Soil Biology & Biochemistry 42 (2010) 1183–1188

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Short Communication

Bacterial diversity and occurrence of ammonia-oxidizing bacteria in the Atacama Desert soil during a "desert bloom" event

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ARTICLE INFO

Article history:
Received 16 October 2009
Received in revised form
13 March 2010
Accepted 17 March 2010
Available online 8 April 2010

Keywords:
Atacama Desert
Desert bloom event
Ammonia-oxidizing bacteria
Bacterial diversity

ABSTRACT

The Atacama Desert, located in northern Chile, is one of the driest deserts on the Earth. However, in some years, short and sporadic rainfall in the southern end of this desert has increased the soil moisture that produces ephemeral "desert bloom". Our goal was to assess the composition of the bacterial community and determine variations in the ammonia-oxidizing bacteria guild diversity from soils collected during the course of the "desert bloom" event. The bacterial composition from this arid soil was determined by cloning and sequencing the 16S rRNA gene. A relatively high diversity of clones belonging to 14 bacterial groups was detected. The ammonia-oxidizers showed a significantly higher diversity of *amoA* gene clones after the "desert bloom" than during or at the beginning of this event. All sequences obtained were related to *Nitrosospira* genera and environmental clones. These results suggest that the diversity of ammonia-oxidizing bacteria in this arid soil can be affected by the occurrence of "desert bloom".

The Atacama Desert occupies a large part of the Chilean territory north of the 29th – parallel and is considered one of the most extreme arid deserts on Earth (McKay et al., 2003). Earlier studies on microbial life in these desert soils have been done in the locality of Yungay that is the most arid region in the northern extent of this desert, where no significant rainfall has occurred for decades (Fritz et al., 1981). There, the level of cultivable microorganisms reported on the surface is extremely low (<100 CFU g^{-1}) (Navarro-González et al., 2003). However, a study carried out in the same area, reported a major abundance of cultivated bacteria at a depth of 20–30 cm and a successful DNA extraction and subsequent 16S rRNA gene PCR (Maier et al., 2004). In these hyper-arid environments, the lack of water and low microbial activity would be responsible for the huge nitrate deposits accumulated in Atacama Desert subsoil zones (Walvoord et al., 2003; Ewing et al., 2007) suggesting a limited nitrogen cycling in this ecosystem.

In arid soils from the southern extent of the Atacama Desert there is less accumulated nitrate compared with the extreme hyperarid region to the north suggesting nutrient cycling by the soil microbiota (Ewing et al., 2007, 2008). In this region, irregular and short rainfall pulses result in increased soil moisture that could support microbial activity. Although, there are no rainfall records for the studied site (Sierra Pajarito), the long-term records available for the nearest city, Copiapó located 55 km north, indicate a mean annual precipitation less than 20 mm (Almeyda, 1948). However, every 2–7 years infrequent higher precipitations result in increased soil moisture that produces a fast growth of dormant seeds with abundant flowering after rainfall (Vidiella et al., 1999). This phenomenon is known as "desert bloom" and usually takes place when an "El Niño" event increases the precipitation (Jaksic, 2001). During 2005 most of the rain was concentrated in early August (Copiapó 19.5 mm), increasing the moisture and inducing a subsequent flowering peak observed in mid-September.

Therefore, the central aim of this research was to assess the bacterial community composition during a "desert bloom" event and determine if changes occurred in the ammonia-oxidizing bacteria (AOB) diversity, a bacterial guild involved in nitrogen cycling. To our knowledge, this is the first report on changes in the bacterial assemblages during a "desert bloom" event in Atacama Desert soil.

