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Interactive effects of forest die-off and drying-rewetting cycles on C and N mineralization

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ABSTRACT

Mediterranean forests will experience more frequent and intense drought periods and extreme rainfall events in the coming decades. Concomitantly, drought-induced forest die-off is likely to increase. Changes in rainfall patterns and forest die-off directly influence soil microbial communities and activity and, consequently, carbon (C) and nitrogen (N) turnover, but their interactive effects have not yet been explored. We investigated the short-, and the long-term interactive effects of forest die-off and drying-rewetting cycles on soil C and N mineralization rates of a Mediterranean woodland. Soil samples collected under and out of the influence of holm oak (*Quercus ilex*) trees with different defoliation degrees (six healthy, six affected and six dead) were incubated under two contrasting water regimes (i.e. drying-rewetting cycles vs. constant soil moisture). Potential soil C and N mineralization responded differently to water regimes, with an overall 55% increase in C mineralization and a 22% decrease in N mineralization in the drying-rewetting cycle treatment compared to the constant moisture treatment. Holm oak decline decreased the response of C mineralization while increased the response of N mineralization to the drying-rewetting cycles at both the short- and the long-term. Moreover, N turnover showed a higher sensitivity to these environmental changes than that of C during most of the year. Our study provides solid evidence that an intensification of the drying-rewetting regimes can result in a decoupling of soil C and N cycles in Mediterranean forests and that forest die-off might enhance this decoupling at both the short- and the long-term, with important implications for the ecosystem functioning.

1. Introduction

Soils represent the largest carbon (C) and nitrogen (N) pools in forest ecosystems (Schlesinger and Bernhardt, 2013). When a dry soil is rewetted, a pulse of microbial activity occurs, with important consequences for soil C and N cycling at ecosystem level (Blazewicz et al., 2014; Borken and Matzner, 2009; Jarvis et al., 2007). This microbial activity pulse, named the *Birch effect* after one of its first observers (Birch, 1958), can be a major contribution to ecosystem C release into the atmosphere (Jenerette et al., 2008). The size of the pulse depends on the intensity and duration of the rainfall and the previous drought event, as well as on the vegetation and soil organic matter content and quality (Huxman et al., 2004; Meisner et al., 2015; Morillas et al., 2017; Song et al., 2017; Wang et al., 2016). Regional- to global-scale climate change projections regarding precipitation dynamics remain relatively uncertain. However, the frequency and intensity of droughts as well as of extreme rainfall events in the Mediterranean region are expected to increase (IPCC, 2013). Also, the rainfall regimes of semiarid areas worldwide are expected to be characterized by a lower number of more concentrated rainfall events (Lafuente et al., 2018). These changes will likely increase the intensity and importance of rainfall pulses and drying-rewetting cycles in the Mediterranean basin, already

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Table 1
Main biogeochemical ($n = 6$) and bacterial functional alpha-diversity ($n = 5$) variables. Values represent the mean (± 1SE). Statistically significant effects of defoliation (P_d) and ecotype (P_e) are represented by bold P values. Different letters represent significant differences among defoliation degrees in each ecotype ($P < 0.05$, ANOVA). Underlined values denote significant differences between ecotypes for the respective defoliation degree and season ($P < 0.05$). TC = total carbon; TN = total nitrogen; SIR = substrate-induced respiration; H'_{bact} = soil bacterial functional Shannon index; S'_{bact} = soil bacterial functional richness, Sp = spring; Su = summer.

		Holm oak ecotype			Grassland ecotype			Mixed models	
		Healthy	Affected	Dead	Healthy	Affected	Dead	P_d	P_e
TC	Sp	3.06 (0.72)	2.34 (0.28)	2.60 (0.31)	1.04 (0.08)	1.38 (0.21)	1.33 (0.18)	0.925	< **0.001**
TN	Sp	0.24 (0.04)	0.19 (0.02)	0.20 (0.02)	0.11 (0.01)	0.10 (0.02)	0.12 (0.01)	0.365	< **0.001**
NH_4^+-N	Sp	5.28 (2.01)	1.83 (0.90)	2.84 (0.85)	0.10 (0.10)	0.08 (0.08)	1.51 (1.36)	0.387	< **0.001**
	Su	7.64 (1.41)a	3.87 (0.70)ab	3.66 (0.71)b	4.15 (2.22)	2.68 (0.60)	4.09 (0.88)	0.293	**0.014**
NO_3^--N	Sp	4.96 (0.73)	5.59 (0.57)	4.24 (0.21)	2.48 (0.59)	2.21 (0.57)	2.39 (0.38)	0.605	< **0.001**
	Su	1.07 (0.22)	1.84 (0.23)	1.75 (0.33)	1.39 (0.22)	1.35 (0.12)	1.85 (0.33)	0.095	0.894
SIR	Sp	31.5 (9.28)	38.7 (4.73)	46.0 (16.0)	17.7 (4.62)	13.8 (2.39)	39.5 (8.37)	0.073	**0.036**
	Su	20.9 (6.67)	16.1 (1.86)	15.6 (2.77)	10.1 (2.32)	8.38 (1.43)	8.42 (1.24)	0.775	< **0.001**
H'_{bact}	Sp	4.47 (0.05)	4.39 (0.06)	4.47 (0.07)	4.09 (0.09)	3.90 (0.12)	4.28 (0.11)	**0.027**	< **0.001**
	Su	4.17 (0.05)	4.07 (0.10)	3.89 (0.06)	4.02 (0.10)	3.68 (0.14)	3.75 (0.09)	0.052	< **0.001**
S_{bact}	Sp	27.8 (0.58)	27.2 (0.80)	27.8 (0.58)	24.0 (1.52)	23.2 (1.46)	26.4 (1.17)	0.212	< **0.001**
	Su	25.0 (0.77)a	23.0 (1.55)ab	19.6 (1.63)b	21.8 (2.11)	17.8 (2.13)	16.8 (2.08)	**0.042**	**0.001**

