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Modelling C and N mineralisation in soil food webs during secondary succession on ex-arable land

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ABSTRACT

The rate of secondary succession after land abandonment depends on the interplay between aboveground and belowground processes. Changes in vegetation composition lead to altered amounts and composition of soil organic matter (SOM) with consequences for the abundance and functioning of the soil food web. In turn, soil food web structure determines the mineralisation rate of nutrients that can be taken up by plants. This study analyses changes in the C and N mineralisation rates along with soil food web structure during secondary succession after land abandonment.

In a previous study, changes in soil food web structure and SOM quantity and quality were measured at different stages of secondary succession on abandoned arable fields (abandoned for 2, 9 and 22 years and a heathland, which is the assumed target of the secondary succession). Based on these measurements we expected the C and N mineralisation rates to increase during secondary succession. The key hypothesis is that with a description of the soil food webs in terms of quantified biomasses, natural death rates, energy conversion efficiencies and diets enables a calculation of C and N mineralisation rates in soils. The basic assumptions connected to this hypothesis are that on a time-scale of years the population sizes are in steady state. We also calculated mineralisation rates per trophic level and energy channel. Based on the same measurements we expected that the contributions by the lower trophic level groups will increase as well as the mineralisation rates by bacterial and fungal energy channels.

Measured C and N mineralisation indeed increased during the 22-year period of abandonment. The calculated C and N mineralisation rates showed the same trend after land abandonment as the measured values.

Calculated contributions to mineralisation of organisms at trophic level 1 increase during secondary succession following land abandonment. The fungal decomposition channel contributed more to N mineralisation than the bacterial decomposition channel, whereas both channels contributed equally to C mineralisation rates. Direct contributions by higher trophic levels to mineralisation decreased during secondary succession. However, higher trophic levels were direct important for N mineralisation and indirect for both C and N mineralisation due to their effect on biomass turnover rates of groups at lower trophic levels.

The increasing total N mineralisation rate of the soil food web, however, does not benefit plants, as during succession plant species that mainly grow under high nutrient availability are replaced by species that can grow in nutrient poor condition.

1. Introduction

The re-establishment of natural species-rich grasslands and heathlands on abandoned agricultural land is a common change in land use in North-West Europe. Such ecological transition through secondary succession can take several to many decades (Walker et al., 2004). The successional changes in vegetation and soil

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depend on each other (Wardle et al., 2004; Kardol et al., 2006). However, relatively little is known about how the composition of the entire soil food web alters and what the consequent changes in process rates are during secondary succession from arable to semi-natural grasslands and heathlands. Changes in plant community composition result in changes in the quantity and quality of soil organic matter (SOM) and, consequently, in changes in the structure of the soil food web (Holtkamp et al., 2008). In return, changed soil food web composition and process rates will influence the amount of mineralised inorganic nutrients that can be taken up by plants (Wardle, 2002). The effects on soil food web composition on mineralisation rates have been analysed for agricultural soils (De Ruiter et al., 1993), prairie grass systems (Hunt et al., 1987) and forest soils (Berg et al., 2001; Schröter et al., 2003). In these studies, food web models have been used to derive mineralisation rates from the food web structure (Hunt et al., 1987). These types of ecosystems show relatively little changes in time, in contrast to secondary successional systems where fast growing early succession plant species are replaced by slow growing later succession plants. Here, we analyse how changes in soil food web composition may affect mineralisation rates during secondary succession from arable land to semi-natural heathland.

We modelled mineralisation rates by groups of soil organisms in the soil food web and analysed how changes in soil food web composition affected these rates. The composition of the soil food webs has been described by Holtkamp et al. (2008). The sites make up a chronosequence of three ex-arable fields, representing early, mid and late secondary succession stages and a reference heathland. For our analysis we used an existing food web model (Hunt et al., 1987). We took measurements of the biomasses of the groups and the total C and N mineralisation rates in order to parameterise and validate the model. With the model we could also estimate mineralisation rates for the various trophic levels (e.g. Hairston and Hairston, 1993) and energy channels (e.g. Moore et al., 1988; Rooney et al., 2006) in the soil food web. This allowed us to relate shifts in food web structure to changes in mineralisation rates (Holtkamp et al., 2008).

