

# Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands

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## Abstract

Nitrogen (N) availability in grasslands varies with agricultural land use. Traditional management regimes of mowing for hay and manuring in subalpine meadows maintain plant communities with exploitative functional strategies suited to fertile soils with fast turnover of nutrients. We investigated whether the neglect of traditional practices has led to a reduction in N availability in two parallel ecosystems (terraced and unterraced fields). Soil nitrate and ammonium contents were assessed using soil cores and ion exchange resins over a 1-year period, and assays of microbial nitrifying and denitrifying enzyme activities, made early in the growing season. A large difference in pH between the two ecosystems, caused by historical ploughing, facilitated greater N availability in terraced than unterraced fields. Abandonment of manuring and mowing caused a reduction in N availability and N transformation processes, which correlated with a shift in the plant community towards more-conservative functional strategies and greater dominance by grasses. We propose that positive feedback between the grassland management regime and dominant plant functional strategy maintained high N availability in these managed subalpine grasslands. When traditional practices of mowing and manuring are neglected, direct management effects combined with the spread of grass species with conservative strategies force down N availability in the soil, reduce microbial activity, change the pH, and lead to a long-term loss of characteristic herbaceous subalpine-meadow species.

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## 1. Introduction

In grasslands, nitrogen (N) availability to plants and microbes varies with the environmental conditions and agricultural land use (Vitousek and Howarth, 1991). Management intervention can influence soil fertility directly through fertiliser inputs (Bahn et al., 1999; Makarov et al., 2003), and indirectly via management-induced changes in plant composition (Collins et al., 1998; Patra et al., 2006). Mowing and grazing accelerate the N cycle (Bardgett et al., 1998; Güsewell et al., 2005), and

encourage increased above- and below-ground plant growth (Leriche et al., 2001) and root exudation (Lipson and Schmidt, 2004). Plants in mown grasslands must complete their life cycle relatively early in the season, thus the recycling of roots from early-season species in mown fields boosts soil nutrient contents sooner than in unmown fields (Bardgett et al., 1998).

Competition for N among plant species and between plants and microbes is intrinsically linked to soil fertility (Bardgett et al., 2005). Changes in the functional composition of plant communities feed back to the rate of N cycling, dependent on plants' strategy for nutrient retention (Hobbie, 1992). N cycling is slowed by plants of conservative strategy, that retain nutrients through reabsorption and foliar longevity and utilise mycorrhizal symbiosis to enhance nutrient acquisition (Chapman

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et al., 2006). This contrasts with an exploitative strategy involving the rapid assimilation of nutrients and early production of nutrient-rich litter (Bardgett et al., 2005).

Species-rich subalpine grasslands present a good model system in which to investigate the ecosystem processes integral to changes in the composition and functional strategy of plant communities (Dale et al., 2005; Lemaire et al., 2005). This information can be used to identify management strategies that maintain the grasslands' integrity, and to assess impacts on ecosystem function and services (Spehn et al., 2005; Quéfier, 2006). Traditionally farmed grassland meadows are characteristic of the European Alps, and have been documented since their habitation (Rousset, 1977). Mowing enables short-lived herbs, that exploit early-season ecological niches (Louault et al., 2005), to flourish, and grazing reduces the dominance of grasses in favour of short-lived rosette species (Bullock et al., 2001 and references therein). But farmers are increasingly abandoning the traditional practices of hay making and grazing (MacDonald et al., 2000). This leaves neglected subalpine grasslands likely to succeed towards shrub- or tussock-grass- dominated communities, and eventually semi-natural forest, associated with loss of fertility (Tappeiner et al., 1999), and plant and animal diversity (Losvik, 1999). In the Austrian Alps, decreased N mineralisation following complete abandonment resulted in succession of a grassland to a dwarf shrub community (Tasser and Tappeiner, 2002). This change was associated with a reduction in pH, and shift from a predominately bacterial to fungal microbial community in the abandoned sites (Zeller et al., 2000).

At our field sites in the French Alps, prior assessment of plant community composition in subalpine grasslands under various grazing, mowing, and manuring regimes identified distinct changes in plant functional composition, even in adjacent fields (Quéfier et al., 2006). Community-aggregated leaf traits (Garnier et al., 2004), such as leaf N content, indicated that the subalpine plant communities

studied were increasingly N limited as management intensity decreased (Table 1; Quéfier et al., 2006). However, foliar nutrient concentrations are not always reliable indicators of nutrient limitation in alpine systems, since use of stored nutrients may supersede "luxury consumption" of soil nutrients in slow-growing plants (Bowman et al., 2003).