TC and TN are expressed in %; NH_4^+-N and NO_3^--N are expressed in mg N kg soil^{-1}; SIR is expressed in mg C kg soil^{-1} h^{-1}.

characterized by a large intra-annual variation in soil water content that largely regulates ecosystem functioning (Gallardo et al., 2009). Whilst recent studies have suggested that small rainfall pulses and drying-rewetting processes may be the main driver of soil C and N cycling in Mediterranean environments (Rey et al., 2017; Song et al., 2017; Wang et al., 2016), the effects of drying-rewetting cycles on both C and N mineralization rates of Mediterranean forest soils have not yet been well elucidated (Wang et al., 2016).

Mediterranean forests are representative of one of the most widely distributed semi-arid areas throughout the world (Jarvis et al., 2007) and are considered biodiversity hotspots. Intensified droughts are increasing tree defoliation and mortality in these forests (Carnicer et al., 2011; Lloret et al., 2004). On the short-term, soil microbial–driven C and N mineralization could rise followed by rapid N losses due to stimulated decomposition of litter, roots and dead wood (Edburg et al., 2012; Lloret et al., 2014; Xiong et al., 2011). On the long-term, repeated drought-induced mortality events, along with an unsuccessful recruitment of the dominant tree species in these forests may lead to a vegetation succession process where trees would be replaced by understory species (Ibáñez et al., 2015; Saura-Mas et al., 2014). This succession process would have an impact on ecosystem functioning, and therefore on critical local and global ecosystem services, even more severe than the short-term direct effects of tree defoliation and mortality (Anadón et al., 2014; Ávila et al., 2016; Díaz, 2014). However, the impacts of forest die-off on soil microbial functioning both at the short- and long-term are still far from being understood (Ávila et al., 2016; Rodríguez et al., 2017). More importantly, although there is increasing evidence that multiple environmental changes can generate effects that are no predictable from single-factor studies (Doblas-Miranda et al., 2017; Matesanz et al., 2009; Morillas et al., 2015), how forest die-off may influence the response of microbial functioning to changing rainfall patterns has not been yet studied.

Herein, we aimed to investigate the short- and long-term interactive effects of forest die-off and drying-rewetting cycles on soil microbial activity, as determined by C and N mineralization rates, of a holm oak (*Quercus ilex*) woodland. To do so, we collected and biogeochemically characterized soil samples under (holm oak ecotype) and out (grassland ecotype) of the influence of selected holm oak trees with different defoliation degrees. Then, we measured soil potential C and N mineralization rates under two different water regimes (i.e. constant soil moisture vs. drying-rewetting cycles). The comparison among samples collected in the holm oak ecotype allowed us to explore the short-term effects of holm oak decline (HOD). The comparison among samples collected in both (holm oak vs. grassland) ecotypes allowed us to explore the HOD long-term effects under a plant succession scenery (Rodríguez et al., 2017). Based on previous studies that showed different sensitivity of N- and C-related processes to environmental changes (e.g. Durán et al., 2013; Morillas et al., 2015, 2017; Rodríguez et al., 2017; Tan and Wang, 2016), we hypothesized that soil C and N mineralization would response differently to drying-rewetting cycles, as well as to the interaction of HOD and soil water regime. Further, given the seasonality in soil water availability of Mediterranean ecosystems, and its influence on biogeochemical cycles, we hypothesized that the response of C and N mineralization to these environmental changes would vary depending on the time of the year (spring vs. summer).

2. Material and methods

2.1. Study site

The study was carried out in a holm oak woodland located in the central part of the Iberian Peninsula, southwest of Madrid (40°23′N, 4°11′W; 630–660 *m* above sea level). Climate is continental Mediterranean with mean annual temperature of 15 °C and mean annual precipitation of 558 mm (Ninyerola et al., 2005). Most rainfall concentrates from autumn to spring, while summers are warm and dry. Atmospheric N deposition in the study area is around 5–6 kg N ha^{-1} year^{-1} (Im et al., 2013; Ochoa-Hueso et al., 2013, p.). Soil is a Cambisol, sandy and slightly acid (pH ~ 6.3), with low total C and N content (Table 1). Aboveground vegetation is characterized by a tree density of ~180 trees ha^{-1}, mostly composed of *Quercus ilex* ssp. *Ballota* L. (holm oak) with scarce *Juniperus oxycedrus* Sibth. & Sm (cedar). The understory is dominated by *Retama sphaerocarpa* L., *Lavandula stoechas* ssp. *pedunculata* (Mill.) Samp. ex Rozeira, and diverse pasture species (see Rodríguez et al., 2017 for more information about the study site).

This region suffered a severe drought in 2005 (European Environment Agency, 2008), with a 55% decrease in the average annual rainfall. This drought resulted in a strong event of holm oak defoliation (around 20–30% of the total population) and mortality (15%) that persists (Valladares, unpublished data). Consequently, this woodland shows a successional chronosequence that goes from a range of holm oak trees with different defoliation degree (holm oak ecotype) to a grassland ecotype, with contrasting soil biogeochemistry and microbial diversity characteristics (Table 1).