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Coupling of microbial nitrogen transformations and climate in sclerophyll forest soils from the Mediterranean Region of central Chile

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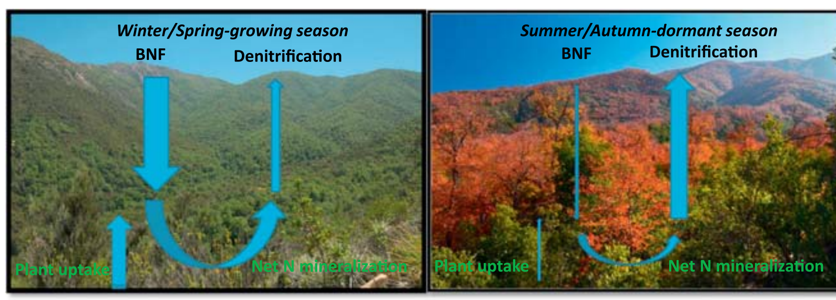
HIGHLIGHTS

- Microbial N transformations evidence a strong seasonal pattern.
- Diazotrophic activity and net N mineralization decrease during summer drought.
- Denitrification increase during summer drought.
- Water addition in field experiments increase diazotrophic activity.
- Predicted increase in summer drought period may lead to a depletion of soil N.

GRAPHICAL ABSTRACT



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ABSTRACT

The Mediterranean region of central Chile is experiencing extensive "mega-droughts" with detrimental effects for the environment and economy of the region. In the northern hemisphere, nitrogen (N) limitation of Mediterranean ecosystems has been explained by the decoupling between N inputs and plant uptake during the dormant season. In central Chile, soils have often been considered N-rich in comparison to other Mediterranean ecosystems of the world, yet the impacts of expected intensification of seasonal drought remain unknown. In this work, we seek to disentangle patterns of microbial N transformations and their seasonal coupling with climate in the Chilean sclerophyll forest-type. We aim to assess how water limitation affects microbial N transformations, thus addressing the impact of ongoing regional climate trends on soil N status. We studied four stands of the sclerophyll forest-type in Chile. Field measurements in surface soils showed a 67% decline of free-living diazotrophic activity (DA) and 59% decrease of net N mineralization rates during the summer rainless and dormant season, accompanied by a stimulation of in-situ denitrification rates to values 70% higher than in wetter winter. Higher rates of both free-living DA and net N mineralization found during spring, provided evidence for strong coupling of these two processes during the growing season. Overall, the experimental addition of water in the field to litter samples almost doubled DA but had no effect on denitrification rates. We conclude that coupling of microbial mediated soil N transformations during the wetter growing season explains the N enrichment of sclerophyll forest soils. Expected increases in the length and intensity of the dry period, according to climate change models, reflected in the current mega-droughts may drastically reduce biological N fixation and net N mineralization, increasing at the same time denitrification rates, thereby potentially reducing long-term soil N capital.

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1. Introduction

Mediterranean-type ecosystems are currently subjected to increasing drought stress due to more intense heat and seasonal droughts, a phenomenon that is common to all five regions of the world where they occur (IPCC, 2013). Over the past three decades, central Chilean climate has been marked by the occurrence of an extensive "mega-drought", which is driven to large extent by anthropogenic climatic forcing (Boiser et al., 2016). Such "mega-drought" has important consequences for the storage and provision of water and nutrients in managed and natural ecosystems, for the frequency of both human-set as well as wildfires affecting ecosystems and human property, and for the long-term survival of tree populations in the region (CR2, 2015).

Element cycles such as nitrogen (N) are strongly driven by biotic and climatic variables that are subjected to strong seasonal and supra-annual fluctuations in Mediterranean-type ecosystems. These ecosystems are characterized by limited N availability because of reduced moisture levels during the extended dry summer period and the poor chemical quality of senescent organic matter, which slows down recycling in sclerophyll woodland soils by influencing decomposition and mineralization processes. Accordingly, water and nutrient availability, N availability in particular, are the most frequent limiting factors for primary productivity in Mediterranean-type ecosystems (Sardans and Peñuelas, 2013; Delgado-Baquerizo et al., 2016).

The main process supplying "new" N to remote, less polluted ecosystems, such as Artic, Sub-Artic, southern temperate, and Sub-Antarctic forests, is biological nitrogen fixation (BNF) (DeLuca et al., 2002; Pérez et al., 2003; Rousk et al., 2015, 2017; Pérez et al., 2017). This process is ordinarily carried out by diazotrophic bacteria, either free-living or symbiotic, which are endowed with the nitrogenase enzyme complex that enables them to transform atmospheric molecular N_2 directly to ammonia. Heterotrophic and autotrophic soil organisms, on the other hand, decompose fixed organic N, which becomes dissolved in the soil solution and mineralized into inorganic N forms, such as ammonium and nitrate that can be readily taken up by microbes and plants, thereby being retained within the ecosystem (Chapin et al., 2002). However, microbial-mediated dissimilatory nitrate reducing processes can cause N losses from the ecosystem via denitrification, which is carried out by denitrifying bacteria that reduce nitrate to nitrous oxide (N_2O), a potent greenhouse gas (Chapin et al., 2002). All of these oxidizing-reducing series of processes are mediated by a wide array of microbial enzymes that are strongly regulated by multiple feedbacks related to substrate availability, as well as by local changes in air temperature and soil moisture levels. Consequently, key microbial-mediated N transformations, such as BNF, net N mineralization, and denitrification processes that are essential for maintaining soil N pools, can be altered under current global change (Vitousek, 1994).