For this study we cloned and sequenced the 16S rRNA gene and the functional gene *amoA*, from soil samples obtained at "Sierra Pajarito" (27°59′S, 70°34′W), in the southern end of the Atacama Desert. In this area, we selected a specific habitat i.e. soil associated with *Calandrinia longiscapa* ("pata de guanaco"), a native plant, which grew and bloomed during the flowering event. Ten soil samples were collected from a site where *C. longiscapa* grew in dense patches (ca. 0–15 cm depth) at the beginning ("**B** samples") in August 2005, during ("**D** samples") in September 2005 and after ("**A** samples") the "desert bloom" event in April 2006 when the plant cover had disappeared completely. The samples were homogenized to obtain a compound sample for each time in order

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0038-0717/$ – see front matter © 2010 Published by Elsevier Ltd.
doi:10.1016/j.soilbio.2010.03.025

Table 1
Comparison of the edaphic factors associated to the three sampling times. Data are means ± standard errors of three independent replicates.

Sampling time	pH	Organic matter (%)	Ammonium[b] ($\mu g\ NO_3$-N g^{-1})	Nitrate[c] ($\mu g\ NH_4$-N g^{-1})	Cultivable bacteria (CFU g^{-1})
Beginning blooming	7.13 ± 0.03	0.20 ± 0.02	3.10 ± 0.15	3.92 ± 0.72	$1.7 \times 10^6 \pm 7.0 \times 10^5$
During blooming	7.11 ± 0.03	0.21 ± 0.02	3.19 ± 0.29	6.84 ± 0.72	$2.2 \times 10^6 \pm 1.5 \times 10^5$
After blooming	7.00 ± 0.02	0.18 ± 0.03	3.02 ± 0.00	2.26 ± 0.00	$2.6 \times 10^6 \pm 1.5 \times 10^6$
Statistical parameters[a]	$F = 2.64$ $P = 0.1506$	$F = 1.03$ $P = 0.4123$	$F = 0.60$ $P = 0.5764$	$F = 46.28$ $P = 0.0002$	$F = 0.62$ $P = 0.5680$

[a] *F* ratio and *P* values according to one-way ANOVA.
[b] The values indicate nitrogen from nitrate and are referred to dry weight of soil.
[c] The values indicate nitrogen from ammonium and are referred to dry weight of soil.

to reduce the spatial heterogeneity at a small scale (Webster et al., 2002; Girvan et al., 2003). From three of the ten samples, a fraction of soil was not turned into composite sample for measurement of pH, organic matter, nitrate, ammonium and plate count of cultivable bacteria. The collected soil was homogenized, sieved and stored at −20 °C for DNA extraction and at 4 °C for chemical analysis and cultivation.

Microbial suspensions were prepared by adding 1 g of fresh soil to sterile PBS buffer and shaking overnight. Dilutions from soil suspensions were plated on nutrient agar and incubated at 28 °C for 48 h to determine the number of cultivable microorganisms in each sample. Soil total organic matter (TOM) content was assessed by colorimetric determination following wet potassium dichromate digestion and soil pH was measured potentiometrically in water (Forster, 1995). Ammonium and nitrate contents were determined by colorimetric methods following potassium chloride and water extraction, respectively (Nelson, 1983; Yang et al., 1998).

DNA was purified from 0.25 g of soil using the UltraClean Soil DNA extraction kit (MoBio Laboratories). The 16S rRNA gene was PCR-amplified using the universal primers fD1 and rP2 (Weisburg et al., 1991) from DNA of the **A** samples. The *amoA* gene was amplified from soil genomic DNA of the **B**, **D** and **A** samples using a nested PCR (Yeager et al., 2005). The first PCR was performed using the forward primer amoA-2F and the reverse primer amoA-5R (Webster et al., 2002); for the second reaction, primers amoA-1F and amoA-2R (Rotthauwe et al., 1997) were used. The amplicons were purified using the Wizard® DNA Clean-Up System (Promega) and the clone libraries were constructed using the TOPO TA cloning kit (Invitrogen). Clones were screened by PCR-RFLP using the *Hae*III restriction enzyme (Promega). Those clones with a distinct RFLP pattern were sequenced. The DNA sequences obtained using an ABI PRISM 3100 Avant-Genetic-Analyzer Prism sequencer were used to search in the GenBank database using the BLAST-n tool. Alignment of the DNA sequences was performed by ClustalW (Thompson et al., 1994) using the BioEdit software (Hall, 1999). Phylogenetic analysis of sequences was performed with the program TREECON (Van de Peer and De Wachter, 1994). The genetic distances were calculated by the Jukes & Cantor index (Jukes and Cantor, 1969) and the tree topologies were inferred using the Neighbor-Joining algorithm (Saitou and Nei, 1987). The robustness of the tree topologies was tested by bootstrap analysis with 1000 resamplings.

