

Aerosol-nutrient-induced picoplankton growth in Lake Tahoe

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[1] Lake Tahoe is an oligotrophic lake appreciated for its transparent waters, yet the Lake's clarity has been declining for several decades due in part to eutrophication. At the same time, a shift from nitrogen (N) toward phosphorus (P) limitation of phytoplankton has occurred that could be due to atmospheric deposition of nutrients with high N:P ratios. Atmospheric particle samples collected during 2005–2006 had a mean soluble N:P ratio of 192:1, well above the Redfield ratio of 16:1 typically required by phytoplankton. Samples collected during the Angora Fire that occurred in 2007 were particularly enriched in N relative to P, with a mean ratio >2800:1. A bioassay incubation experiment was conducted using locally collected atmospheric total suspended particulate (TSP) matter. TSP samples with high ammonium (NH_4^+) and low P content favored the growth of picoplankton (cells <3 μm) and opportunistic filamentous cyanobacteria, whereas larger nanophytoplankton (cells 3–20 μm) were better competitors when more P was available. Picoplankton growth can increase primary productivity without causing a large increase in chlorophyll (chl *a*) or biomass. Aerosol-nutrient-induced picoplankton growth (together with shifts in grazing dynamics and stratification trends) may contribute to the uncoupling between primary productivity, chl *a*, and biomass that has been observed in Lake Tahoe in the last several decades and, in particular, following the Wheeler and Angora Fires. The chemical composition of aerosols has a marked impact on ecosystem dynamics in Lake Tahoe with potential consequences to lake productivity and microbial community dynamics.

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1. Introduction

[2] Lake Tahoe is a large, subalpine lake situated in the Sierra Nevada mountain range on the border of California and Nevada. Lake Tahoe is known and valued for its scenic beauty and remarkable water clarity, a characteristic that results from the specific geographic, geological, and morphometric properties of the surrounding watershed [Goldman, 1988]. The nutrient-poor soils, erosion-resistant substrate, high ratio of lake to total watershed surface area (1.6:1), and largely forested watershed all limit the amount of

nutrients that enter the lake [Jassby *et al.*, 1994]. These factors, along with its large volume (156 km³) and great depth ($Z_{\text{mean}} = 313$ m), make Lake Tahoe a naturally oligotrophic water body where phytoplankton are nutrient limited.

[3] Since the 1960s, the clarity of Lake Tahoe has decreased dramatically. The Secchi depth, which is the average depth below which a 25 cm diameter white disk disappears from view as it is lowered and raised through the water column, has decreased by about 30%, from deeper than 30 m in the mid-1960s to approximately 20 m in recent years [Goldman, 1988; Swift *et al.*, 2006]. The human population around Lake Tahoe has simultaneously increased from less than 5000 in 1960 to 55,000 permanent residents and over 3 million visitors annually in 2010 (www.census.gov) [Goldman *et al.*, 1988]. The ensuing land use changes and increased anthropogenic emissions are both suspected to contribute to Tahoe's loss of clarity by increasing sediment loads as well as nutrient loading, which stimulate productivity [Jassby *et al.*, 1994, 1995; Reuter *et al.*, 2009; Sahoo *et al.*, 2010].

[4] Nutrient addition experiments to lake water conducted as early as 1959 showed that primary production in the lake was limited by nitrogen (N) availability [Goldman *et al.*, 1988]. Long-term water chemistry monitoring shows the ratio of N to phosphorus (P) in lake water in the mid-1900s

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was below the Redfield ratio of 16N:1P that phytoplankton generally require for growth (although individual taxa may prefer different ratios), also consistent with N limitation. However, beginning in the early 1980s, a shift toward increased N input and occasional P limitation began, along with a consistent decline in the Lake's P concentrations. Present-day nutrient addition experiments indicate that phytoplankton are P limited during October through April, although colimitation for N and P occurs periodically throughout the year [Goldman *et al.*, 1993; G. Schladow, personal communication, 2011]. Only in the stratified summer months of May through September is N limitation still observed.

