

## Research Article

# Evidence of an atmospheric forcing on bacterioplankton and phytoplankton dynamics in a high mountain lake

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**Abstract.** We quantified dry and wet atmospheric deposition of soluble reactive phosphorus (SRP) to the Southwest Mediterranean region during one year and assessed its effect on bacterial abundance and phytoplankton specific biomass during one ice-free period in a high mountain lake located in an area highly influenced by Saharan dust outbreaks. Dry deposition of SRP represented 79% of total SRP inputs and it showed a seasonal pattern similar to Saharan dust export to this region, with maxima during spring and summer. Bacterial abundance was significantly correlated with SRP atmospheric deposition, suggesting the influence of this input on bacterioplankton dynamics. The field evidence was

experimentally corroborated using bacterial regrowth cultures performed with dust-amended lake water. Dust addition significantly increased SRP concentration in lake water and it stimulated bacterial abundance. Regarding phytoplankton community, only one species, the chrysophyte *Chromulina nevadensis*, was significantly related to SRP inputs and, consequently, there was a significant decrease in phytoplankton species diversity after atmospheric SRP inputs. Since changes in climate will presumably lead to an alteration in dust export, these results point to the need of further studies on the potential effects of this alteration on bacterioplankton and phytoplankton dynamics in remote oligotrophic systems.

**Key words.** Saharan dust; atmospheric phosphorus; mountain lake.

## Introduction

Every year, massive airborne plumes of dust from the Sahara desert are exported to the Mediterranean region, with maximum loads during spring and summer (Moulin et al., 1997). The deposition of this mineral dust constitutes an important route by which limiting nutrients are delivered to both terrestrial

(Swap et al., 1992; Okin et al., 2004) and aquatic ecosystems (Ridame and Guieu, 2002; Morales-Baquero et al., 2006). In aquatic systems, recent efforts to understand the biogeochemical role of dust inputs have focused on their impact on ocean autotrophic productivity, given their potential to generate new production (Ridame and Guieu, 2002; Bonnet et al., 2005). In contrast, heterotrophic bacteria have received less attention within current research on the atmospheric forcing on biogeochemical cycles, although it is well recognized that, in oligotrophic systems, prokaryote heterotrophs are a large compo-

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ment of microbial biomass (e.g. Cotner and Biddanda, 2002).

Dust deposition was first acknowledged as a source of nutrients to lakes in the seventies (Peters, 1977). However, in comparison to marine ecosystems, the impact of dust deposition on lake biogeochemistry has been less studied (Morales-Baquero et al., 2006). High mountain lakes are expected to be particularly sensitive to dust deposition due to their extreme oligotrophy and low mineralized waters (Psenner, 1999). Sierra Nevada is a high-mountain site located in the Southwest Mediterranean region (Spain). Due to its geographical location and altitude, it receives a high rate of dust deposition associated with Saharan dust outbreaks (Morales-Baquero et al., 2006; Pulido-Villena et al., 2006). There are around 50 oligotrophic and dilute lakes located between 2800 and 3100 m above sea level (asl) in this mountain site and previous research on these remote lakes has revealed a significant influence of Saharan dust inputs on lake biogeochemistry (Morales-Baquero et al., 2006, Pulido-Villena et al., 2006).

The main goal of this study was to investigate the responses of bacterioplankton and phytoplankton to atmospheric inputs of phosphorus in a remote oligotrophic lake. We quantified dry and wet atmospheric deposition of soluble reactive phosphorus over Sierra Nevada Mountains and, simultaneously, we examined bacterial abundance and phytoplankton community structure in a Sierra Nevada high mountain lake during one ice-free period. In addition, we set up a bacterial regrowth culture using lake water amended with mineral dust to assess the availability of dust-derived phosphorus to bacterioplankton.

