



Can changes in soil biochemistry and plant stoichiometry explain loss of animal diversity of heathlands?



J.J. Vogels^{a,b,*}, W.C.E.P. Verberk^b, L.P.M. Lamers^c, & H. Siepel^{b,d}

^a Bargerveen Foundation, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

^b Department of Animal Ecology and Physiology, Radboud University Nijmegen, The Netherlands

^c Department of Aquatic Ecology and Environmental Biology, Radboud University Nijmegen, The Netherlands

^d Plant Ecology and Nature Conservation Group, Wageningen University, The Netherlands

ARTICLE INFO

Article history:

Received 16 February 2016

Received in revised form 22 August 2016

Accepted 29 August 2016

Available online 16 September 2016

Keywords:

Acidification

Ecological stoichiometry

Heathland fauna

Nitrogen deposition

N:P ratio

Sod-cutting

ABSTRACT

Increased atmospheric deposition rates of nitrogen (N) and sulphur (S) are known to affect soil biogeochemistry and cause a decline in plant biodiversity of heathlands. Concomitant declines of heathland invertebrates are mainly attributed to changes in vegetation composition and altered habitat structure. While there may also be effects on animals through altered plant chemistry, these have received little attention up to now. Here, we remedy this by quantifying soil nutrient and acid buffering status, vegetation composition and structure, plant nutrient stoichiometry, and densities and species richness of Diptera and Carabidae in two large heathland systems. Soil acid buffering status appeared to be a key driver for plant P availability. Sod-cutting was found to further increase plant N:P ratios, suggesting increased P-limitation. Vegetation N:P ratio was negatively linked to invertebrate density and species richness, and was found to impact fauna more strongly than vegetation structure and plant species richness. The relationship between invertebrates and plant C:N ratio was weaker and less consistent, suggesting that for invertebrates, plant P is generally more limiting than N. Our results imply that the role of plant stoichiometry is underestimated in explaining declines of heathland invertebrates, and we here provide a novel mechanistic model including this pathway. Management should therefore not only focus on restoring habitat structural complexity, attention should be paid to restoring plant stoichiometry. This can be achieved through restoring biogeochemical soil conditions, especially by mitigating soil acidification, while measures solely focusing on removal of accumulated N by means of sod-cutting should be avoided.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Heathland landscapes in Northwest Europe are under considerable pressure from land use change (Diemont, 1996) and atmospheric pollution by nitrous oxides (NO_x), ammonia/ammonium (NH_y) and sulphur dioxide (SO₂) (Cowling, 1982; Elser, 2011), which greatly surpass the critical loads for these systems (Bobbink et al., 2010; Bobbink and Roelofs, 1995). High deposition of N and S compounds has strongly altered soil chemistry of heathlands and acidic grasslands, not only by increasing ammonium (NH₄⁺) and nitrate (NO₃⁻) availability, but also by accelerating soil acidification, which has resulted in increased mobilization of aluminium (Al) and the accumulation of NH₄⁺ (Bobbink et al., 1998; Houdijk et al., 1993). As a result, vegetation has shifted towards grass dominance at the expense of herbaceous species (Bobbink et al., 1998; Bobbink and Roelofs, 1995; De Graaf et al., 1997; De Graaf et al., 1998; Heil and Bruggink, 1987; Heil and Diemont, 1983; Houdijk et al., 1993; Roelofs,

1986), with a concomitant overall loss of plant biodiversity (De Graaf et al., 2009; Kleijn et al., 2008; Roem et al., 2002). Restoration management of heathlands generally involves removal of the N-rich top layer (sod-cutting), to reduce the competitive advantage of fast-growing tall-grasses in favour of dwarf shrubs and herbaceous vegetation (Diemont, 1996).