[5] In addition to changes in nutrient inputs, the cause for this shift in lake chemistry and ecology may also be linked to long-term changes in the Lake's mixing regime [Coats *et al.*, 2006; Winder and Hunter, 2008]. Density stratification from warming of the Lake's surface waters has generally increased since the 1970s and has led to a reduction in the amount of nutrients introduced through mixing with deep waters. Over the same period, primary productivity has increased; however, this increase has not been associated with an increase in chlorophyll *a* (chl *a*) levels [Goldman, 1988; G. Schladow, personal communication, 2011]. The cause for the decoupling between productivity and chl *a* is currently unknown. It could be attributed to shifts in grazing rate or phytoplankton community structure. The latter possibility is supported by observations of a shift from larger diatoms toward smaller diatoms (e.g., *Cyclotella* sp. 4–25 μm in diameter) and filamentous and coenobial chlorophytes in surface waters, particularly during intense stratification [Winder *et al.*, 2009; Carney *et al.*, 1988].

[6] Because the supply of nutrients to surface waters from deep mixing decreases as stratification increases, other nutrient sources assume greater importance. Atmospheric deposition is a known source of nutrients to many aquatic environments [Paerl *et al.*, 1995; Wolfe *et al.*, 2001; Duce *et al.*, 2008; Mackey *et al.*, 2010] and has been identified as an important source of nutrients to Lake Tahoe [McGauhey *et al.*, 1963; Jassby *et al.*, 1994, 1995]. Current estimates show that of Tahoe's exogenous nutrient sources, ~55% of N and ~15% of P derive from atmospheric sources (G. Schladow, personal communication, 2011). Atmospheric nutrient input can occur in the form of either "wet" or "dry" deposition. Wet deposition delivers scavenged aerosols and gases to the water surface via rain or snow. Fine aerosols, some gases, and particulate material such as crustal "dust," anthropogenic emissions, or ash from fires can all be components of dry deposition and serve as a source of nutrients to phytoplankton upon solubilizing in lake water. The N in Tahoe's atmospheric deposition (wet or dry) originates both within and outside of the basin [Eliot-Fisk *et al.*, 1996; Tarney *et al.*, 2001; Gertler *et al.*, 2006], whereas atmospheric P tends to be generated within the basin and is associated with larger particles [Cahill and Wakabayashi, 1993; Gertler *et al.*, 2006]. The ratio of N:P in ambient atmospheric material is generally higher than the Redfield ratio. Accordingly, the transition from N to P limitation observed in the 1980s has been attributed to the influence of atmospheric nutrient deposition, which is depleted in soluble P relative to soluble N [Jassby *et al.*, 1994, 1995].

[7] In bottle incubation experiments where leachate from aerosols was added to Lake Tahoe water, an increase in

primary productivity was observed [Goldman *et al.*, 1990], demonstrating the influence of dry atmospheric aerosol deposition on phytoplankton growth. In situ responses of phytoplankton to dry deposition (gaseous and aerosol) following major fires in the region have also been documented. In 1985, the Wheeler Fire in the Los Padres National Forest burned over 50,000 ha and contributed substantial input of ash to Lake Tahoe. Goldman *et al.* [1990] found that primary productivity in the surface mixed layer increased from ~10 $\text{mg C m}^{-3} \text{ d}^{-1}$ to over 30 $\text{mg C m}^{-3} \text{ d}^{-1}$ following this event, possibly due to aerosol nutrient enrichment, relief from photoinhibition, or both. The Angora Fire of 2007 increased dry deposition rates approximately fivefold above normal levels but had a negligible effect on chl *a* despite contributing up to 8.4 metric tons of N and 0.8 metric tons of P to the lake [Oliver *et al.*, 2011]. Based on these observations, it is clear that atmospheric dry deposition can have variable effects under different conditions or that unidentified variables are at play.

[8] To better understand the mechanism by which atmospheric deposition affects microbial growth in Lake Tahoe surface waters, we monitored nanophytoplankton and picoplankton concentrations during a 3 day incubation experiment with bulk aerosol (total suspended particles) and nutrient additions. Picoplankton are important members of aquatic microbial communities and can have photoautotrophic, chemoautotrophic, or heterotrophic energy requirements. As such, they contribute to primary [Malone *et al.*, 1991; Bell and Kalff, 2001; Winder, 2009] and secondary production [Cole *et al.*, 1988], as well as to the recycling of organic nutrients [Azam, 1998]. In Lake Tahoe, eukaryotic and cyanobacterial picophytoplankton undergo seasonal succession, with picocyanobacteria dominating in the stratified summer months [Winder, 2009]. However, to our knowledge, the response of picoplankton to atmospheric aerosol deposition has not been characterized previously in Lake Tahoe.