## Materials and methods

### Atmospheric deposition of soluble reactive phosphorus (SRP)

Separate samples of dry and wet deposition were collected weekly during 2001 using two MTX<sup>®</sup> ARS 1010 automatic deposition samplers placed in two different sites of the study area. One sampler was installed in a high-altitude site in the Sierra Nevada Mountains (37°03'N, 3°23'W) at 2900 m asl, near to the study lake. Due to extreme meteorological conditions during most part of the year, it was sampled only during the ice-free period of 2001 (from 24 July to 18 September). Another sampler was installed in a more accessible site in the Sierra Nevada Mountains (36°34'N, 3°17'W) at 1000 m asl and was sampled throughout the year. On each sampling date, dry and wet deposition buckets from both collectors were replaced and taken to the laboratory. Dry deposition

was collected by rinsing the bucket with 1000 mL of ultrapure water. Dry and wet deposition samples were filtered through Whatman GF/F filters and SRP was analysed spectrophotometrically after Murphy and Riley (1962). SRP concentration ( $\mu\text{mol L}^{-1}$ ) measured in weekly deposition samples was converted to units of daily deposition rates ( $\mu\text{mol m}^{-2} \text{d}^{-1}$ ) using an equation described elsewhere (Morales-Baquero et al., 2006). This approach for determining atmospheric deposition of SRP implies that the term “dry deposition” designates, in fact, the fraction of phosphorus contained in dry deposition that is dissolvable in ultrapure water. To assess if this approach applies to what would happen in the lake surface after a dry deposition episode, we performed a leaching experiment using dry deposition collected in the study area and comparing its dissolution behaviour in ultrapure water and 0.2  $\mu\text{m}$ -filtered lake water. After a contact time of 2 hours (well above the 10-min contact time at which most dissolvable phosphorus is released, Ridame and Guieu (2002)), the dissolvable phosphorus released was not significantly different between both types of water ( $F_{(1,4)} = 1.7$ ;  $p = 0.265$ ). Hereafter, the following terms will be used to refer to the different forms of SRP atmospheric deposition: dry deposition (dissolvable fraction of atmospheric phosphorus), wet deposition (fraction of atmospheric phosphorus dissolved in rainwater), and total deposition (sum of dry and wet deposition).

### Study lake and sampling

La Caldera Lake (Table 1) is located in the Sierra Nevada Mountains (Spain) at 3050 m asl and is ice-covered during 8–9 months every year. It is a seepage lake in a rocky watershed with no terrestrial vegetation covering its catchment and, hence, nutrient inputs from the catchment are expected to be negligible (Kopáček et al., 2000). It is an ultraoligotrophic lake with an extreme phosphorus limitation of both the bacterioplankton and phytoplankton community (Carrillo et al., 1995; Reche et al., 1997; Pulido-Villena et al., 2003). Secchi depth equals maximum depth (10 m) and it does not stratify during the ice-free period. Simultaneously to the sampling of the collector at 2900 m asl, La Caldera Lake was weekly sampled during the ice-free period of 2001 to determine bacterial abundance and species-specific phytoplankton biomass. In addition, on 21 August, the lake was also sampled to perform bacterial regrowth cultures. All samples were collected from central station pumping water from depths of 9, 7, 5, 3 and 1 m and mixing it in equal parts to produce a single integrated sample.

**Table 1.** Main characteristics of the study lake for the ice-free period of 2001.

Lake area (km <sup>2</sup> )	0.021
Catchment area (km <sup>2</sup> )	0.235
Maximum depth (m)	10
Mean depth (m)	3
	Average (range)
ANC <sup>1</sup> (meq L <sup>-1</sup> )	0.25 (0.24–0.28)
Ca <sup>2</sup> (μmol L <sup>-1</sup> )	113 (106–118)
NO <sub>3</sub> <sup>-1</sup> (μmol L <sup>-1</sup> )	15.7 (12.4–20.6)
SRP <sup>1</sup> (μmol L <sup>-1</sup> )	0.03 (n.d.-0.13)
TN <sup>3</sup> (μmol L <sup>-1</sup> )	30.8 (18.4–41.0)
TP <sup>3</sup> (μmol L <sup>-1</sup> )	0.15 (0.04–0.33)
DOC <sup>1</sup> (μmol L <sup>-1</sup> )	46.4 (23.3–89.7)
Chl-a <sup>3</sup> (μg L <sup>-1</sup> )	0.75 (0.23–1.57)

<sup>1</sup> Data from Pulido-Villena (2004).<sup>2</sup> Data from Pulido-Villena et al. (2006)<sup>3</sup> Data from Morales-Baquero et al. (2006)

