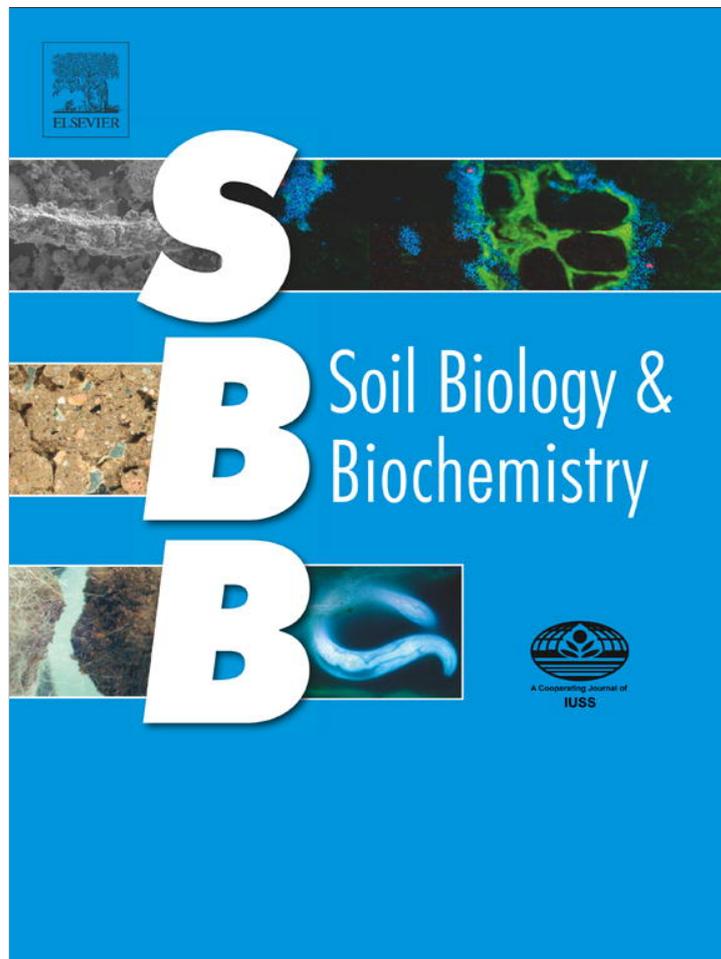


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Short communication

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

Benjamin W. Sullivan^{a,*}, Paul C. Selman^b, Stephen C. Hart^c^a School of Forestry, Northern Arizona University, USA^b Department of Natural Resources and Environmental Management, University of Hawai'i at Manoa, Honolulu, HI 96822, USA^c School of Natural Sciences & Sierra Nevada Research Institute, University of California, Merced, 5200 North Lake Rd., Merced, CA 95343, USA

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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.

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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; Selman 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

* Corresponding author. Present address: College of Forestry and Conservation, The University of Montana, 32 Campus Drive, Missoula, MT 59812, USA.

E-mail addresses: ben_sullivan@nau.edu (B.W. Sullivan), selman@hawaii.edu (P.C. Selman), shart4@ucmerced.edu (S.C. Hart).

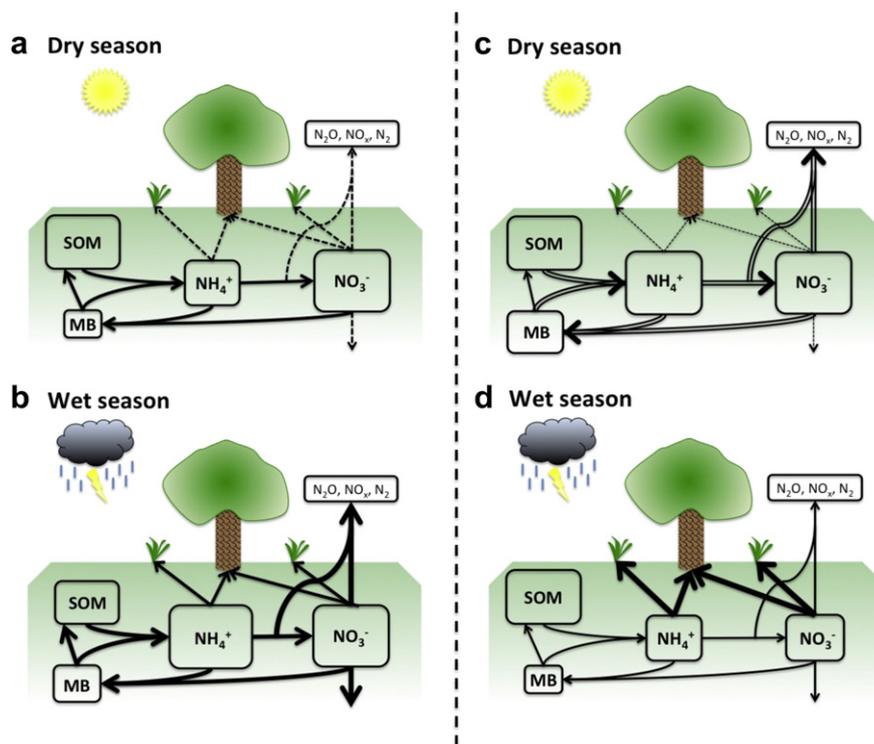


Fig. 1. Conceptual model of soil nitrogen (N) dynamics in arid and semiarid ecosystems. Panel a and panel b were adapted from Austin et al. (2004; a and b) and represent seasonal N dynamics during dry seasons (Panel a) and after precipitation pulses (Panel b). Panel c depicts dry season N dynamics; the 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_2O), 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