The simultaneous decline of heathland animal diversity is commonly attributed to the loss of plant biodiversity and grass encroachment following eutrophication and acidification. Mechanisms thought to underlie the vegetation-driven negative effects on fauna include changes in microclimatic conditions (Schirmel et al., 2011; Vanreusel and Van Dyck, 2007; Wallis de Vries and van Swaay, 2006), loss of open habitat (Öckinger et al., 2006; van Turnhout, 2005), and a decrease of nectar and host plants (Öckinger et al., 2006; Vanreusel et al., 2007; Wallis de Vries, 2004). However, much less attention has been paid to the question whether eutrophication and acidification might also affect heathland animals directly through deposition-mediated shifts in plant macronutrient stoichiometry. In nutrient-poor terrestrial environments, increased N deposition can lead to substantial increases in plant-available N relative to phosphorus (P) and can, thus, potentially increase the N:P ratio of plant biomass. Pitcairn et al. (2001) found a significant

* Corresponding author at: Bargerveen Foundation, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands.

E-mail address: j.vogels@science.ru.nl (J.J. Vogels).

positive relationship between foliar N content of *Calluna vulgaris* and annual N deposition levels. In the poorly buffered heathland ecosystem, however, soil acidification could also affect plant N:P stoichiometry in a different way, as under increasing acidity, plant P availability will generally decrease through stronger formation of Al- and Fe-bound P (Blume et al., 2016). Shoot P concentrations of plants can also be significantly lowered as a result of Al toxicity (De Graaf et al., 1997; Foy et al., 1978). In addition, reduced mycorrhizal infection as a result of acidification and/or increased soil NH_4^+ concentrations will significantly lower P uptake rates (Pearson and Stewart, 1993). Both the increase in foliar N content due to higher N inputs and the lower P availability related to soil acidification can increase plant N:P ratios, and reinforce one another. Stoichiometric studies of heathlands have primarily focused on the effects of changes in plant stoichiometry on interspecific plant competition and plant community structure (Britton and Fisher, 2007; Roem and Berendse, 2000; Roem et al., 2002; Von Oheimb et al., 2010). Increased P-limitation in heathlands has been found to decrease plant species richness (Roem and Berendse, 2000), with many herbaceous and/or graminoid plant species with relatively low mean N:P ratios declining or disappearing in stands on soils with low P-availability. Plants with high mean N:P ratio and/or plants that show a higher plasticity in tissue N:P ratio (e.g. *C. vulgaris*, *Molinia caerulea*) show much lower declines or may even increase in cover. Thus, increased P-limitation for plants can lead to 1) reduced plant species richness due to the disappearance of plant species that require high P availability, and 2) shifts towards increased N:P ratios in more tolerant plant species. The question whether increased heathland vegetation N:P ratios may also significantly impact higher trophic levels has, however, still largely been unexplored.

Interestingly, Elser et al. (2000) showed that terrestrial herbivore N:P ratios are significantly lower than autotroph N:P ratios, indicating that for herbivores in terrestrial ecosystems shortage of P rather than N is more likely. Animals exhibit compensatory feeding behaviour when faced with nutritionally imbalanced foods (Behmer, 2009; Berner et al., 2005; Mayntz et al., 2005; Raubenheimer and Simpson, 1993). Compensatory feeding alleviates fitness reductions of ingesting nutritionally imbalanced foods, thereby obscuring the importance of a balanced diet for consumers (Berner et al., 2005). Studies on compensatory feeding have focused mainly on behavioural responses for dietary carbohydrate and protein and the majority of stoichiometric studies feature C:N ratios. Evidence for compensatory feeding for low levels of dietary P is weak, even though increased dietary P content can significantly enhance fitness (Cease et al., 2016; Perkins et al., 2004; Visanuvimol and Bertram, 2010, 2011). Possibly, increasing food intake to compensate low P content is not as tightly regulated as for carbohydrates and protein. Consequently, an increase in plant N:P ratio will further exacerbate low dietary P content, as compensatory feeding will be less in herbivores feeding on plants with elevated N (protein) content, further reducing their P-intake (Berner et al., 2005).

Animals may be affected by increases in vegetation N:P ratio in multiple ways (Elser et al., 2009; Elser et al., 2010). Most straightforward, if increased P-limitation for plants results in a loss of plants having relatively low N:P ratios, species that specialize on these plants will be affected. However, if N:P ratios of plants that remain also increase, all herbivorous species are expected to be subject to increased P-limitation, also adversely affecting generalist herbivore growth rates, densities and community structure (DeMott and Gulati, 1999). Detritivorous species can also be considered to be generalist species; they feed on decomposing litter and fungal hyphae and will also be impacted by altered vegetation N:P ratio, as the N:P ratio of fresh litter is largely determined by that of living tissue. Finally, the impacts of increased vegetation N:P ratios could also cascade towards higher trophic levels, reducing carnivore diversity. This could simply result from reduced prey availability, but also from stoichiometric imbalances in their prey (see e.g. Jensen et al., 2011; Mayntz et al., 2005; Mayntz and Toft, 2001; Raubenheimer et al., 2007).