[9] In this study we investigated the responses of the natural microbial community, including phytoplankton and nonphotosynthetic microbes, to atmospheric nutrient input using a bioassay incubation experiment with locally collected total suspended particle (TSP) samples and nutrient additions. Observations of microbial community composition and changes in water chemistry during the experiment show that (1) aerosol nutrients are soluble and bioavailable to the microbial community and (2) the addition of atmospheric aerosols causes changes in microbial community structure and impacts the growth rates of specific taxonomic groups. We discuss these results in light of monitoring data collected during the Angora Fire in 2007 and compare chemical characteristics of aerosols collected during fire and nonfire periods.

2. Materials and Methods

2.1. Aerosol Collection and Analysis

[10] Atmospheric aerosol samples were collected from November 2005 to August 2006 using a total suspended particles (TSP) air sampler located 200 m from the lake shore at the Tahoe City Field Station (Tahoe City, CA). The sampler was located 5 m above ground in an area protected from direct road dust or other disturbance impact and had an

airflow rate of $\sim 85 \text{ m}^3 \text{ h}^{-1}$. The soluble nutrient contents of 39 samples collected between November 2005 and August 2006, each representing about 1 week of aerosol accumulation, were analyzed. Samples were stored frozen prior to analysis. To further explore aerosol chemical composition near Lake Tahoe and expand the temporal representation of our data set, we also used aerosol data from the Interagency Monitoring of Protected Visual Environments (IMPROVE) site at Bliss State Park (38.97°N , 120.1°W). IMPROVE aerosol samples are collected for 24 h every 3 days [Malm *et al.*, 1994]. Aerosol composition is available for aerosols with aerodynamic diameters less than $2.5 \mu\text{m}$ ($\text{PM}_{2.5}$).

[11] To establish the transport history of air masses reaching Lake Tahoe, back trajectories were generated using the Hybrid Single-Particle Lagrangian Integrated Trajectory 4 (HYSPLOT-4) model (provided by the National Oceanographic and Atmospheric Administration Air Resources Laboratory) and meteorological data from the Eta Data Assimilation System archive (R. R. Draxler and G. D. Rolph, HYSPLIT (Hybrid Single-Particle Lagrangian Integrated Trajectory), 2011, <http://ready.arl.noaa.gov/HYSPLIT.php>, NOAA Air Resources Laboratory, Silver Spring, Maryland; G. D. Rolph, Real-time environmental applications and display system (READY), 2011, <http://ready.arl.noaa.gov>, NOAA Air Resources Laboratory, Silver Spring, Maryland). The 3 day back trajectories were initialized at 500 m above model ground level (amgl) every 4 h for the period of interest. It is important to note that individual trajectories are not representative of air parcel movement within the atmospheric boundary layer because parcels quickly lose their identity through mixing processes. The HYSPLIT model can only be used to describe regional-scale air mass motions.

[12] Aerosol samples were also collected during the Angora Fire which began on 24 June 2007, burned over 1250 ha near the south shore of Lake Tahoe, and was contained by 2 July. Aerosol samples (PM_{10}) were collected during the fire over 24 h periods at eight locations within the Lake Tahoe Basin including two from lake buoys located in open water (buoy TB-1 $39^\circ 09.231' \text{N}$, $120^\circ 00.275' \text{W}$ and buoy TB-4 $39^\circ 09.370' \text{N}$, $120^\circ 04.276' \text{W}$). Two samples were collected at each site on different days during the period 25–28 June. All samples were collected on acid-cleaned Teflon filters using MiniVol collection units.

