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Short communication

New evidence that high potential nitrification rates occur in soils during dry seasons: Are microbial communities metabolically active during dry seasons?

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ABSTRACT

Emerging research is challenging existing paradigms of nitrogen (N) cycling in arid and semiarid ecosystems that experience distinct seasonal patterns in precipitation. We measured equal or greater potential nitrification rates in the dry season than the wet season in chemically and physically distinct soils along a three million year substrate age gradient in Arizona. These surprising and counterintuitive results are supported by recently published work in California Mediterranean grasslands. Considered together, these studies call attention to the need to measure process rates during the dry, non-growing season of xeric ecosystems. Several mechanisms may be responsible for these patterns, but we highlight the importance of understanding the contribution of archaeal ammonia oxidizers to nitrification in these seasonally dry ecosystems.

Arid and semiarid ecosystems cover one-third of the Earth's surface (Archibold, 1995), and many of these areas experience distinct seasonal precipitation patterns. In the last decade, a series of reviews have sought to draw attention to the importance of biogeochemical cycling in pulse driven ecosystems that experience less than 600 mm of precipitation y^{-1} (Austin et al., 2004; Collins et al., 2008; Borken and Matzner, 2009). Partly in response to this call for investigation, new research is challenging classical paradigms and advancing our understanding of nitrogen (N) cycling in water-limited ecosystems. Traditionally, it has been assumed that rates of soil N transformations are higher after rain events than during dry periods (Austin et al., 2004, Fig. 1a, b). It is important to note, though, that much of this research has focused on precipitation "pulses" in dry ecosystems rather than longer-term seasonal trends (Austin et al., 2004; Collins et al., 2008; Borken and Matzner, 2009). Below, we highlight unexpected observed seasonal dynamics of N cycling in water-limited ecosystems.

Higher fluxes of N were recently reported during dry periods than wet periods of the year in a California grassland that experiences a Mediterranean climate (Parker and Schimel, 2011). The patterns described by Parker and Schimel (2011) cast doubt on our understanding of seasonal dynamics of N cycling, but the scope of their inference was limited to California grassland soils. In this short communication, we present new results from four semiarid sites that support patterns observed by Parker and Schimel (2011). By introducing this supporting evidence, we broaden the limited scale of inference of Parker and Schimel (2011) to include semiarid sites with different vegetation types and timing and duration of dry and wet seasons than Mediterranean California grasslands. In addition, we seek to draw attention to several mechanisms that may result in these seasonal patterns.

The Substrate Age Gradient of Arizona (SAGA; Selmants and Hart, 2008, 2010) is a well-constrained three million year chronosequence located in piñon-juniper woodlands in northern Arizona. Northern Arizona, like many other semiarid or arid regions, has distinct dry and wet seasons. The typical climate of northern Arizona during the plant growing season (usually March to November) consists of warm, dry early summers followed by a warm, wet late summer "monsoon" precipitation pattern (Sheppard et al., 2002). The SAGA exhibits strong gradients of soil texture, water holding capacity, and

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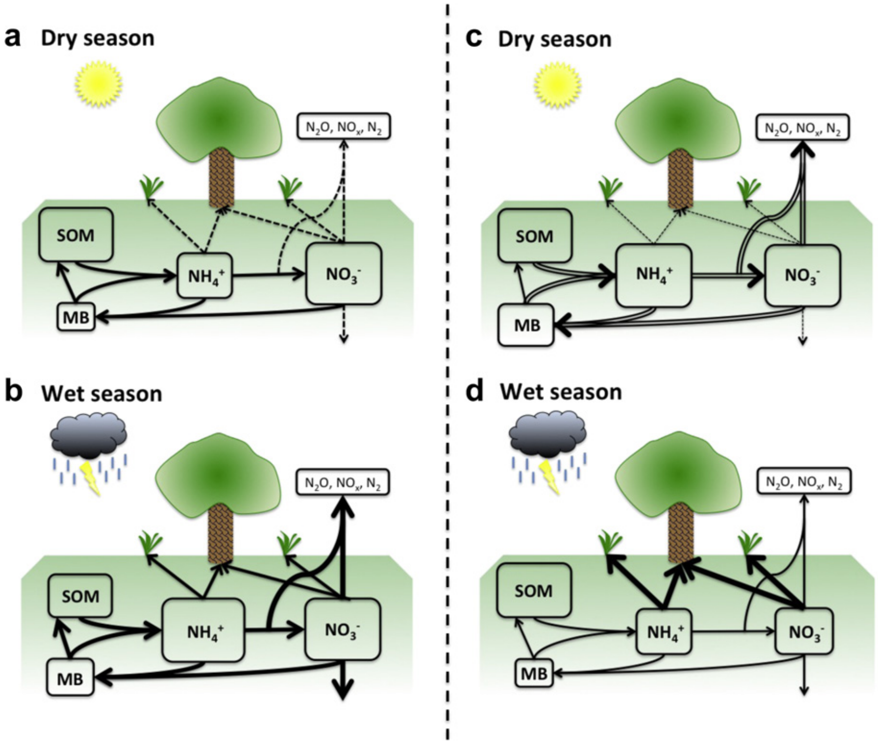

