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Continuous and cumulative acidification and N deposition induce P limitation of the micro-arthropod soil fauna of mineral-poor dry heathlands

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ABSTRACT

Phosphorus content of mineral-poor sandy soils is steadily decreasing due to leaching caused by continuous and cumulative acidification and N deposition. Sod-cutting as a traditional restoration measure for heathland vegetation appears to increase P limitation, as most of the P present is in the organic matter being removed by sod-cutting. Mineral weathering, the natural inorganic source of P, becomes limiting or has even ceased as a result of the depletion of minerals. Previous investigations indicate a P limitation of the macrofauna under these circumstances. If this also holds for the soil fauna, hampering of decomposition may occur. To test experimentally whether soil fauna is indeed limited by the amount of P in the system, we set up an experiment in sod-cut heathland in which we added P or Ca (as Dolokal), resulting in: P + Ca+, P + Ca-, P-Ca+ and P-Ca- (control) treatments and an extra reference block in the original grass encroached heathland vegetation. The Ca treatment was added because liming is used to recover from acidification effects, but as a side effect Ca may also bind P. Three growing seasons after the addition of P and Ca, we found a significant increase in herbivores and predators among the soil fauna, with herbivore numbers higher in the P+/Ca-plots than in the P+/Ca + plots, indicating a lower availability of P in the presence of added Ca. Predators increased in all P+ plots. Fungivorous browsers responded negatively to the treatment after three growing seasons, both to P and to Ca addition. Phoretic species responded rapidly either to fewer numbers (when these are fungivorous browsers) or to greater numbers (when these are herbivorous browsers) to P addition. P addition induced also an allometric effect, via the medium-sized species increasing in greater numbers than both the larger and smaller species.

1. Introduction

Acidification and N deposition are considered major threats for the conservation of dry heathlands in Western Europe (Bobbink et al., 1998; Bobbink and Roelofs, 1995; De Graaf et al., 1997; De Graaf et al., 1998; Heil and Diemont, 1983). Critical loads of N deposition for dry heathland are exceeded for decades (Bobbink and Roelofs, 1995; Bobbink et al., 2010), resulting in a shift from a dwarf shrub dominated vegetation to a grass encroached vegetation in which herb species have also become much rarer (De Graaf et al., 2009; Kleijn et al., 2008; Roem et al., 2002). These shifts are explained by lifting the N limitation of particular plant species (Roem et al., 2002) and by differences in sensitivity to Al toxicity of others: N deposition causes severe acidification in the top soil, which releases Al at pH lower than 4.2 (Bobbink et al., 1998; Houdijk et al., 1993). The focus in restoration management has been to combat these changes by removing as much N as possible by sod-cutting (Diemont, 1996) in order to restore the former N limited ecosystem.

Sod cutting has been proven highly efficient in restoring ericaceous dwarf shrub dominance in grass encroached vegetation (Diemont, 1996). However, plant species diversity, especially herb diversity, hardly recovers. Aerts (1990) and later Roem and Berendse (2000), Britton and Fisher (2007) and Von Oheimb et al. (2010) showed the importance of N:P stoichiometry for interspecific competition among plant species. In a recent study, Vogels et al. (2017) found an impoverished invertebrate fauna correlated with an increased N:P ratio in the dominant plant species. They found a response of increased plant N:P ratio in both herbivorous and detritivorous Diptera and

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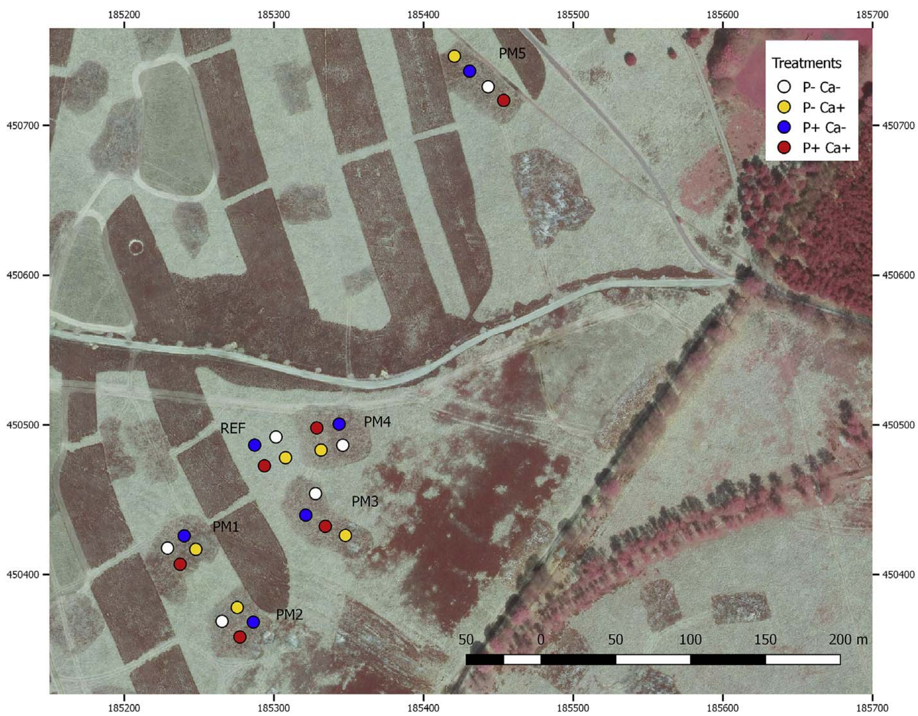