[13] To extract the soluble fraction of aerosol from the collected TSP, a 47 mm circular subsample of each filter was placed on an acid-washed filter tower, and 100 mL MilliQ water was passed through the sample allowing 10 s of exposure under gentle vacuum pressure as described by Buck *et al.* [2006] and Buck and Paytan [2012]. A 10 mL aliquot of the MilliQ water filtrate was analyzed for NO_3^- , NH_4^+ , and soluble reactive phosphorus (SRP, mostly PO_4^{3-}) on a flow injection autoanalyzer (FIA, Lachat Instruments Model QuickChem 8000). The reported NO_3^- values include a negligible contribution from NO_2^- . Peak areas were calibrated using standards prepared in MilliQ water over a range of $0\text{--}60 \mu\text{mol L}^{-1}$ for NO_3^- and $0\text{--}15 \mu\text{mol L}^{-1}$ for NH_4^+ and SRP. The detection limits based on 3 times the standard deviation of five blank (pure MilliQ water) measurements were $0.42 \mu\text{mol N L}^{-1}$ for NO_3^- with a precision of ± 0.2 ; $0.1 \mu\text{mol P L}^{-1}$ for SRP with a precision of ± 0.02 ; and $0.24 \mu\text{mol N L}^{-1}$ for NH_4^+ with a precision of ± 0.15 . All samples were blank corrected.

2.2. Incubation Setup and Sampling

[14] A nutrient and aerosol addition bioassay experiment was conducted with natural microbial assemblages from Lake Tahoe during July 2010. A depth-integrated composite water sample was collected from the upper 20 m of the water column at the UC Davis Lake Tahoe Index Station ($39^\circ 05.708' \text{N}$, $120^\circ 09.421' \text{W}$). The Index Station is a long-term sampling station on the western side of the Lake offshore of the outlet of Blackwood Creek. The station is approximately 0.2 km offshore and 0.3 km southeast of the town of Tahoe Pines. Equal volumes of water from 2, 5, 8, 11, 14, 17, and 20 m were prefiltered through an $80 \mu\text{m}$ screen to remove larger grazers and combined to provide a water sample representative of the surface mixed layer. Grazers were removed following standard procedures for conducting nutrient limitation experiments in Lake Tahoe [Hackley, 2011] such that the response to nutrient additions could be easily assessed and selective grazing on certain species would not affect the community composition of nanophytoplankton. Water was dispensed into acid-cleaned, sample-rinsed, clear 500 mL polycarbonate bottles (12 bottles per treatment). Five sample bottles were also collected to define ambient baseline conditions. Nutrient additions were made with final concentrations of $1.5 \mu\text{mol L}^{-1}$ NaNO_3 (hereafter NO_3^-), $3 \mu\text{mol L}^{-1}$ NH_4^+ delivered as $(\text{NH}_4)_2\text{SO}_4$ (hereafter NH_4^+), or $0.4 \mu\text{mol L}^{-1}$ NaH_2PO_4 (hereafter PO_4^{3-}). These concentrations were calculated to be approximately fivefold higher than ambient mixed layer concentrations of these nutrients for the month of July. Nutrient treatments included NO_3^- alone, NH_4^+ alone, PO_4^{3-} alone, $\text{NO}_3^- + \text{PO}_4^{3-}$, and $\text{NH}_4^+ + \text{PO}_4^{3-}$.

[15] Dry atmospheric aerosol deposition is a function of aerosol properties, atmospheric conditions, and surface characteristics. Thus, it is highly heterogeneous in both space and time. Two aerosol samples with different nutrient contents and air mass back trajectories were selected from the set of TSP aerosol samples collected. Aerosol type 1 was collected between 19 and 25 May 2006, and aerosol type 2 was collected between 20 and 25 December 2005 (Figure 2). Additions of aerosol were made to approximate levels that would accumulate within the mixed layer over 1 week. To calculate the appropriate amount of aerosol to add to the water, we used a deposition rate of $\sim 140 \text{ mg m}^{-2} \text{ d}^{-1}$ based on the upper range of TSP concentrations we measured from our nonfire aerosol samples, and assumed a deposition velocity of 2 cm s^{-1} for TSP [Jacobson, 2005] and a mixed layer depth of 20 m based on the thermocline for the stratified period [Coats *et al.*, 2006]. It is important to note that the mountainous terrain surrounding Lake Tahoe is very different from an ideal flat surface for which deposition models are intended. Accordingly, the deposition rates assumed here are used only to approximate the amount of material that could accumulate in surface waters and to aid our experimental design for determining how much aerosol to add to the incubation bottles. This amount of aerosol simulates a strong deposition event during nonfire periods or a relatively small amount of deposition during a fire when TSP loads are much higher. Aerosol filters of the appropriate size were added directly to the incubation bottles, and control bottles included blank filter additions.

