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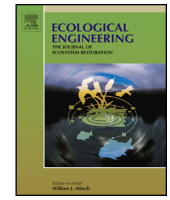

Effect of nutrient additions and site hydrology on belowground production and root nutrient contents in two wet grasslands

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Belowground production can be a significant part of total plant biomass and represents a significant pool of carbon and other nutrients. Changes in root biomass and nutrient contents can influence root decomposition and nutrient turnover rates, thereby impacting ecosystem processes and functions. In-growth core bags were used in a long-term nutrient addition study to determine net belowground primary production (NBPP), root nutrient (C, N and P) percentages and stoichiometry under different nutrient treatments in two wet grasslands with either mineral or organic soil. It was hypothesized that fertilization will lead to reduced NBPP, but increased root nutrient contents, and that these differences will be greater over time. The fertilizer was added in two half doses in a growing season over seven years with NBPP and the nutrient measures sampled in years 2, 3, 5 and 7. Between-year differences in the measured parameters were tested by repeated measures ANOVA, while one-way ANOVAs were run to compare between-treatment differences in each year within each site. Linear regressions were run to relate NBPP, root nutrient content and the stoichiometric ratios to changes in site hydrology. NBPP and root nutrient contents changed over time, especially in the organic soil grassland, but were largely unaffected by the nutrient additions. Site hydrology, sometimes interacting with the nutrient treatments, appeared to be the more important factor. Prolonged flooding of the two grasslands in the latter two years of measurements led to significantly reduced NBPP, and N and P% especially in the organic soil site. The response of wet grassland belowground structures to changing hydrologic conditions, in tandem with nutrient addition, may be useful in developing management plans to deal with the expected effect of climate change on water availability at the local and regional scales.

1. Introduction

The production of belowground structures can be a significant portion of total plant biomass. These belowground structures can be significant pools of carbon and other nutrients, and the subsequent death and decomposition of these structures can represent large inputs of these nutrients to ecological systems (Persson, 1979; Vogt et al., 1998; Boyd and Svejcar, 2012). Root production and the rate of root turnover can greatly affect various ecosystem processes, including nutrient flows and fluxes such as carbon sequestration (Gill and Jackson, 2000; Bai et al., 2010). Recently, there has been increased interest in belowground production. Various factors, such as increased CO_2 (Milchunas et al., 2005; Arndal et al., 2013; Sonderegger et al., 2013), greater or lesser moisture levels (Zhang and Zak, 1998; Fiala et al., 2009; Bai et al., 2010) and nutrient additions (Dukes et al., 2005; Moar and Wilson, 2006; Blue et al., 2011), have been found to greatly influence root production and nutrient turnover rates. Increased nutrient availability is known to result in changes to plant biomass allocation patterns, favoring aboveground production at the expense of belowground structures (Saggar et al., 1997; Detenbeck et al., 1999). The roots produced are of higher quality (lower C:N ratio) with faster turnover rates resulting in more rapid nutrient cycling within a particular system (Olde Venterink et al., 2002; Kaštovská et al., unpublished data).

A majority of studies on belowground production have been conducted in forested and upland grassland habitats (see appendix in Gill and Jackson, 2000 and later studies such as Milchunas et al., 2005; Meinen and Leuschner, 2009; Dodd and Mackay, 2011; Ladwig et al., 2012, etc). Such studies in wetlands have occurred mostly in riparian meadows (Martin and Chambers, 2002; Kiley and Schneider, 2005; Blank et al., 2006; Boyd and Svejcar, 2012), with non-riparian, non-forested wetland systems, such as wet grasslands, being under-represented. Overall, most nutrient addition studies have generally been of short duration, usually a year or less, with only a few studies investigating the effect of long-term

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(>1 year) nutrient additions on primary production or plant nutrient contents (e.g., Ladwig et al., 2012).

Wet grasslands are highly productive, graminoid-dominated wetlands, which can have either low or high vegetation species diversity, depending on the heterogeneity of the plant community mosaic (Ružíčká, 1994; Prach and Straškrabová, 1996; Joyce and Wade, 1998). In Europe, wet grasslands are maintained by human activities, therefore any change in management practices can greatly impact the state of these systems (Joyce and Wade, 1998; Tallowin and Jefferson, 1999). The area of European wet grasslands has declined over the last 60 years due to agricultural intensification, conversion to upland arable land, or abandonment (Joyce and Wade, 1998; Tallowin and Jefferson, 1999; Prach, 2008).

Only a few studies in wet grasslands have focused on belowground production (Fidelis et al., 2013). These studies found that belowground production was negatively affected by late season mowing (Dumortier et al., 1996), but enhanced under greater fire frequency (Fidelis et al., 2013), while flooding could have either a positive (Barbosa et al., 2012) or negative (Fidelis et al., 2013) impact on root growth. No studies have investigated the effect of nutrient additions on belowground production in wet grasslands.