Fig. 1. Aerial false-colour photo, taken in 2013, showing the lay-out of the experimental plots in De Hoge Veluwe National Park. Light blue surfaces are sod-cut. REF, reference (uncut) plots and replicates (PM) represent P +/Ca + red, P+/Ca-blue, P-/Ca + yellow and P-/Ca-grey plots of 15 × 15 m^2. Distance between marginal numbers is 100 m.

herbivorous and carnivorous Carabidae. However, as detritivorous Diptera may feed on dead organic matter, fungal hyphae, or both, it remains unclear whether soil animals with different sizes, diets and life history strategies respond differently to sod-cutting and altered stoichiometry.

N:P ratios of terrestrial herbivores are significantly lower than those in plants (Elser et al., 2000), even in situations where these ratios have not become excessively high in plants. This indicates that P is more limiting for animals than N. An unforeseen effect of sod-cutting may therefore be that P limitation has become more severe for a large part of the fauna, as most of P was bound in the, by sod-cutting, removed organic matter in the humus form. Weathering, if still possible in the top soil by the presence of sufficient minerals, will take many years: Zehetner et al. (2008) found that about 50% of apatite P was taken up in organic matter in 500 years in Romania.

Barendregt and Siepel (2016) draw attention to the possible rigidity effects of nature conservation in keeping the same vegetation on the very same spot, as natural processes, such as acidification of the top soil continue and even are enforced by human influences. Mol et al. (2003) calculated that human-induced acidification in soils during the industrialized decades was equivalent in terms of leaching and weathering of minerals with the past 11,000 years. So, P containing minerals (e.g. apatite) in the top soil may be completely weathered and leached if P is not incorporated in organic matter. In heathlands, most P is bound in the organic matter in the A-horizon (Härdtle et al., 2009). However, most of the organic matter is removed by sod-cutting to combat the continuous influx of N, resulting in a possible severe P limitation. Under these conditions, only plant species can survive that are extremely efficient in P reallocation (indicated by a high N:P ratio in their tissues). As the fauna is even more susceptible to P limitation, effects must be seen there first. As also suggested in Vogels et al. (2017) an unforeseen negative side-effect of sod cutting may therefore be that P limitation has become more severe for a large part of the fauna.

Predominant fungi in heathlands are saprophytic, or form either ectomycorrhizal or ericoid mycorrhizal connections to plant roots. In the latter case they provide the plants with nutrients, particularly P via uptake from mineral soil (ectomycorrhiza) and/or from resistant organic matter (ericoid mycorrhiza) (Smith and Read, 2008). P contents in fungi therefore are thought to be higher than in plants. So, it is hypothesized that fungivorous soil animals suffer less from P limitation than herbivorous animals do. Furthermore, larger animals need more P to complete their development, thus effects of P might be allometric. Mulder (2010) and Mulder and Elser (2009) show that larger animals especially suffer from P limitation as they found a clear allometric effect in occurrence of animal species under P limited conditions.

To test experimentally whether soil fauna is indeed limited by the amount of P in the system, we set up a full factorial experiment in sod-cut heathland. Liming in heathlands is often practised to restore the buffer capacity of the soil to acidification, however excess of Ca may inhibit P availability to plants (Haynes, 1982; Kooijman and Besse, 2002). Thus, in the experiment we added P or Ca (as Dolokal), addition noted as + and no addition as -, resulting in: P-Ca- (control), P + Ca-, P-Ca+ and P + Ca + treatments and an extra reference block in the original grass encroached vegetation (with *Molinia caerulea* dominance). Here 'control plots' refer to the sod-cut experiment without any addition and 'reference plots' refer to the original not sod-cut vegetation with or without additions. We focussed on the micro-arthropod soil fauna and formulate the following hypotheses: we hypothesize herbivores to respond positive to P addition, fungivores not to respond to P addition, but slightly to Ca addition and predators to respond positive to P addition, as a consequence of increased herbivore numbers. Concerning life-history tactics, we hypothesize a faster response in thelytokous reproducing species than in sexual reproducing species, as the former have a faster reproduction, and a positive response of the better colonizers (phoretic species). Moreover, following the allometric rule of Mulder (2010), we hypothesize the most numerous positive response in populations of the larger species.

2. Material and methods

2.1. Site description and experimental design

Experimental plots were created in National Park De Hoge Veluwe, in the centre of the Netherlands (52°.2'.30″ N; 5°.49'.50″E). Plots are located on the gentle slope of a push moraine ridge with some cover sand. Soil type is a spodic dystrudept (Soil Survey Staff, 1999),