The 16S rRNA gene sequences have been deposited in the GenBank database under accession numbers EU603370–EU603376; EU603378; EU603380; EU603382; EU603385–EU603386; EU603389–EU603397; GU552158–GU552241 and the *amoA* sequences under accession numbers EU616583–EU616619.

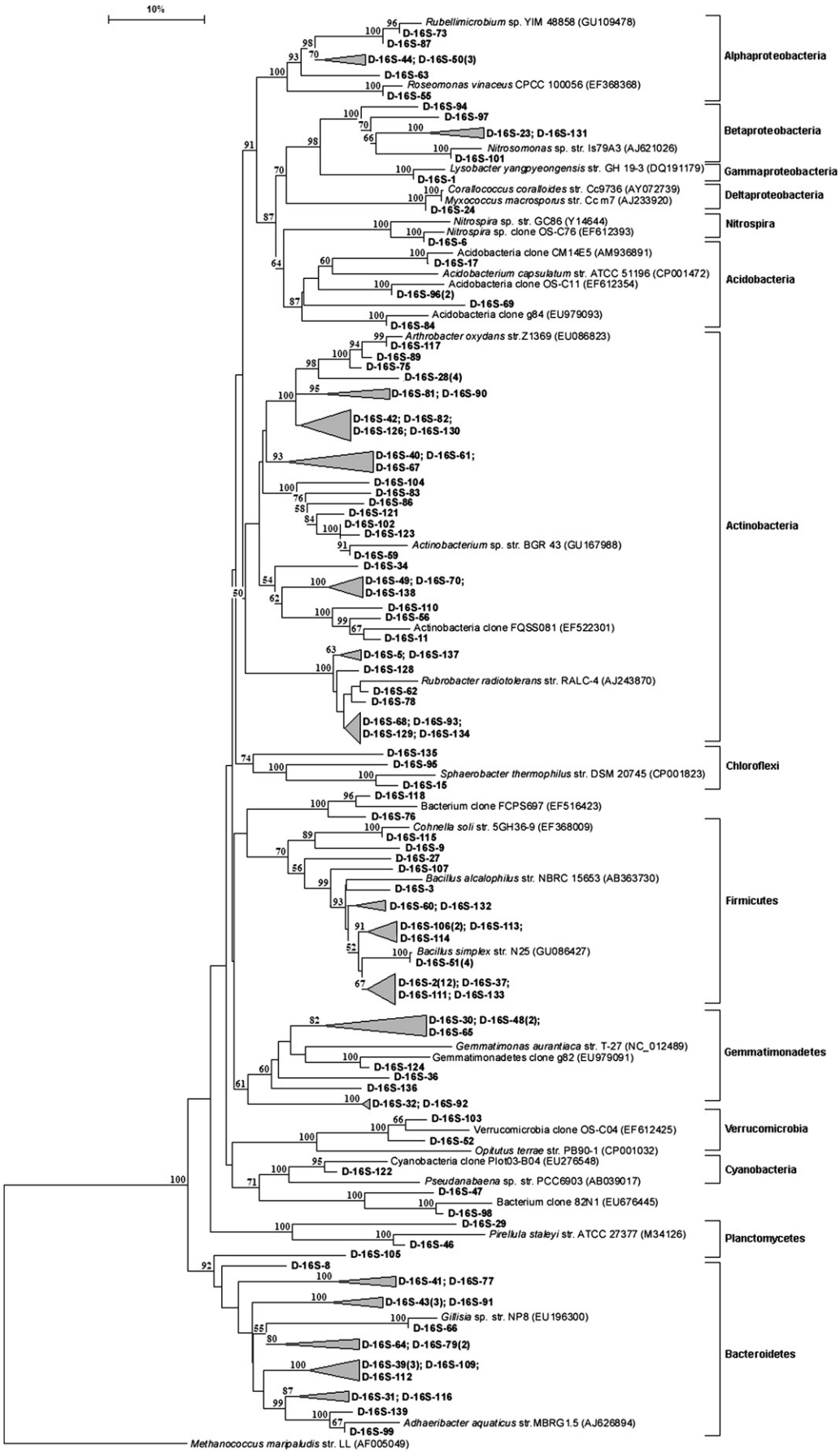
To evaluate the richness and evenness of AOB at each sampling time, we determined the Shannon index (H') (Begon et al., 1990) in the MVSP program version 3.12 h (GeoMem, Blairgowrie, United Kingdom) using the number of distinct *amo*A gene clones obtained.

