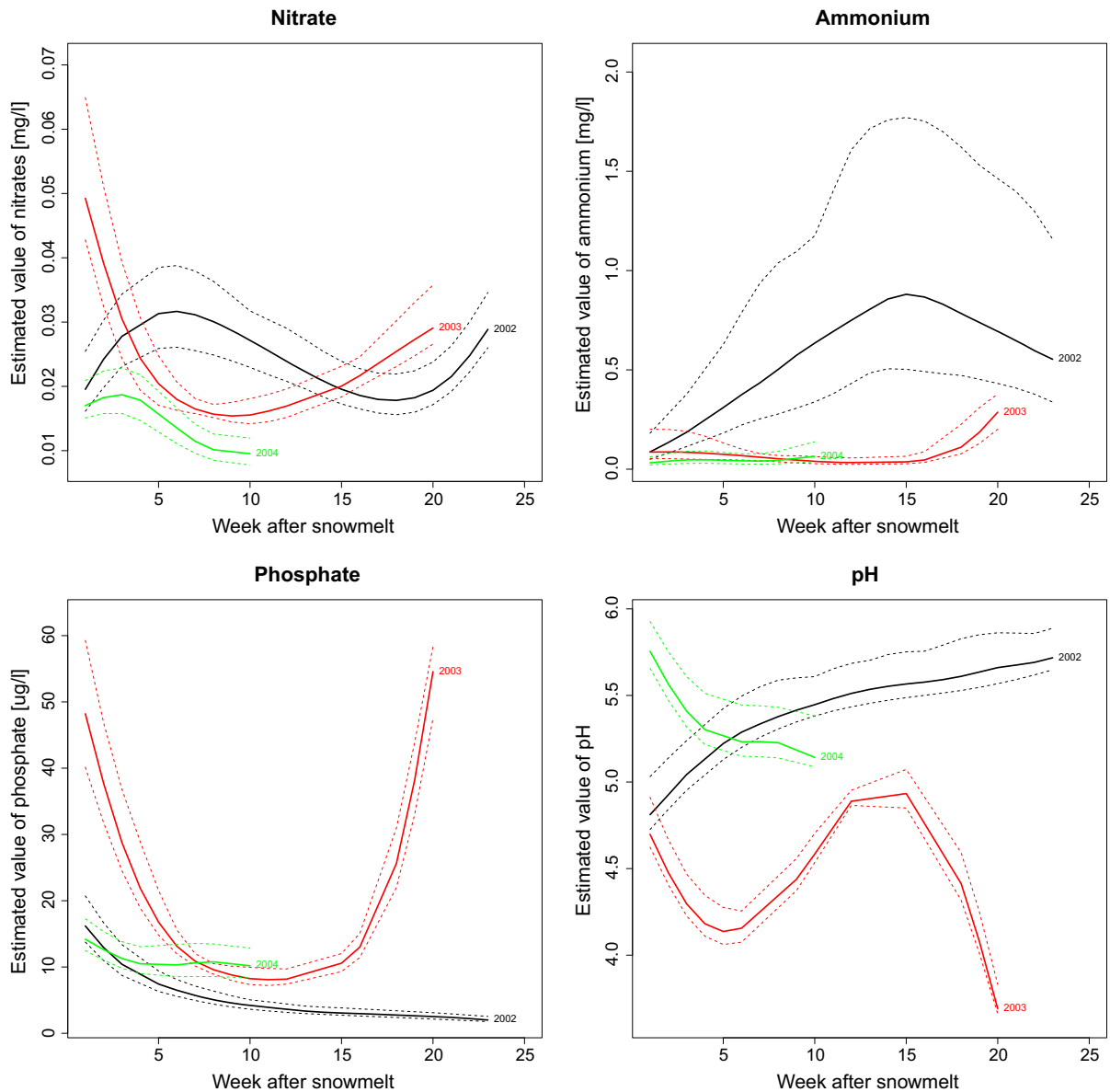
Nitrate

Ammonium

Phosphate

pH

Fig. 3 Estimated mean values of chemical parameters of the soil solution as a function of time. The values are predicted values from a mixed model with third-order polynomial effect of week, and interaction between week and the categorical variable year. Week is counted from snowmelt. Dotted lines indicate 95% confidence intervals of expected values. For significance tests, see Table 2

patches of nutrient availability. The high temporal variation is thus superimposed on a system that is essentially spatially homogeneous, both at fine scale and over larger (metres and more) distances.