During the secondary succession, the quantity of SOM and the quantity of microbial biomass increases for at least 22 years (Holtkamp et al., 2008), leading to an increase in decomposition and C mineralisation rates. Therefore we expected that measured C mineralisation rates will increase after land abandonment. Nitrogen mineralisation rates, together with SOM quantity and microbial biomass, also depend on the C to N ratio of both SOM and its consumers. The C to N ratio of SOM being a measure of SOM quality (Moore et al., 2004), may vary among the stages in secondary succession, although it may not necessarily increase or decrease with years since abandonment (Holtkamp et al., 2008). In the present case of secondary succession, there was no decrease in SOM quality, the fungal biomass increases, while the biomass of bacteria did not change significantly (Van der Wal et al., 2006b; Holtkamp et al., 2008). Because of the increase in fungal biomass with no changes in bacterial biomass, we expect that the model will predict an increase in N mineralisation rates with time since abandonment. Fungi and bacteria are known to have generally the highest mineralisation rates among soil organisms, because of their high turnover rate and high biomass (De Ruiter et al., 1993; Bloem et al., 1994; Neher, 1999). Because the fungal biomass will increase with time since abandonment, contributions to mineralisation rates by fungi are expected to increase as well.

To analyse the effect of the soil food web structure on the C and N mineralisation rates, we defined trophic levels and energy channels in the soil food web. The biomass of the two lowest trophic levels, comprising roots, SOM and microorganisms, increases after land abandonment (Holtkamp et al., 2008). In contrast, the biomass at the two higher trophic levels, comprising bacterivores, fungivores and predators, does not increase or even decrease. Hence, contributions to mineralisation rates by higher trophic levels are expected to decrease.

An energy channel consists of species from which their consumed biomass originates from the same primary energy source (Moore et al., 1988). We defined a bacterial channel that consists of high quality, easy decomposable SOM, bacteria, bacterial consumers and predators, and a fungal channel that consists of low quality SOM, fungi, fungal consumers and predators, and a root channel with roots, root herbivores and predators. The biomass of both the bacterial and fungal channels increases after land abandonment (Holtkamp et al., 2008). Therefore, we expect that mineralisation rates by both channels will increase after land abandonment. Because of the decrease in plant productivity when secondary succession proceeds, the root channel biomass will decrease after land abandonment and therefore mineralisation rates by this channel were expected to decrease.

2. Methods

2.1. Areas and sampling

Three ex-arable fields, abandoned in 2002, 1995 and 1982, and a heathland (as a reference natural ecosystem), were chosen based on a similar agricultural history and physical characteristics (Holtkamp et al., 2008). The fields were located in the same geographical region in the central part of the Netherlands on well-drained sandy soil originating from glacial deposits (Kardol et al., 2005; Van der Wal et al., 2006b). In this paper, we refer to the field abandoned in 2002 as young, abandoned in 1995 as mid-aged, and abandoned in 1982 as old field. We defined field age as the number of years since abandonment (so that our fields had a field age of 2, 9 and 22 years respectively).

At four sampling dates in April, June, September and November 2004, soil samples of 25 cm wide $\times$ 25 cm long $\times$ 10 cm deep were collected. At each sampling date, at each field within a 50 $\times$ 50 m area we collected four such samples from randomly chosen positions. Each sample was minimally 10 m away from another sample and minimally 20 m away from the edge of the field. In total, we collected 4 (fields) $\times$ 4 (seasons) $\times$ 4 (samples within field) = 64 samples. Although we recognise that mobile organisms such as micro-arthropods might disperse over large ranges, the active dispersal of most of these organisms is rather limited (Norton, 1994; OConnor, 1994). Therefore, we assumed independency between samples that were taken from plots when being 10 m away from each other.

Each sample was hand-sieved (Ø 4 mm) and mixed, after which sub-samples for C (kg C/ha/10 cm (depth)/yr) and N (kg N/ha/10 cm (depth)/yr) mineralisation rates analyses were taken. We measured the mineralisation rates following procedures described by Van der Wal et al. (2006a). For C mineralisation rates, the mass of CO_2 released over a 48-h period was measured. These lab incubations should be seen as potential mineralised C. For N mineralisation rates, the mass of inorganic N at the start and after 25 days was measured, where the difference in mass between these dates was taken as the measure of N mineralisation rate (or possibly immobilisation). Because mineralisation was measured at 20 °C and the average soil temperature was 8 °C, we scaled mineralisation rates as in Andrén et al. (1990) with a Q_{10} value, i.e. the factor by which mineralisation rates change per 10 °C, of 2.5 (Tjoelker et al., 2001) to have a first order estimate of annual mineralisation rates.

Soil organic matter and soil organism biomass was measured by Holtkamp et al. (2008) for the same samples as mentioned above. Soil organic matter was divided in three fractions: recalcitrant (R),