### Bacterial abundance and phytoplankton biomass

Samples for bacterial abundance (BA) were fixed in the field with neutralised 0.2 μm-filtered formaldehyde to a final concentration of 2%. BA was determined by epifluorescence microscopy using DAPI fluorochrome stain (Porter and Feig, 1980). At least 450 cells in 30 random fields were counted per filter. Phytoplankton samples were fixed in the field with a Lugol's solution. A 50-mL aliquot was sedimented and the cells were counted in 50 randomly selected fields at 1000x magnification using an inverted microscope. For each sample, at least 20 cells of each species were measured to estimate cell volume according to an appropriate geometric shape. Cell volumes were converted to biomass using a conversion factor of 150 fg C μm<sup>-3</sup> (Vadstein et al., 1988). Phytoplankton species diversity was calculated using the Simpson index (Simpson, 1949; Magurran, 2004) in terms of biomass:

$$D = \sum_{i=1}^S \frac{n_i(n_i - 1)}{N(N - 1)} \quad (1)$$

where  $n_i$  is the biomass of the  $i$ -species,  $N$  is the total phytoplankton biomass and  $S$  is the total number of species. Since this index may be counterintuitive (the bigger the value of  $D$ , the lower the diversity), we used the Simpson reciprocal index,  $1/D$ .

### Experimental design

To perform the bacterial regrowth cultures, lake water was initially filtered through Whatman GF/F filters. This filtration removed 85% of *in situ* bacterial abundance and all bacterivores and phytoplankton (checked by epifluorescence microscopy). Filtered lake water was amended with mineral dust collected in

the study area during one week to a final concentration of 9 mg L<sup>-1</sup>. Unamended water was kept as a control. Incubations were performed in triplicate in dark conditions at 15°C during 68 hours. Samples for SRP concentration were taken at the beginning and at the end of incubations. Samples for bacterial abundance (BA) were taken sequentially during the incubations. BA and SRP concentration were determined as described above.

### Statistical analyses

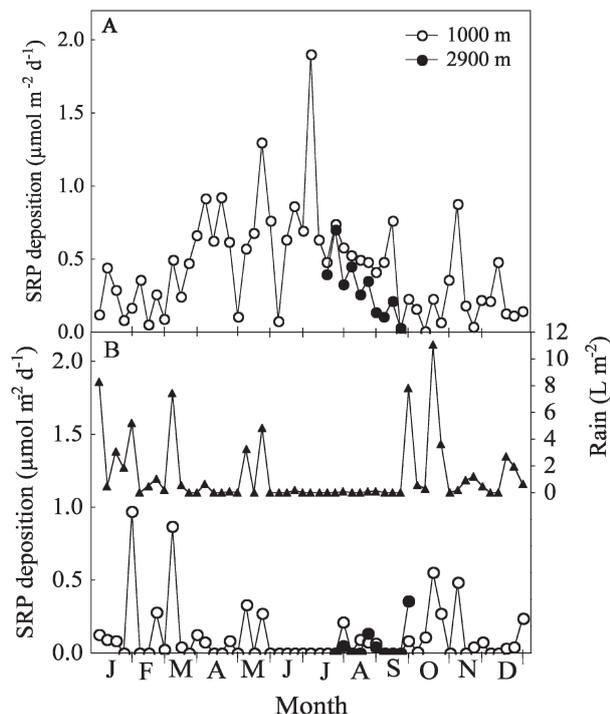
To explore the response of bacterioplankton and phytoplankton to SRP atmospheric inputs, we performed Pearson's correlation analysis among BA, phytoplankton species biomass and total (dry + wet) atmospheric deposition of SRP collected at 2900 m asl. For the statistical treatment of the results of the bacterial regrowth cultures, one-way repeated measures ANOVAs were performed (Underwood, 1997). This analysis is useful for experiments where there may be a within-subject effect (incubation time) and a between-subjects effect (dust addition), since it allows to test the interaction between both effects, that is, the effect of dust addition through incubation time.