This implies that nutrient supply for plants has a very fast turnover for one position, but with no clear differentiation among these positions (see e.g. also Chagnon et al. 2018). This suggests that root

proliferation is unlikely to follow the rapid dynamics in the availability of soil resources, as it is known to be much slower than the observed nutrient dynamics (van Vuuren et al. 1996; von Wirén et al. 1997; Hodge et al. 1999; Fransen and de Kroon 2001). We therefore hypothesize that such a highly dynamic resource environment would force plants to develop a more or less regular and homogeneous, extensive and

Fig. 5 Principal components analysis of interrelationships among the four soil solution variables. Points indicate individual samples. First and second axes explain 40.6% and 33.1% of the total variation
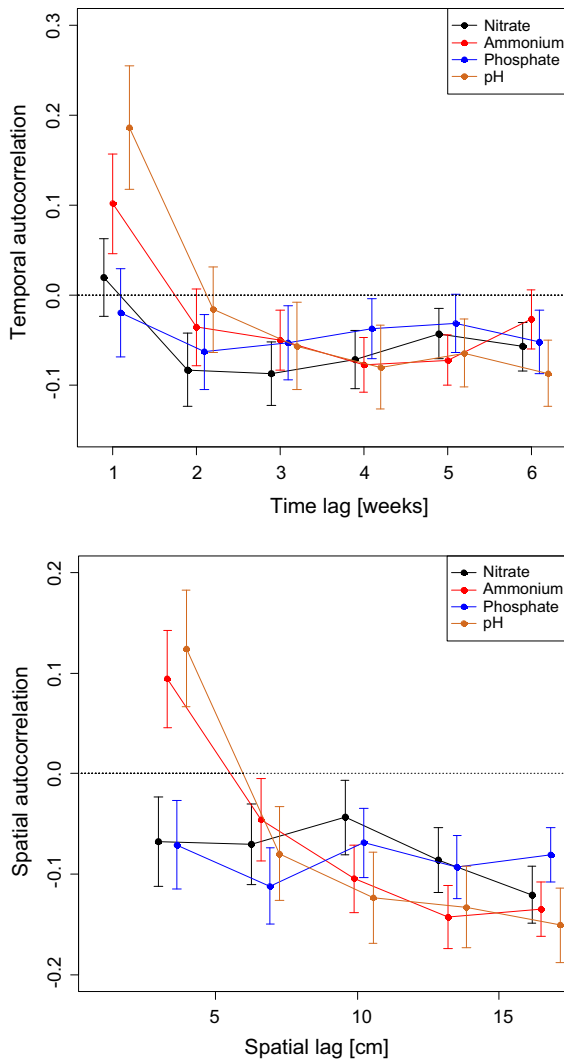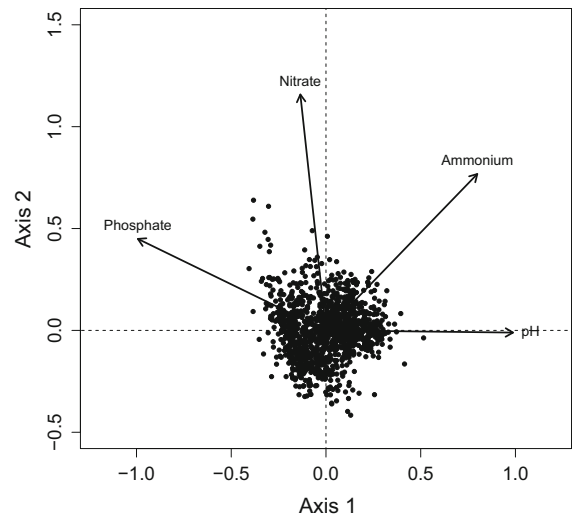
Fig. 4 Temporal and spatial autocorrelations of four chemical parameters of the soil solution. Bars indicate 95% quantiles calculated over all positions and years for temporal correlations and calculated over all transects and years and weeks

temporally stable distribution of roots, which will adjust physiologically to short-term changes in nutrient availability as suggested also by conceptual considerations (Alpert and Simms 2002) or simulation models (Magyar et al. 2007). This is supported by existing data from the site. They revealed highly spatially homogeneous root distribution of many species (Herben et al. 2018) as well as homogeneous distribution of absorption zones identified by a tracer element (Pecháčková et al. 2003), supporting the absence of root response to environmental heterogeneity.

Importantly, large share of this temporal variation was due to the effect of year, and interaction of year and week, indicating that seasonal course of nutrient

Table 3 Correlation matrix (Pearson correlation) between the variables

	Volume	Nitrate-N	Ammonium-N	Phosphate-P
Nitrate-N	− 0.077			
Ammonium-N	− **0.341**	**0.317**		
Phosphate-P	0.186	**0.292**	− **0.257**	
pH	− 0.207	− 0.048	**0.291**	− **0.381**

All variables except pH were log-transformed. Correlation coefficients greater than 0.25 (i.e. $R^2 > 0.05$) are shown in bold. All values are highly significant ($P < 0.001$). $N = 1279$