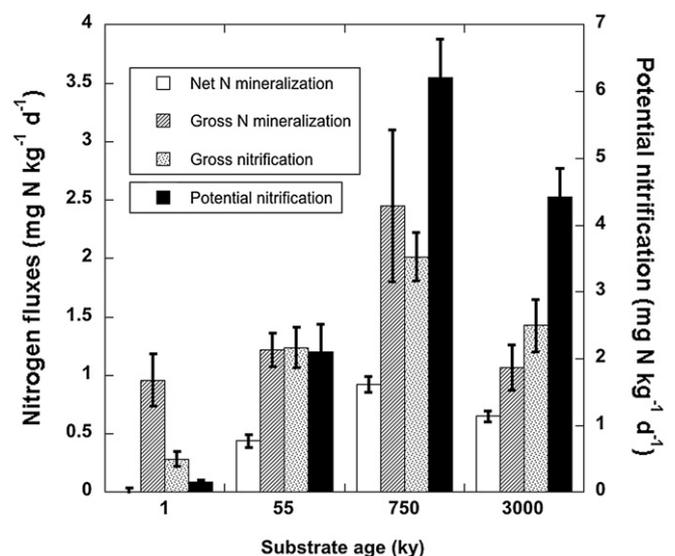


Fig. 2. Net nitrogen (N) mineralization, gross N mineralization, gross nitrification, and potential nitrification rates in the mineral soil (0–15 cm) among sites of the semiarid Substrate Age Gradient of Arizona (modified from Selmants and Hart, 2008) in 2004. Data are presented as means \pm one standard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

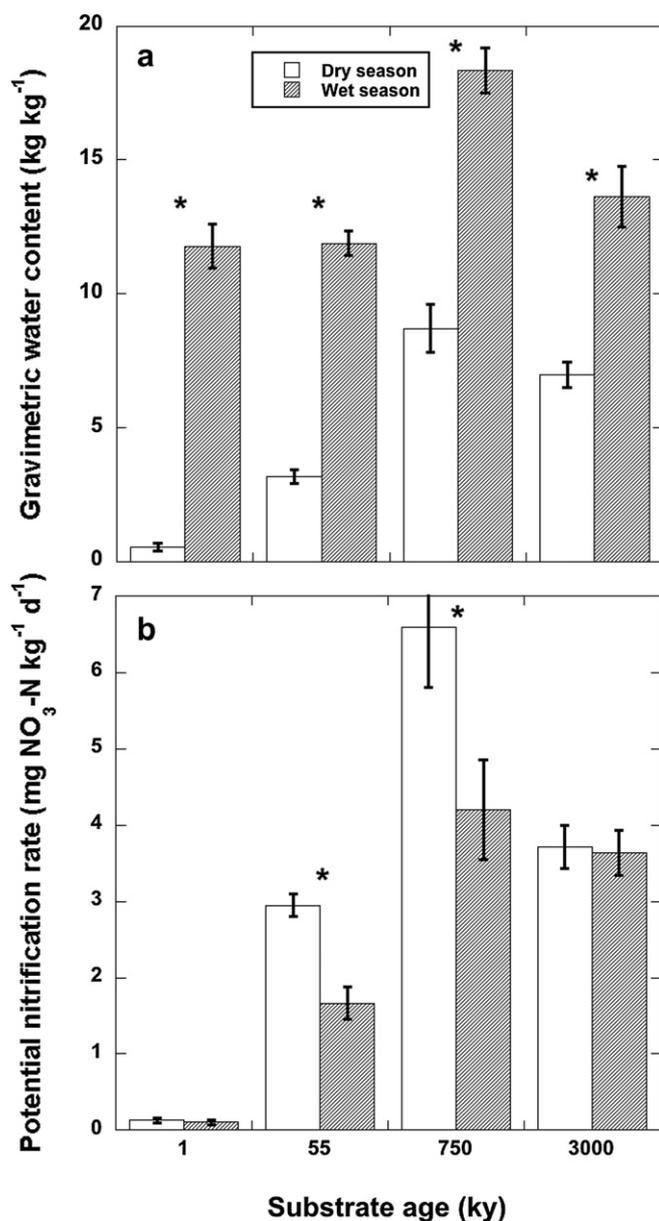


Fig. 3. Novel seasonal patterns of (a) gravimetric soil water content and (b) potential nitrification rates in the mineral soil (0–15 cm) among sites of the semiarid Substrate Age Gradient of Arizona. Data are presented as means \pm one standard error. Asterisks represent statistical differences between seasons within a site using repeated measures analysis of variance ($P < 0.05$).