### Results

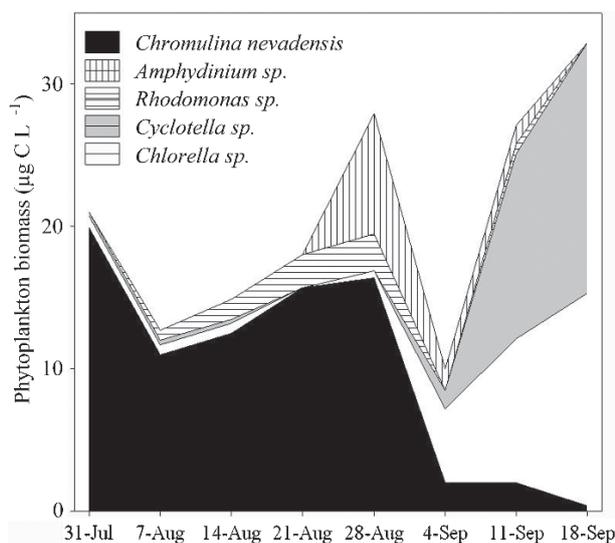
Dry deposition of soluble reactive phosphorus (SRP) at 1000 m asl ranged from non-detectable values (< 0.06 μmol m<sup>-2</sup> d<sup>-1</sup>) to 1.9 μmol m<sup>-2</sup> d<sup>-1</sup> and it showed a clear seasonal pattern with maximum values during spring and summer (Fig. 1A). Wet deposition of SRP ranged from 0 (no rain event) to 1.0 μmol m<sup>-2</sup> d<sup>-1</sup> and did not exhibit any seasonal trend (Fig. 1B). During the ice-free period, dry deposition of SRP at 2900 m asl ranged from non-detectable values to 0.7 μmol m<sup>-2</sup> d<sup>-1</sup> (Fig. 1A) and wet deposition of SRP varied from 0 to 0.4 μmol m<sup>-2</sup> d<sup>-1</sup> (Fig. 1B). The average contribution of dry deposition to total SRP inputs was 79%.

Total deposition of SRP at both study altitudes was significantly correlated to total deposition of particulate matter collected in the study area during the same period ( $n = 62$ ;  $r = 0.46$ ;  $p < 0.01$ ; data from Morales-Baquero et al., 2006). The proportion of SRP to total phosphorus (TP; data from Morales-Baquero et al., 2006) measured in dry and wet deposition samples varied widely during the period of study ( $0.36 \pm 0.20$ ), being < 60% in most analysed samples (Fig. 2).

Phytoplankton community was dominated by the chrysophyte *Chromulina nevadensis* (> 80% of total biomass) during most part of the study ice-free period. The chlorophyte *Chlorella* sp. and the diatom *Cyclotella* sp. became the dominant species of the commun-

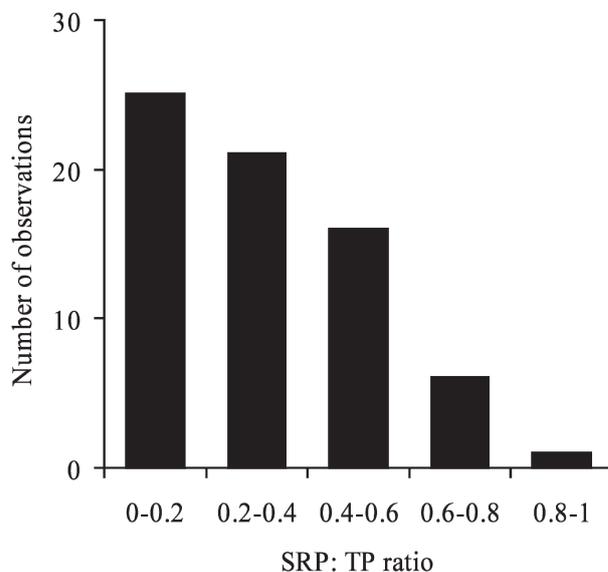


**Figure 1.** Seasonal dynamics of dry (A) and wet (B) atmospheric deposition of soluble reactive phosphorus (SRP;  $\mu\text{mol m}^{-2} \text{d}^{-1}$ ) in the study site at 1000 m asl during 2001 and at 2900 m asl during the ice-free period of 2001. Panel B also shows precipitation data registered at 1000 m asl during the study period.