To compare the difference in the edaphic parameters between the three sampling times a one-way analysis of variance (ANOVA) followed by Tukey's test was used. The sampling time was used as the independent variable and each edaphic factor was considered as dependent variables. The analysis was carried out using the GraphPad Prism version 4.0 (GraphPad Software, Inc). The Shannon indexes were compared between sampling times according to the *t*-test proposed by Hutcheson (1970). Additionally, the effect of the "desert bloom" event on the AOB community was evaluated in a phylogenetic context by *P*-test significance (Martin, 2002) using the Bonferroni correction for multiple comparisons. This analysis was performed at the UniFrac website (http://bmf.colorado.edu/unifrac) (Lozupone and Knight, 2005).

Soil TOM content was very low in all samples (0.18–0.21%) without significant differences between the three sampling times ($F = 1.03$; $P = 0.4123$) (Table 1). These values were higher than those previously reported for the most extreme arid area from Yungay, Atacama Desert (Lester et al., 2007); although they were low compared with TOM content from other desert soils (Feng et al., 2002). The pH was slightly alkaline and remained unchanged in the three sampling times ($F = 2.64$; $P = 0.1506$), likewise, the ammonium content also remained unchanged ($F = 0.60$; $P = 0.5764$). On the other hand, the nitrate content was higher during the event and had the lowest value after flowering ($F = 46.28$; $P = 0.0002$), however, was significantly lower than those reported in the more arid regions of Yungay to the north where the values ranged from 44 to 130 $\mu g\ g^{-1}$ (Lester et al., 2007). These differences in the nitrate content during and after the "desert bloom" event could be related to an increase of microbial activity in response to labile carbon release from plant roots. Changes in soil nitrogen content caused by plant cycling (Schlesinger et al., 1990; Hartsough et al., 2001) and precipitation (Zaady, 2005) have been reported. Bowman and Steltzer (1998) suggested that fast-growing grass species exhibit high turnover of fine roots, promoting more fertile conditions. Another possible explanation for decrease in nitrate content could be leaching to subsoil zones (Walvoord et al., 2003), however in desert soil it was assumed to be insignificant (Peterjohn and Schlesinger, 1990).

Cultivable bacteria numbers were in the range of $1.7–2.6 \times 10^6$ CFU g^{-1}. These values are in accordance with those found for aerobic bacterial populations in deserts around the world (Bhatnagar and Bhatnagar, 2005). Given the variations of

Fig. 1. Phylogram of representative 16S rRNA gene sequences recovered from soil samples at the end of the "desert bloom" event. The numbers in parentheses after clone names indicate the number of clones that showed the same restriction pattern. Clones without this designation had a unique digestion pattern. *Methanococcus maripaludis* LL (AF005049) was used as outgroup. Genetic distances were calculated by the Jukes & Cantor index and tree topologies were inferred using the Neighbor-Joining algorithm. The robustness of the tree topologies was tested by bootstrap analysis with 1000 resamplings, values larger than 70 are shown. Clones obtained are shown in bold. Accession numbers for sequences from public databases are shown in parentheses.