Fig. 1. Conceptual model of soil nitrogen (N) dynamics in arid and semiarid ecosystems. Panel a and panel b were adapted from Austin et al. (2004; a and b) and represent seasonal N dynamics during dry seasons (Panel a) and after precipitation pulses (Panel b). Panel c depicts dry season N dynamics; the hollow arrows depict the concept of an "empty pipe." An empty pipe signifies that the microbial community is active and capable of generating large fluxes, but these fluxes may or may not occur depending on substrate availability (production and transport in the soil). However, under the optimum laboratory conditions created by potential assays, these microbial communities are capable of generating large fluxes. Panel d depicts wet season N dynamics, which are 'potentially' smaller than dry season fluxes, but may be larger in net fluxes due to greater substrate availability (a "full pipe"). Pool sizes of soil organic matter (SOM), microbial biomass (MB), ammonium (NH$_4^+$), and nitrate (NO$_3^-$) are represented by the size of the box. Large fluxes are indicated by wide arrows, small fluxes are indicated by small arrows, and negligible fluxes are indicated by dashed arrows. Nitrous oxide (N$_2$O), various nitrogen oxides (NO$_x$), and dinitrogen (N$_2$) are depicted as the major fluxes of N from soil to the atmosphere.

carbon (C), N, and phosphorus (P) availability described in detail by Selmants & Hart (2008, 2010). Tree canopy interspaces are dominated by blue gramma grass (*Bouteloua gracilis* (Wild. ex Dunth) Lag. ex Griffiths) at the three oldest sites and by woody shrubs (*Fallugia paradoxa* (D. Don) Endl. ex Torr. and *Rhus trilobata* Nutt.) at the youngest site. The soil substrates that comprise the sites are 1 ky, 55 ky, 750 ky, and 3000 ky old. Pools and fluxes of C and N in soils increase between 1 and 750 ky and decline by 3000 ky in a pattern consistent with ecosystem retrogression (Selmants and Hart, 2008; Peltzer et al., 2010). Selmants and Hart (2008) found that fluxes of nitrogen, including net N mineralization, gross N mineralization, gross nitrification, and potential nitrification, all followed this retrogressive pattern during the wet season (Fig. 2).

We measured potential nitrification using the shaken soil-slurry method (Belser and Mays, 1980) as modified by Hart et al. (1994). Ammonium (NH$_4^+$) oxidation is the conversion of NH$_4^+$ to nitrite and is the rate-limiting step of nitrification. Ammonium oxidation is mediated by ammonia oxidizing bacteria and archaea (AOB/AOA). Relative differences in potential nitrification rates should reflect relative differences in the size of the AOB/AOA community because of the slow growth of AOB/AOA (Belser and Mays, 1980; Hart et al., 1994). We collected soil from 12 canopy interspaces (10 m diameter; Selmants and Hart, 2008) on each substrate age once during the dry early summer (June 15th) and once during the wet late summer (August 15th) of 2008. We used repeated measures analysis of variance to determine within-site seasonal differences in gravimetric soil water content and potential nitrification rates, indicated by a significant effect of time on the factor of interest.

Though gravimetric soil water content was consistently higher in the wet season than the dry season at all sites ($F > 38.59$; $P < 0.01$; Fig. 3a), mean dry season potential nitrification rates were as high or

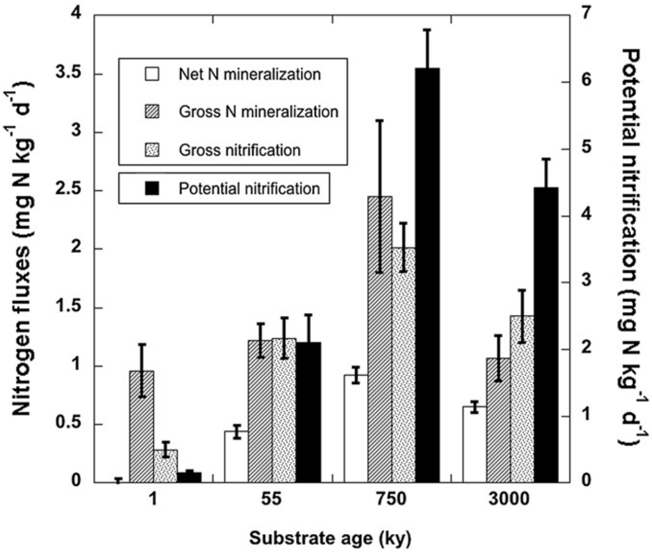

Fig. 2. Net nitrogen (N) mineralization, gross N mineralization, gross nitrification, and potential nitrification rates in the mineral soil (0–15 cm) among sites of the semiarid Substrate Age Gradient of Arizona (modified from Selmants and Hart, 2008) in 2004. Data are presented as means ± one standard error.