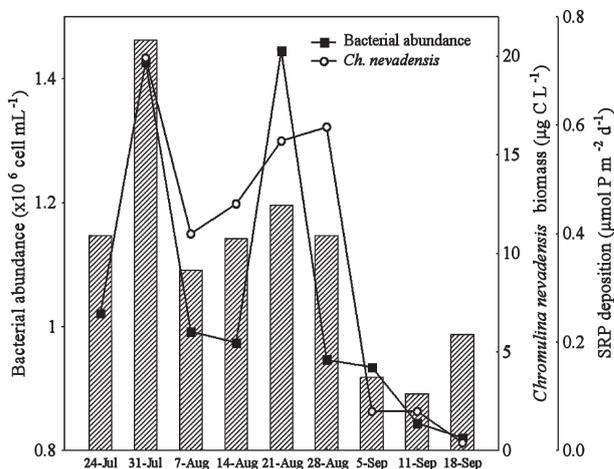


**Figure 3.** Temporal variation in the biomass of the most representative phytoplankton species in La Caldera Lake during the ice-free period of 2001.

ity at the end of the ice-free period. Other species such as *Rhodomonas* sp. and *Amphidinium* sp. were less representative (Fig. 3). Bacterial abundance (BA) ranged from  $0.8 \times 10^6$  to  $1.5 \times 10^6$  cell  $\text{mL}^{-1}$  with maximum values coinciding with peaks in SRP atmospheric inputs (Fig. 4).



**Figure 2.** Frequency distribution of the soluble reactive phosphorus to total phosphorus ratio (SRP: TP ratio) in total (dry + wet) atmospheric deposition samples collected during 2001 ( $n = 62$ ).

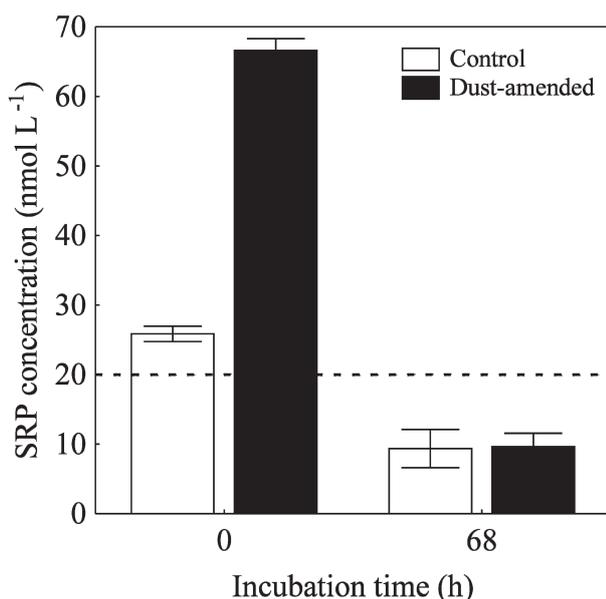


**Figure 4.** Temporal dynamics of total (dry + wet) atmospheric deposition of soluble reactive phosphorus (SRP;  $\mu\text{mol m}^{-2} \text{d}^{-1}$ ; filled bars), bacterial abundance (BA;  $\times 10^6$  cell  $\text{mL}^{-1}$ ) and *Chromulina nevadensis* biomass ( $\mu\text{g C L}^{-1}$ ) in La Caldera Lake during the ice-free period of 2001. Result of the Pearson's correlation analysis between BA and *Ch. nevadensis* biomass:  $n = 8$ ;  $r = 0.76$ ;  $p < 0.05$ .

Correlation analysis revealed multiple interactions between BA, phytoplankton specific biomass and total (dry + wet) atmospheric inputs of SRP (Table 2). BA and the chrysoyte *Chromulina nevadensis* biomass exhibited a coupled dynamic (Fig. 4) and both were significant and positively related to total

**Table 2.** Results of Pearson's correlation analysis between total (dry + wet) atmospheric deposition of soluble reactive phosphorus (SRP;  $\mu\text{mol m}^{-2} \text{d}^{-1}$ ) and bacterial abundance (cell  $\text{mL}^{-1}$ ) and biomass of dominant phytoplankton species ( $\mu\text{g C L}^{-1}$ ) in La Caldera during the ice-free period of 2001.