Examples of climatic alterations are frequently reported for Mediterranean-type regions. In fact, a global comparison of arid and semiarid regions shows that an observed increase in the aridity index has caused a drop in the pools of total N and C, and N mineralization rates in soils (Delgado-Baquerizo et al., 2013, 2016). A recent global meta-analysis reported enhanced gaseous N losses from soils, as nitric oxide emissions via denitrification, in response to experimental drought (Liu et al., 2017). Moreover, temporal variability of N pulses in Mediterranean ecosystems could mean even greater vulnerability to global change (Sardans and Peñuelas, 2013). In highly seasonal, arid and semi-arid environments, under high industrial N deposition, as in the northern hemisphere, nutrients are supplied in pulses following rain events, which in Mediterranean regions are restricted to the winter months (Fenn et al., 2003). In the North American chaparral, it is well documented that available soil N increases after the first winter rain, causing an abrupt pulse of hydrological N losses, mainly because of the decoupling of N inputs and plant uptake during the dormant season (Vourlitis et al., 2009). As a consequence, despite the high dry N deposition occurring during the dry season, the decoupling of rainfall and N inputs maintains N limitation in North American Mediterranean-type ecosystems (Ochoa-Hueso et al., 2014; Homyak et al., 2014). In contrast, soils from the Mediterranean region in central Chile are often considered N-rich, when compared with other Mediterranean-climate regions of the world, and with the California chaparral in particular (Miller, 1981; Rundel, 1982; Shaver, 1983; Stock and Verboom, 2012; Sardans and Peñuelas, 2013).

The main goal of this study is to disentangle the patterns of the major microbial N transformations, i.e., free-living N fixation, N mineralization, and denitrification, and their correspondence with the Mediterranean-climate seasonal contrasts in the sclerophyll forest-type from Central Chile. We will experimentally assess how water supply regulates BNF and denitrification processes.

We asked the following three questions about soil N transformations:

1. How do microbial N transformations differ among seasons in the Mediterranean-type ecosystem of central Chile? We expect to find evidence for a pronounced decline of BNF, N mineralization and denitrification during the dry summer and dormant season.
2. Does experimental water addition to sclerophyll forest soils in the field increase the rates of BNF and denitrification? We expect to find evidence for water limitation of both processes.
3. Is the coupling of microbial N transformations during the wetter growing season a key factor explaining the reported higher N status in Chilean Mediterranean-climate soils?

Answering these questions will reveal whether the coupling of microbial N transformations and seasonal climate could determine the amount of soil N that would become available for plant uptake during the growing season, and eventually determine the retention or loss of soil N capital. Moreover, understanding the responses of both BNF and denitrification processes to experimentally enhanced water supply, and to the seasonal variation in the patterns of net N mineralization, will be useful information to predict the vulnerability of Mediterranean-type ecosystems to increasing summer drought, as such tendency predicted by climate change models for central Chile.

2. Materials and methods

2.1. Study sites

We studied four stands of the sclerophyll forest-type, located on the Coastal Range at the Nature Reserve "Roblería del Cobre de Loncha" (RCL), where the co-dominant trees in the canopy were evergreen sclerophyllous trees and deciduous *Nothofagus obliqua* (southern beech). The Reserve is located 80 km southwest of the city of Santiago (Fig. 1) in the Mediterranean region of central Chile. Mean annual precipitation is 454 mm with a mean annual temperature of 16.6 °C. The majority of the annual precipitation (63%) falls during the austral winter, from June to August, with only 0.66% of it falling during the austral summer months, December–March (https://es.climate-data.org). Field campaigns were conducted each season (summer, fall, winter and spring) from September 2015 (late winter) to March 2016 (early autumn). This was a year with low annual precipitation, reaching only 170 mm, according to records from the closest meteorological station to the study site (Santiago). Seasonally, 78% of the rain fell during the winter months (June–August), with complete lack of rain from early summer, December 2015, to early autumn, March 2016 (www.meteochile.cl). A decline of about 30% in mean annual precipitation, has been occurring since 2010 in central Chile and climatologists have called this climatic anomaly a "mega-drought" (Boiser et al., 2016; CR2, 2015).

Geological substrate for all sites are primarily granitic/granodioritic mixed with volcanic sediments. Soil type belongs to typical Xerochrepts developed over colluvium material (FAO-UNESCO, 1987). The Nature