10%
Rubellimicrobium sp. YIM 48858 (GU109478)
D-16S-73
D-16S-87
D-16S-44; D-16S-50(3)
D-16S-63
Roseomonas vinaceus CPCC 100056 (EF368368)
D-16S-55
Alphaproteobacteria
D-16S-94
D-16S-97
D-16S-23; D-16S-131
Nitrosomonas sp. str. Is79A3 (AJ621026)
D-16S-101
Betaproteobacteria
Lysobacter yangpyeongensis str. GH 19-3 (DQ191179)
D-16S-1
Gammaproteobacteria
Corallococcus coralloides str. Cc9736 (AY072739)
Myxococcus macrosporus str. Cc m7 (AJ233920)
D-16S-24
Deltaproteobacteria
Nitrospira sp. str. GC86 (Y14644)
Nitrospira sp. clone OS-C76 (EF612393)
D-16S-6
Nitrospira
Acidobacteria clone CM14E5 (AM936891)
D-16S-17
Acidobacterium capsulatum str. ATCC 51196 (CP001472)
Acidobacteria clone OS-C11 (EF612354)
D-16S-96(2)
D-16S-69
Acidobacteria clone g84 (EU979093)
D-16S-84
Acidobacteria
Arthrobacter oxydans str.Z1369 (EU086823)
D-16S-117
D-16S-89
D-16S-75
D-16S-28(4)
D-16S-81; D-16S-90
D-16S-42; D-16S-82;
D-16S-126; D-16S-130
D-16S-40; D-16S-61;
D-16S-67
D-16S-104
D-16S-83
D-16S-86
D-16S-121
D-16S-102
D-16S-123
Actinobacterium sp. str. BGR 43 (GU167988)
D-16S-59
D-16S-34
D-16S-49; D-16S-70;
D-16S-138
D-16S-110
D-16S-56
Actinobacteria clone FQSS081 (EF522301)
D-16S-11
D-16S-5; D-16S-137
D-16S-128
Rubrobacter radiotolerans str. RALC-4 (AJ243870)
D-16S-62
D-16S-78
D-16S-68; D-16S-93;
D-16S-129; D-16S-134
Actinobacteria
D-16S-135
D-16S-95
Sphaerobacter thermophilus str. DSM 20745 (CP001823)
D-16S-15
Chloroflexi
D-16S-118
Bacterium clone FCPS697 (EF516423)
D-16S-76
Cohnella soli str. 5GH36-9 (EF368009)
D-16S-115
D-16S-9
D-16S-27
D-16S-107
Bacillus alcalophilus str. NBRC 15653 (AB363730)
D-16S-3
D-16S-60; D-16S-132
D-16S-106(2); D-16S-113;
D-16S-114
Bacillus simplex str. N25 (GU086427)
D-16S-51(4)
D-16S-2(12); D-16S-37;
D-16S-111; D-16S-133
Firmicutes
D-16S-30; D-16S-48(2);
D-16S-65
Gemmatimonas aurantiaca str. T-27 (NC_012489)
Gemmatimonadetes clone g82 (EU979091)
D-16S-124
D-16S-36
D-16S-136
D-16S-32; D-16S-92
Gemmatimonadetes
D-16S-103
Verrucomicrobia clone OS-C04 (EF612425)
D-16S-52
Opitutus terrae str. PB90-1 (CP001032)
Verrucomicrobia
Cyanobacteria clone Plot03-B04 (EU276548)
D-16S-122
Pseudanabaena sp. str. PCC6903 (AB039017)
Cyanobacteria
D-16S-47
Bacterium clone 82N1 (EU676445)
D-16S-98
D-16S-29
Pirellula staleyi str. ATCC 27377 (M34126)
D-16S-46
D-16S-105
Planctomycetes
D-16S-8
D-16S-41; D-16S-77
D-16S-43(3); D-16S-91
Gillisia sp. str. NP8 (EU196300)
D-16S-66
D-16S-64; D-16S-79(2)
D-16S-39(3); D-16S-109;
D-16S-112
D-16S-31; D-16S-116
D-16S-139
Adhaeribacter aquaticus str.MBRG1.5 (AJ626894)
D-16S-99
Bacteroidetes
Methanococcus maripaludis str. LL (AF005049)

cultivable biomass reported from this region, ranging from very low to 10^7 CFU g^{-1}, it is clear that microbial concentrations can vary over many orders of magnitude depending on location (Rainey et al., 1999; Navarro-González et al., 2003; Maier et al., 2004).