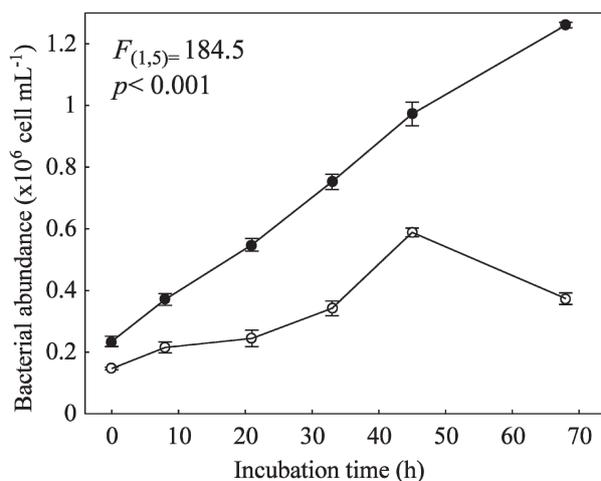
	Bacterial abundance	<i>Chromulina nevadensis</i>	<i>Chlorella</i> sp.	<i>Cyclotella</i> sp.	<i>Rhodomonas</i> sp.	<i>Amphydinium</i> sp.
SRP deposition	$n = 9$ $r = 0.807$ $p = 0.009$	$n = 8$ $r = 0.905$ $p = 0.002$	$n = 8$ $r = -0.621$ $p = 0.100$	$n = 8$ $r = -0.552$ $p = 0.156$	$n = 8$ $r = 0.273$ $p = 0.513$	$n = 8$ $r = -0.053$ $p = 0.901$



**Figure 5.** Concentration (mean value  $\pm$  standard error,  $n = 3$ ) of soluble reactive phosphorus (SRP,  $\text{nmol L}^{-1}$ ) in the control and dust-amended experimental bottles at the beginning and end of the incubations. Dotted line represents the detection limit of the analytical method.

(dry + wet) SRP deposition (Table 2, Fig. 4). Since *Ch. nevadensis* was the only phytoplankton species that exhibited a relationship with total SRP deposition, a significant and negative relationship was found between total SRP deposition and phytoplankton species diversity ( $n = 8$ ;  $r = 0.86$ ;  $p < 0.01$ ).

Figure 5 shows SRP concentration (mean value  $\pm$  standard error) measured in the control and dust-amended treatments of the performed regrowth cultures at initial and final incubation times. At the beginning of the incubations, SRP concentration was significantly higher in the dust-amended treatment than in the control treatment ( $F_{(1,4)} = 410.7$ ;  $p < 0.001$ ). At the end of incubations, SRP concentration reached values below detection limits in both control and dust treatments. The results of the one-way repeated measures ANOVA showed a significant and positive effect of dust addition on bacterial abundance through incubation time (Fig. 6).



**Figure 6.** Variation in bacterial abundance (mean value  $\pm$  standard error) over the incubation time in control (empty symbols) and dust-amended (filled symbols) treatments. Result of the performed one-way repeated measures ANOVA.

## Discussion

Several studies have emphasized the major importance of Saharan dust as a supplier of soluble phosphorus to the West Mediterranean region (Bergametti et al., 1992; Ridame and Guieu, 2002). In the study area, SRP dry deposition exhibited a similar seasonal trend to that reported for Saharan dust transport to the Mediterranean region, with maxima in spring and summer (Moulin et al., 1997). Moreover, SRP total deposition was significantly related to particulate matter collected in the study area that is dominated by Saharan dust, especially during spring and summer (Morales-Baquero et al., 2006). Anthropogenic sources (e.g. industrial activities and biomass burning), which are a significant contributor to SRP inputs in the Mediterranean region (Migon and Sandroni, 1999), are expected to be negligible in the study area, particularly at the high-altitude site, a remote and unpopulated area with little vegetation.

Dry deposition has been traditionally considered as a negligible pathway of dust deposition in the western Mediterranean (Löye-Pilot and Martin, 1996) although it can represent up to 56% in the eastern areas of the basin (Kubilay et al., 2000). In the

particular case of P inputs, most studies have overlooked dry deposition by just focusing on P delivered by rain (Migon and Sandroni, 1999; Bartoli et al., 2005). In this study, dry deposition represented the dominant fraction of SRP atmospheric inputs (79%), indicating that, at least in arid and semiarid areas such as the southwest Mediterranean region, the single consideration of wet events might lead to a serious underestimation of phosphorus inputs, precluding the success of the attempts to evaluate its impact on biological productivity.

