Geophysical Research Abstracts
Vol. 16, EGU2014-16375, 2014
EGU General Assembly 2014

N enrichment decouples the relation between N and P cycling in the rhizoplane but not in the bulk soil: evidence from an N-manipulation field experiment in a Mediterranean ecosystem

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Increasing deposition of reactive nitrogen (N) is a major threat to global ecosystems' stability. Due to the N cascade, the 'extra' N affects the air, water and soil, climate and ecosystems' stability and biodiversity, costing 70-320 billion € per year in Europe alone. Within the European Union, the Mediterranean Basin is a N-limited biodiversity hotspot where N deposition is expected to increase threefold by 2050. However, most of our knowledge of the impacts of increased N availability on ecosystems comes from northern Europe and America. Since Mediterranean-type ecosystems appear on the 'neglected ecosystems list', in 2007 a unique N-manipulation field experiment (N dose and form) was set up in southern Europe (Portugal). The study site is located in Arrábida Natural Park, Portugal (38°29'N, 9°01'W). Vegetation consists of a dense maquis with skeletal soil (15-20 cm deep). We applied 3 N-treatments: 40 and 80 kg N ha-1 yr-1 of ammonium nitrate ($NH4NO_3$) and 40 kg N ha-1 yr-1 of ammonium (1:1 mix of NH4Cl and (NH4)2SO4). Each treatment had 3 replicates (400 m2 plots).

Since Mediterranean ecosystems are co-limited by N and phosphorus (P), increasing N availability is expected to alter N and P cycling, i.e. the no longer limiting N is likely to be channelled into P acquisition. Under increased N availability, we expect that phosphatase production and maintenance is no longer tied to the degradation of N-containing macromolecules. To explore this hypothesis, the extracellular enzyme activity (EEA) patterns of the dominant plant species' roots and surrounding soils were compared.

We used a novel technique for EEA profiling to measure the activity of acid phosphatase and N-related enzymes (N-Acetylglucosaminidase and Leucine aminopeptidase). The proportions of roots and soil were determined per 100 g soil-root agglomerate to extrapolate the total turnover of each compartment.

The total EEAs expressed per agglomerate were similar in soil and root compartments, even though the latter only contributed 2% to the total. This highlights the importance of the root surface (rhizoplane) as a compartment for nutrient cycling within the ecosystem. In the rhizoplane, linear correlations between N-related enzymes and phosphatase activity observed under natural conditions were lost upon addition of N, while in the soil, and despite the N additions, the linear correlations between N-related enzymes and phosphatase activity were maintained. Since most of the applied N is temporarily stored in the biotic compartment, the plant probably has enough N available to invest in rhizoplane phosphatases or provide microorganisms with the nutrients needed to exhibit higher activities. In contrast, as the inorganic N has been taken up by the plants, the soil microorganisms have to rely on N-containing polymers. Our data suggest that the additions of N decoupled the relation between activities of phosphatase and N-related enzymes in the rhizoplane but not in the bulk soil.