Along a gradient of fertility, differences in rates of N cycling are expressed as changes in the abundance of the various forms of soil N (nitrate, ammonium, and organic N), and in the rates of N transformation processes (Schimel and Bennett, 2004). The objective of our study was to test whether the reductions in soil fertility with cessation of mowing and manuring suggested at our study sites by plant indicators (Table 1) are confirmed by changes in N form, availability, and key microbial processes. Foliar traits suggest a continuum of decreasing fertility with neglect of manuring and mowing. The mown fields produce exploitative plant communities containing more tall fast-growing herbaceous plants (Table 1; Quéfier et al., 2006). In the unmown fields, the plant communities are dominated by the tussock grasses *Festuca paniculata*, and *Bromus erectus*, which exhibit conservative functional strategies (Quéfier et al., 2006). Accordingly, we predicted a decrease in both ammonium and nitrate availability in the unmown fields. In this case, immobilisation should dominate the microbial community, and plants and microbes should strongly compete for soil N (Schimel and Bennett, 2004) so that nitrifying and denitrifying enzyme activities should be restricted.

To test these hypotheses, we performed a suite of measurements to survey soil N concentrations and availabilities throughout the year, and assessed key microbial activities on soil samples taken early in the growing season, which corresponds with a period of high N availability critical for plant growth. We monitored soil N using ion exchange resins at multiple depths over a 12-month period to track seasonal trends, in conjunction with

Table 1  
Soil characteristics (0–10 cm depth) and ecosystem properties of the five management treatments

Historical cultivation	Terraced			Unterraced	
	Fertilised mown	Mown	Unmown	Mown	Unmown
Current management					
Stoniness (%) > 2 mm	13 ± 8 <sup>A</sup>	21 ± 10 <sup>B</sup>	23 ± 14 <sup>B</sup>	0 ± 1 <sup>C</sup>	1 ± 1 <sup>C</sup>
Hotspots of NO <sub>3</sub> (% occurrence)	14.7 ± 4.2 <sup>A</sup>	8.0 ± 1.6 <sup>A</sup>	10.2 ± 3.0 <sup>A</sup>	15.3 ± 4.4 <sup>A</sup>	9.6 ± 3.4 <sup>A</sup>
Hotspots of NH <sub>4</sub> (% occurrence)	10.7 ± 1.9 <sup>A</sup>	4.4 ± 0.7 <sup>B</sup>	5.3 ± 1.6 <sup>B</sup>	6.2 ± 0.8 <sup>B</sup>	2.2 ± 0.7 <sup>C</sup>
Soil water content (%) May 2005	60.1 ± 3.2 <sup>A</sup>	61.6 ± 1.3 <sup>A</sup>	62.2 ± 1.2 <sup>A</sup>	63.1 ± 1.4 <sup>A</sup>	60.4 ± 2.0 <sup>A</sup>
Soil water content (%) July 2004	20.8 ± 2.0 <sup>A</sup>	19.4 ± 1.5 <sup>A</sup>	18.3 ± 2.0 <sup>A</sup>	26.9 ± 1.4 <sup>B</sup>	28.6 ± 1.5 <sup>B</sup>
Organic carbon (%)	14.2 ± 1.9 <sup>A</sup>	16.4 ± 1.1 <sup>B</sup>	15.7 ± 0.5 <sup>B</sup>	12.4 ± 1.0 <sup>C</sup>	10.6 ± 0.4 <sup>C</sup>
NNI (%)	70.3 ± 0.9 <sup>A</sup>	64.5 ± 3.5 <sup>B</sup>	55.0 ± 4.5 <sup>C</sup>	68.7 ± 1.4 <sup>B</sup>	65.7 ± 3.7 <sup>B</sup>
LNC (%)	2.29 ± 0.07 <sup>A</sup>	1.75 ± 0.03 <sup>B</sup>	1.59 ± 0.04 <sup>C</sup>	1.42 ± 0.05 <sup>D</sup>	1.34 ± 0.04 <sup>D</sup>
Annual litter decomp. (% loss)	60.8 ± 1.5 <sup>A</sup>	55.1 ± 0.6 <sup>B</sup>	48.1 ± 7.7 <sup>BC</sup>	53.3 ± 2.2 <sup>B</sup>	43.9 ± 4.0 <sup>C</sup>
Early-season net primary production (g m <sup>-2</sup> )	73.5 ± 3.9 <sup>A</sup>	47.7 ± 5.0 <sup>BC</sup>	39.5 ± 6.1 <sup>C</sup>	74.1 ± 3.8 <sup>A</sup>	56.4 ± 8.6 <sup>B</sup>

Community-aggregated leaf nitrogen content (LNC), and ecosystem processes from Quéfier et al. (2006). Nitrogen nutrition index (NNI) is the % canopy N content relative to a critical value representing no N limitation (see Duru et al., 1997; Quéfier et al., 2006). The % occurrence of hotspots among samples for each land use is given. Letters indicate a significant difference among land uses.

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