Mineral nutrients are being increasingly considered as a controlling resource for bacteria (Rivkin and Anderson, 1997; Smith and Prairie, 2004). Indeed, bacterioplankton abundance and production in La Caldera Lake is strongly limited by phosphorus (Reche et al., 1997; Pulido-Villena et al., 2003), which explains the observed correlation between bacterial abundance (BA) and SRP deposition during the study period. This correlation provided important evidence of the influence of dust-derived phosphorus on bacterioplankton dynamics. In particular, two Saharan dust events, registered on 31 July and 21 August, which delivered a SRP input of 5.3 and 3.2  $\mu\text{mol m}^{-2}$ , respectively, were followed by important increases in BA (Fig. 3). Considering a lake mean depth of 4 m, the first event (31<sup>st</sup> July) would have yielded an increase in lake SRP concentration of 1.3  $\text{nmol L}^{-1}$ . Using a carbon (C): P Redfield ratio of 106, this increase in SRP could have caused an increase in biomass of 138  $\text{nmol C L}^{-1}$ . By comparison, the increase in bacterial biomass during the same period, estimated after applying a range of conversion factors of 4–9 fg C cell<sup>-1</sup> typical of P-limited bacteria populations (Gundersen et al., 2002), was between 134 and 300  $\text{nmol C L}^{-1}$ . Likewise, the SRP input associated to the second Saharan dust event (21 August), could have supported an increase in biomass of 95.4  $\text{nmol C L}^{-1}$ , slightly lower than the observed increase in bacterial biomass (167–375  $\text{nmol C L}^{-1}$ ). It must be noted that this estimate is only a lower limit; not only is SRP the available fraction of the P pool but soluble non-reactive P may also be available to aquatic biota (Benitez-Nelson, 2000 and references therein) and can represent a significant fraction of the atmospheric P delivered by rain in the Mediterranean region (Migon and Sandroni, 1999). During the period of study, SRP represented < 60% of TP in most of the analysed samples and, in the particular case of the two Saharan dust events studied, it accounted for only 9 and 12%, respectively. This result suggests that the fraction of atmospheric P that is available to bacteria might be higher than that measured as SRP. On the other hand, the slightly lower atmospheric SRP input compared to calculated bacterial demand could be

alternatively explained if the atmospheric SRP deposited in the lake catchment was ultimately delivered to the lake. However, this indirect input is not expected to be significant since previous research in Sierra Nevada Mountains has shown a negative relationship between lake SRP concentration and catchment area, suggesting a probable SRP retention by Sierra Nevada soils (Morales-Baquero et al., 1999).

The performed regrowth cultures supported the field evidence that dust-derived phosphorus was available to bacterioplankton. The addition of mineral dust to La Caldera lake water had a strong fertilising effect, increasing SRP concentration by 40  $\text{nmol L}^{-1}$ . At the end of the incubation, SRP was exhausted, most likely consumed by heterotrophic bacteria which exhibited a 5-fold increase in their abundance. Since the first indirect suggestions of the importance of dust deposition in lakes (Psenner, 1984), this result represents, to our knowledge, the first experimental evidence for the availability of atmospheric nutrients to aquatic bacteria. Indeed, in oceanic systems, bacterial response to atmospheric inputs has been largely overlooked with respect to autotrophic communities and only a few attempts have been carried out (Klein et al., 1997; Herut et al., 2005). In freshwater ecosystems, no work on the impact of mineral dust inputs on bacterial dynamics has been published yet. Our results undergo, however, a quantitative limitation and must be cautiously interpreted. Since the goal of bacterial regrowth cultures was to experimentally assess the availability of dust-derived phosphorus to bacterioplankton, the experiment was over-scaled, that is, the dust concentration used for the amendment (9  $\text{mg L}^{-1}$ ) was higher than a typical episode of Saharan dust deposition to the study area. Nevertheless, the results of the combined approach used in this study (field observation and experimental assessment), even if they may not be conclusive, constitute an important first step towards the understanding of the role of dust inputs on bacteria dynamics in P-limited aquatic systems.