In this study, we therefore explored whether plant macronutrient stoichiometry, as related to soil chemistry, can explain changes in community composition and diversity of animals of lowland heathlands. We assessed how these stoichiometric impacts compare to the effect of vegetation structure and composition using a multimodel inference approach as proposed by Burnham and Anderson (2002). We first investigated how soil chemistry is related to both C:N and N:P ratio of the vegetation, and to vegetation composition. Modelling included contrasting hypotheses that were based on soil chemical parameters found to be most important in predicting vegetation diversity and richness in previous studies dealing with N and acid deposition in heathland ecotypes (Bobbink et al., 1998; De Graaf et al., 2009; De Graaf et al., 1997; De Graaf et al., 1998; Kleijn et al., 2008; Roelofs, 1986; Roem and Berendse, 2000; Roem et al., 2002). We tested whether vegetation responses were related to either increased soil N availability (H1), increased soil acidity (H2), reduced soil P availability (H3), and their combinations: N availability in relation to acidity (H4); N in relation to P availability (H5); acidity in relation to P availability (H6); or combined effects of N, P availability and acidity (H7; Table 1). Soil chemical parameters used were: NO_3^- , NH_4^+ , $\text{NH}_4:\text{NO}_3$ -ratio for N availability hypotheses, plant available P for P availability hypotheses and pH, Al^{3+} , Ca^{2+} and Al:Ca-ratio for soil acidity hypotheses. In order to test whether changes in vegetation N:P ratio were mainly the result of changes in species composition (e.g. loss of low N:P ratio species) or whether intra-specific changes in plant N:P ratio also contributed, we contrasted the results for the N:P-ratio of the vegetation as a whole with those obtained when using the N:P ratio of the most common plant species, *C. vulgaris*. Next, we related animal taxon richness and abundance data (Diptera and carabid beetles) to vegetation C:N and N:P stoichiometry, structure and composition. We chose Diptera and carabid beetles because they represent widespread species groups in heathland ecosystems, are typically present in high abundance, encompass different trophic levels and, for carabid beetles, trophic level as well as other relevant autecological information are available at species level (Turin, 2000). We tested whether animal responses were related to either plant nutrient ratios (H1-F); 2) plant species richness (H2-F); plant species richness and vegetation structure (H3-F); or combinations of plant macronutrient ratio, vegetation structure and/or plant species richness (H4-F; Table 2). Subsequently, we explored the effect of different management types on vegetation community structure and plant C:N and N:P stoichiometry. The study was carried out in the Netherlands, which is one of the regions in Europe that has very high atmospheric N and acid deposition rates (EMEP, 2015).

2. Material and methods

2.1. Research locations

In order to account for regional variation, this study was performed in two large open heathland reserves in the Netherlands, the Dwingelderveld heathland reserve (Lat: 52.796°, Lon: 6.393°) and the Strabrechtse Heide heathland reserve (Lat: 51.403°, Lon: 5.619°). In both areas, 30 sites covering an area of 10 m × 10 m were selected for soil and plant chemistry sampling, vegetation relevés and sampling of Diptera and Carabidae, giving a total of 60 sites. Plant communities in the selected sites consisted of *Genisto-Callunetum* (n = 42), *Ericion tetralicis* (n = 15) and *Nardo-Galion* (n = 3) communities on loamy soils or long-term (>25 years) abandoned crop fields on sandy soils.

2.2. Management

Of all sites, management practice carried out over a period of 30 years and information of historical land use were provided by the managers of both reserves. Management of the heather dominated sites included sod-cutting (topsoil removal), grazing, a combination of both, controlled burning, or no management for at least 30 years.

Download English Version:

<https://daneshyari.com/en/article/5743069>

Download Persian Version:

<https://daneshyari.com/article/5743069>

[Daneshyari.com](https://daneshyari.com)