higher at all SAGA sites than wet season rates (Fig. 3b). At the 55 ky-old and 750 ky-old sites, dry season potential nitrification was significantly higher during the dry season than the wet season ($F = 18.55$, $P < 0.01$ and $F = 15.61$, $P < 0.01$, respectively). Potential nitrification rates in both dry and wet seasons followed the previously established gradient of soil N availability (Fig. 2; Selmants and Hart, 2008); rates increased from the 1 ky-old to the 750 ky-old site, before declining by the 3000 ky-old site. The rates of potential nitrification we measured in August 2008 are remarkably similar to potential nitrification rates measured by Selmants and Hart (2008) during August 2004, indicating a high degree of interannual stability of the size of the AOB/AOA community. Our results are notable because we measured high dry season potential nitrification rates despite very different soil physical and chemical characteristics over three million years of soil development among the SAGA sites (Selmants and Hart, 2008, 2010).

Considered in light of the patterns reported by Parker and Schimel (2011), our results indicate that high potential rates of N transformations may occur generally in seasonally dry soils, and are cause to reconsider the model of seasonal N transformations proposed by Austin et al. (2004; Fig. 1c, d).

Because potential nitrification rates are indicative of the size of the AOB/AOA community (Hart et al., 1994), it would appear that the community size of AOB/AOA is at least as large, if not larger, in the dry season than the wet season despite extremely low soil water content during the dry season (less than 0.01 kg kg^{-1} at the 1 ky-old site). This pattern may reflect a broader trend of the of the entire microbial community; in addition to higher rates of nitrification, Parker and Schimel (2011) also found that microbial biomass was greater during the dry season than the wet season.

Several mechanisms may be causing these unexpected seasonal patterns, including competition between plants and AOB/AOA for NH_4^+ during the wet season when plants are metabolically most active (Kaye and Hart, 1997; Dore et al., 2008), higher predation and pathogen activity during the wet season (the mechanism proposed by Parker and Schimel, 2011), and differences in the AOB/AOA community structure, a mechanism that has not previously been reviewed. Based on a quantitative assessment of ammonia monooxygenase gene copies, ammonia oxidizing archaea outnumbered AOB at five sites with annual precipitation less than 600 mm in volcanically derived soils with different vegetation types along a nearby elevation gradient in northern Arizona (Adair and Schwartz, 2008). In particular, AOA were more abundant than AOB in the dry season at a site located among the SAGA with the same piñon-juniper woodland vegetation as the SAGA (Adair and Schwartz, 2008). In order to be able to tolerate extremely dry conditions, AOA must exhibit high affinity for NH_4^+ in order to be abundant during the dry season. Substrate supply is typically lowest during the dry season due to diffusional limitation (Stark and Firestone, 1995), and AOB/AOA are limited to the NH_4^+ immediately available within local microsites (Schimel and Bennett, 2004). A recent laboratory study showed that AOA grow at NH_4^+ concentrations 100 times lower than AOB (Martens-Habbena et al., 2009). The combined evidence of increased AOA abundance during the dry season (Adair and Schwartz, 2008), the high affinity of AOA to tolerate low NH_4^+ concentrations (Martens-Habbena et al., 2009), and our result demonstrating potential rates of nitrification as high or higher during the dry season than the wet season suggests that AOA may be adapted to extremely dry conditions as a mechanism to avoid competition for NH_4^+ .

This growing body of research indicates that microbial communities responsible for N transformations may be large and metabolically active despite extremely dry soil conditions and low rates of plant growth during dry seasons in arid and semiarid ecosystems. Net and gross rates of N transformations showed similar among-site patterns at the SAGA as potential nitrification during the wet season (Selmants and Hart, 2008), but it remains unclear if potential rates become decoupled from net and gross rates during the dry season. For instance, Parker and Schimel (2011) measured higher dry season net nitrification rates than wet season rates; yet Davidson et al. (1990) found that while potential nitrification rates stayed high several months into the dry season, net nitrification declined dramatically at the beginning of the dry season. The pattern of Davidson et al. (1990) is consistent with the “empty pipe” concept we propose (Fig. 1c, d): the microbial community may be large and metabolically active during the dry season. Maintenance of metabolic activity during the dry season may allow for a competitive advantage because rapid utilization of resources during pulse precipitation events (as in Fig. 1b, modified from Austin et al., 2004) could allow microbes to outcompete plants for mineral N (Kaye and Hart, 1997). Future research must consider pools and fluxes of N and microbial community dynamics during

the dry season in xeric ecosystems, and should explore the relative effect to the N cycle of the three mechanisms described above.

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