Regarding the relationship between atmospheric P inputs and the phytoplankton community, it is important to emphasize that only one species, *Chromulina nevadensis*, showed a significant correlation with SRP deposition. This increase in the biomass of one species after SRP inputs led to a decline in phytoplankton species diversity. Due to the episodic nature of Saharan dust outbreaks, P atmospheric inputs to the study area may be compared to pulsed additions of nutrients. These additions generally provoke a species-specific response (Duarte et al., 2000; Lagus et al., 2004) and a consequent decline in species diversity (Cottingham et al., 1998; Klug and Cottingham, 2001). However, the observed response of the chrysophyte

*Ch. nevadensis* to P-inputs diverges from the expected pattern of a shift in phytoplankton composition from chrysophytes to chlorophytes after nutrient enrichment (Cottingham et al., 1998; Vuorio et al., 2005; Hessen et al., 2006). It is likely that atmospheric P inputs were not large enough to induce an eutrophication-type shift in phytoplankton community structure. Another plausible explanation to this response of *Ch. nevadensis* could be that it did not respond directly to P inputs but it profited from bacterial stimulation. When both bacteria and phytoplankton growth rates are P-limited, bacterioplankton can be a stronger competitor for the limited inorganic P (Rivkin and Anderson, 1997; Thingstad et al., 1999; Mindl et al., 2005). Under this scenario, mixotrophy offers a strategy to circumvent this competition for P with bacteria by obtaining P directly from the bacteria through phagotrophic ingestion (Jansson, 1998; Nygaard and Tobiesen, 1999). Such a situation of both bacteria and phytoplankton being P-limited is typically encountered in La Caldera Lake (Carrillo et al., 1995; Reche et al., 1997; Pulido-Villena et al., 2003) and the mixotrophic behaviour of *Ch. nevadensis* in La Caldera Lake has already been reported (Medina-Sánchez et al., 2006). Bacterivory rates can vary in response to mineral nutrient availability, although there is no consensus on the direction of these variations. Thus, bacterivory rates can decrease with nutrient supply (e.g. Urabe et al., 1999) but can also increase as an indirect effect of bacteria stimulation after nutrient enrichment (Isaksson et al., 1999). This could explain the observed connections between atmospheric inputs of soluble reactive phosphorus, bacterioplankton and mixotrophic phytoplankton in La Caldera Lake. Bacterioplankton would have successfully competed for the pulsed P atmospheric inputs increasing their abundance. At this time, mixotrophic phytoplankton could have profited from the increase in BA to access the P, leading to the increase in *Ch. nevadensis* biomass observed after the inputs. The correlation between BA and *Ch. nevadensis* biomass would, then, reflect a mixotrophic relationship and the relationship between P inputs and *Ch. nevadensis* biomass would, therefore, be an indirect effect derived from the coupled dynamic between BA and P inputs.

The results obtained in this study point to an atmospheric forcing of bacterioplankton and phytoplankton dynamics mediated by the atmospheric inputs of P. Nevertheless, it is worthy to remark that other nutrients delivered to the lake by atmospheric deposition could have contributed to the observed responses in bacterial abundance and phytoplankton biomass. In particular, Saharan dust exhibits a significant content in Fe (Jickells et al., 2005), a micro-

nutrient which limits productivity in wide areas of the globe, including freshwater ecosystems (Martin et al., 1994; Vrede and Tranvik, 2006). Although La Caldera Lake is mainly P-limited, potential Fe limitation has never been explored and no data on dissolved Fe concentration are available yet. The frequent occurrence of Saharan events in the lake area (Rodriguez et al., 2001; Morales-Baquero et al., 2006), together with a small lake volume (which affects the amount of water in which aerosol is diluted), rule out a low concentration of Fe. However, since Fe availability is restricted by its low solubility, further research on the role of Fe in the lake functioning would be desirable.

In summary, the results obtained in this work strongly suggest the significant influence of atmospheric inputs of P on bacterioplankton dynamics in oligotrophic systems. In addition, they suggest that these pulsed inputs could provoke changes in phytoplankton community structure reducing species diversity, although the ultimate cause of these changes remains uncertain. Although P appeared responsible for the observed changes, other dust-derived nutrients such as Fe could have also played an important role. Anyhow, since changes in climate will presumably lead to an alteration of mineral dust export to ecosystems (Prospero and Lamb, 2003), further research is needed to achieve an accurate understanding of the potential effects of these changes on bacterioplankton and phytoplankton dynamics in remote oligotrophic systems.

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