A relatively high diversity of 16S rRNA gene clones belonging to 14 bacterial groups was detected. Actinobacteria (29.6%), Firmicutes (22.7%), Bacteroidetes (15.9%) and Proteobacteria (11.4%) were the most abundant groups according to clone library (Fig. 1). Previous reports from the Atacama Desert based on DNA and PLFA showed that the microbial community was primarily composed of Actinobacteria, Proteobacteria and Firmicutes (Lester et al., 2007; Connon et al., 2007). However, Drees et al. (2006) found a higher abundance of Gemmatimonadetes in the hyperarid core while in our library represents only 6.8%. Additionally, only one of the sequences was related to cyanobacteria, a unique community of desert microbes found to inhabit translucent rocks in discrete island-patches (Warren-Rhodes et al., 2007). Finally, two clones were related to nitrifying microorganisms, D-16S-6 to *Nitrospira* and D-16S-101 to *Nitrosomonas*.

All *amoA* sequences analyzed were related to *Nitrosospira* cluster 3 (Stephen et al., 1996), which have been detected as the dominant AOB group in a number of neutral pH arable fields receiving fertilizers (Bruns et al., 1999; Mendum et al., 1999; Kowalchuk et al., 2000) (Fig. 2). However, they were grouped in different sub-clusters; some of them containing clones obtained in a specific sampling time e.g. sub-cluster VII grouped clones obtained from samples **B** related to *Nitrosospira* sp. Nsp2; some clones obtained from samples **D** were associated with *Nitrosospira multiformis* in the sub-cluster III and clones obtained from samples **A** formed the sub-cluster II related to an environmental clone (QY-A5) found in a soil under long-term fertilization practices (He et al., 2007) and the sub-cluster IV without a sequence related in the database. The other sub-clusters contain clones from different sampling times. Clones A11 and D26 are not part of the clusters described.

On the other hand, according to the *t*-test proposed by Hutcheson (1970), Shannon diversity index was significantly higher ($P < 0.05$) in **A** samples than **B** and **D** samples with values of 2.68, 1.92 and 1.89, respectively. In addition, pooling all the sequences from **B** (25 sequences), **D** (19 sequences) and **A** (28 sequences)