concentrations changed rather inconsistently between years. Only phosphate-P had a marked early-spring concentration peak in all three studied years. Nitrate-N had a similar early-spring increase in one of the three years only whereas ammonium-N tended to increase during the season, especially in 2002. This situation is similar to the temporally inconsistent variation pattern in nutrient concentrations found in other grasslands (Rychnovská 1993; Giese et al. 2011; Leimer et al. 2016) or other temperate ecosystems (Davy and Taylor 1974; Farley and Fitter 1999), implying that a sufficient duration of the study is necessary for a reliable description of variation in nutrient availability. As the study was conducted at a reasonably stable grassland site, its temporal dynamics is likely to be driven primarily by variation in climatic variables that affect soil water availability. For example, the above-mentioned early-spring increase in phosphate-P or autumnal rise of all nutrient concentrations are likely the consequence of a "partial sterilisation effect", i.e. death of plants and microbial biomass due to frost or drought and subsequent mineralization of dead biomass after snow-melt or rewetting (Taylor et al. 1982; Magid and Nielsen 1992; Fierer and Schimel 2002; Edwards et al. 2006; Freppaz et al. 2007; Borken and Matzner 2009). Similarly, the tendency of ammonium ion concentrations to increase in drier parts of the season when smaller volumes were collected (see also Giese et al. 2011; Dujardin et al. 2012 for a similar seasonal pattern) can be explained by a combination of drought-triggered decrease of its uptake by plants and microbial organisms and its release from dead organic biomass (see Dujardin et al. 2012 and references therein).

Another important feature of nutrient heterogeneity at the study site was the similar amount of variation in concentrations at fine and coarse spatial scales. We did not find convincing evidence of spatial autocorrelation in nutrient concentrations even at the smallest observed spatial and temporal lags. While the extent of spatial variation at the site can be underestimated due to the largest distance between suction cups being only 5 m, this is unlikely to have a major impact on the conclusion due to its homogeneity—variation at small spatial scales typically captures a large part of the entire spatial variation of homogeneous sites (Ball and Williams 1968; Jackson and Caldwell 1993 and references therein; Ryel et al. 1996).

Dynamics of individual nutrients

Different seasonal courses of individual ions clearly result from differences in their physico-chemical characteristics. Immobile phosphates are usually kept at low concentrations in the soil solution by processes of sorption, fixation and immobilization to soil particles, minerals and into microbial biomass (Marschner 1998; Hinsinger 2001; Kruse et al. 2015; Kreuzeder et al. 2018). Their uptake by plants and their mycorrhizal symbionts follows a rather consistent seasonal dynamic related to the intensity of plant uptake (Klaus et al. 2016). On the contrary, the high mobility of nitrate-N makes it susceptible to accidental rainfalls causing subsequent leakage which in turn results in seasonally inconsistent courses (Rychnovská 1993; Paul 2007; Brady and Weil 2008; Giese et al. 2011). Importantly, collecting soil solution using suction cups provides much more accurate measurement of actual availability of nutrients due to such effects, in contrast to rather conservative estimates of variation of the total amount of nutrients in solid soil samples, which, moreover, typically provide estimates of spatial variation only.

Our data also confirm the well-established fact that ammonium-N is a more available source of nitrogen in acidic soils than nitrate-N (Gigon and Rorison 1972). Exceptionally low nitrate-N concentration in the soil solution at the study site probably results from the intense dilution of the soil solution, as a consequence of the precipitation in the study region (Hruška et al. 2006), and from ammonium-N deposition (Budská et al. 2000). Low nitrate-N implies that the fertility of any microsite at the study site results mainly from the concentrations of ammonium-N and phosphate-P. The negative correlation and rather opposite seasonal course of ammonium-N and phosphate-P concentrations indicate that microsites with a high availability of nitrogen and phosphorus are largely temporally separated.

Implications

This lack of spatial structure in nutrient distribution, combined with its high temporal dynamics and negative correlation of key nutrients, questions the very concept of internally homogeneous, spatially well-defined and temporally stable patches in the field, which has been the pillar of many studies estimating

costs and benefits of plastic responses of roots (Gleeson and Fry 1997; Hutchings et al. 2003; Kembell et al. 2008; McNickle and Cahill 2009). Instead, the results support the concept of soil as a system influenced by independent and similarly strong sources of variation at different spatial/temporal scales (Kotliar and Wiens 1990; Lavelle 2002). In such a system, meristems at different hierarchical levels of plants independently cope with the different hierarchical scales of soil resource variation in accordance with the modular concept of phenotypic plasticity in plants (De Kroon et al. 2005, 2009). A better understanding of the costs and benefits of the plastic responses of plants to variation in soil resources is therefore likely to result from methodological approaches taking into account this multilevel nature of both soil resource variation and a plant's plastic responses.

Consequently, plants under nutrient limitation in an oligotrophic meadow have to cope with a highly dynamic and spatially uncorrelated supply of nutrients which changes considerably between the study years and which has a rather inconsistent seasonal pattern. This means that the best growth strategy for roots under such conditions is to be conservative, combined with physiologically plastic responses of individual roots to nutrient variation. This is supported by existing data on species-specific root distribution at the site (Pecháčková et al. 2003; Herben et al. 2018). For a better understanding of the costs and benefits of these responses and their ecological significance, one should consider rapid dynamics, low predictability in space and time and the multiscale nature of nutrient variation in the soil.

Author contributions SB conceived the experiment; SB with HS, VH, FK and SP designed data collection; SB collected the soil solutions; TH, KJ and SB analysed the data; and SB, TH and KJ wrote the text with contributions from all other authors.

Data availability Data are available in the Electronic Supplemental Material (S6).

Compliance with ethical standards

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

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