A manipulative field experiment was established to investigate the effect of prolonged nutrient additions (over seven years) on belowground production and the nutrient percentages and stoichiometric ratios of the belowground structures in two wet grasslands growing on either organic or mineral soil. This study was part of a larger project investigating how long-term nutrient inputs and soil type affected plant-soil interactions in wet grasslands. Within this larger project, short-term nutrient treatment effects on primary production (both above and belowground) have already been published (Picek et al., 2008; Edwards et al., 2015). In keeping with the results of past nutrient addition studies, it was hypothesized that plants in fertilized plots will have reduced belowground production, but that these structures will have greater nutrient (N, P) contents than those growing in control, unfertilized plots. In addition, it was expected that these differences would become greater over time due to the repeated application of nutrients (hypothesis two).

In addition to the manipulative nutrient addition experiment, there were uncontrolled changes in the hydrologic conditions of the two wet grasslands over the seven years of the study. The first few years of data collection occurred at times of drier site conditions while the wet grasslands were flooded for long periods in the later years of the study. Given that future conditions in Central Europe are predicted to be drier, with changed precipitation patterns, as a result of climate change (IPCC, 2014), and that belowground plant C can be an important input affecting other ecosystem processes and functions, it may be interesting to determine how other factors, such as site hydrology, affect belowground plant production, either singly or when interacting with the experimental nutrient additions. Therefore, this paper describes the response of belowground plant production to a long-term, manipulative nutrient addition experiment overlaid by an observational study of water level effects. Such information could be useful in determining how nutrient additions and site hydrology, either singly or in combination, affect plant nutrient inputs to wet grasslands and what management actions may be required to maintain well-functioning ecosystems.

2. Methods

2.1. Study sites

In situ experiments were conducted in two wet grasslands, one on organic soil and the other having mineral soil, in the Třeboň Basin Biosphere Reserve (TBBR, 49°01′ N and 14°46′ E), Czech Republic. Complete descriptions of the study wetlands are given in Picek et al. (2008). Briefly, the organic site, Záblatské Louky (hereafter referred to as the organic soil site), is located in the inundation area of a large fishpond. Carbon accumulation is typical of poorly flushed marginal wetlands in the TBBR (Prach, 2002). The site is a species poor (11 vascular plant species; H = 0.48) sedge meadow dominated by *Carex acuta* (50–75% cover) and *Carex vesicaria* (10–25%). Other species found in the site include *Phalaris arundinacea* (5%), *Lythrum salicaria* (5%) and *Galium palustre* (5–10%) (based on results of phytosociological relevés, L. Rektoris, personal communication). The moss *Calliergonella cuspidate* is also quite common (25–50% cover). The organic soil site is mown once a year in mid-July.

The second site, Hamr (hereafter referred to as the mineral soil site), is located in the floodplain of a small river (Nežárka) and is frequently flushed. It is a normal situation in floodplains that wetlands on 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 *Glyceria maxima* and *C. acuta* (both with 25–50% cover) with only four other species present (L. Rektoris, personal communication). In this site, *C. cuspidate* is quite rare with less than 1% cover. Water levels are similar to those in local drainage ditches, which are connected with the river. Thus, average water level is lower and more variable in this site than in the organic soil site. The mineral soil site is mown two times during the growing season, in early-June and August. The sites are about 11 km distant from each other and have similar elevations (ca. 400 masl).

2.2. Sampling design

A field experiment was established at the two sites in spring 2006. See Picek et al. (2008) for a full description of the experimental design. Briefly, four blocks were established in each site, with three treatment plots (12.25 m^2) per block. Of these, only two of the nutrient treatments were used in this study, with fertilization treatments of 0 and 300 kg NPK ha^{-1} yr^{-1} (corresponding to unfertilized control and high fertilization treatments, respectively). This differs from earlier studies (Picek et al., 2008; Zemanová et al., 2008; Edwards et al., 2015) which included data from a third, middle nutrient treatment (65 kg NPK ha^{-1} yr^{-1}, corresponding to the Low treatment in those studies). Nutrient addition was administered to randomly selected plots using a commercial NPK fertilizer (Lovofert 15:15:15 NPK, Lovochemie, a.s.), which is recommended for use in wet grasslands. 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 fertilizer application was followed by at least two days with no precipitation. Laboratory analyses of the soil from the sites showed that the added nutrients were immobilized into the plants and soil microbes within 48 h. This rapidity of nutrient uptake appears to be a common feature of wet grasslands (see Rejmánková et al., 2008). Therefore, it was felt that these precautions greatly reduced the chance of the nutrients spreading to adjacent plots even though the sites were occasionally flooded.

Continuous water level measurements were taken from a well established in the center of each site. Water levels were taken at 15 s intervals using the STELA system, which consists 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).

Net belowground primary production (NBPP) was measured in both sites in 2007, 2008, 2010 and 2012 (representing years 2,