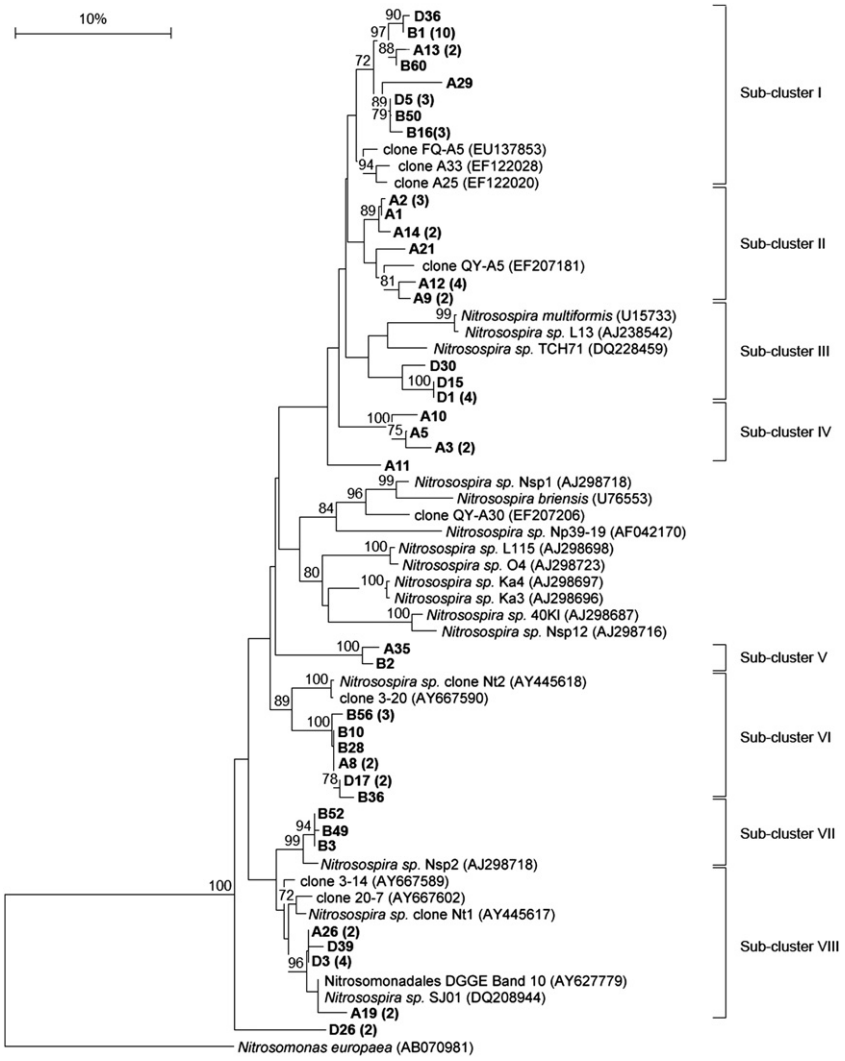


Fig. 2. Phylogram of representative *amoA* gene sequences from soil samples at the beginning (**B** samples), during (**D** samples) and after (**A** samples) the "desert bloom" event. The numbers in parentheses after clone names indicate the number of clones that showed the same restriction pattern. Clones without this designation had a unique digestion pattern. *Nitrosomonas europaea* (AB070981) was used as outgroup. Genetic distances were calculated by the Jukes & Cantor index and tree topologies were inferred using the Neighbor-Joining algorithm. The robustness of the tree topologies was tested by bootstrap analysis with 1000 resamplings, values larger than 70 are shown. Clones obtained are shown in bold. Accession numbers for sequences from public databases are shown in parentheses.

samples and then comparing each sampling time pairwise by the *P*-test, only the sampling times before (**B** samples) and after (**A** samples) were significantly different from each other ($P = 0.03$).

The increased soil moisture and the presence of the plant during flowering could enhance abundance of some clones, become dominant in the community and therefore, reduce the existing diversity of AOB guild. Some studies suggested that the greater water availability could reduce the spatial isolation and increase the competence which could favour the dominance of some clones (Zhou et al., 2002, 2004). Other authors have described changes in microbial community composition in response to plant development (Wieland et al., 2001; Lipson and Schmidt, 2004) and rapid changes in soil moisture (Fierer et al., 2003), among other factors.

AOB have been described in other arid soils; members of the *Nitrosospira* genera are the main ammonia-oxidizers of the Negev Desert soil (Nejidat, 2005). Likewise, ammonia-oxidizing activity has been detected in microbial communities that constitute biological crusts (Johnson et al., 2005) although these microbial assemblages have not been described in Sierra Pajarito.

Microbial community composition research is particularly lacking in deserts (Adams, 2003). According to our knowledge, this is the first report on occurrence of the AOB guild and changes of its composition during the "desert bloom" event in the Atacama Desert indicating potential nitrogen cycling in this ecosystem. Our results suggest that the higher soil moisture and the occurrence of plants during flowering of the desert reduce the diversity of the AOB guild and may promote a shift in nitrate levels. These changes, due to the flowering of the desert, could have long-term consequences in N cycling. Information on changes in the diversity and composition of the soil bacterial community associated with changes in the soil environment is important for understanding and predicting plant productivity and ecosystem health in arid soils.

Acknowledgments

This work was supported by ENL07/16 project from the University of Chile and in part by FONDECYT project N°1080280.

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