[16] Following addition of the nutrient and aerosol treatments, three bottles were immediately sampled for each of the measurements described below (time zero). The

Table 1. Range of Aerosol TSP, Nutrient Contents, and Nutrient Ratios for Samples Collected November 2005 to August 2006 Extracted in MilliQ Water^a

	Aerosol 1	Aerosol 2	Mean			
	(5/2006)	(12/2005)	(All Samples 11/2005 to 8/2006)	SE	Min	Max
TSP ($\mu\text{g m}^{-3}$ air)	11.15	9.95	17.81	1.26	2.73	46.01
NO_3^- (nmol m^{-3} air)	1.13	2.97	1.99	0.18	0.67	5.34
NH_4^+ (nmol m^{-3} air)	8.06	1.05	3.49	0.49	0.72	9.39
SRP (nmol m^{-3} air)	0.09	0.04	0.07	0.01	0.01	0.26
$(\text{NO}_3^- + \text{NH}_4^+)/\text{SRP}$	104.84	113.57	192.50	25.97	48.64	702.03
NO_3^-/SRP	12.88	83.89	71.89	12.32	2.92	306.92
NH_4^+/SRP	91.95	29.68	105.34	14.59	27.76	424.42

^aThe specific values for aerosols 1 and 2 used in the incubation experiment are shown.

remaining bottles (nine per treatment) were incubated within a shallow pool on the deck of R/V *John Le Conte* in the Tahoe City Marina. Lake water was continually pumped through the pool to maintain the bottles at ambient surface water temperatures. A neutral density shade cloth that attenuated irradiance 50% was placed over the pool. Three bottles from each treatment were collected each morning of the experiment at 8 A.M. (3 days total).

2.3. Nutrient Analyses

[17] Nutrient concentrations, including NO_3^- , NH_4^+ , and SRP, were determined in the incubation experiment water. Aliquots (50 mL) were filtered through 0.45 μm syringe cartridge filters and stored frozen until analysis. Nitrate (including trace amounts of NO_2^-) was determined following the hydrazine method [Kamphake et al., 1967; Strickland and Parsons, 1972] with a detection limit of 0.1 $\mu\text{mol N L}^{-1}$ and a precision of $\pm 0.02 \mu\text{mol N L}^{-1}$. Ammonium was analyzed following the indophenol method [Liddicoat et al., 1975; Solorzano, 1969; Brzezinski, 1987] with a detection limit of 0.2 $\mu\text{mol N L}^{-1}$ and a precision of $\pm 0.1 \mu\text{mol N L}^{-1}$. SRP was analyzed following the phosphomolybdate method [Murphy and Riley, 1962] with a detection limit of 0.03 $\mu\text{mol P L}^{-1}$ and a precision of $\pm 0.02 \mu\text{mol P L}^{-1}$. For all of these nutrients, calibration standards were run approximately every 20 samples and $\sim 5\%$ of samples were run in duplicate to check precision.

2.4. Chlorophyll *a* (Chl *a*) Concentration

[18] Concentrations of chl *a* in the incubation experiment were determined fluorometrically on a TD700 fluorometer, following acetone extraction [Mackey et al., 2009], with a detection limit of 0.01 mg m^{-3} .

2.5. Flow Cytometry and Cell Counts

[19] Samples for enumeration of microbial and phytoplankton cells were preserved with 5% formalin. Cell counts were conducted by microscopy to enumerate cells $> 3 \mu\text{m}$ in diameter, primarily nanophytoplankton (cells 3–20 μm in diameter). All of the nanophytoplankton cells were photosynthetic and included both eukaryotic and cyanobacterial taxa. A settling chamber was used to concentrate cells (for cell counts only) from approximately 100 mL of sample water by gravity settling over a 72 h period. Cells were identified to the species level using a Zeiss AxioObserver A1 inverted compound microscope, equipped with both phase contrast and differential interference contrast objectives. Cells were enumerated and measured at 630X magnification. All cells in the sample were identified and enumerated such that no

group was excluded from the counts. The presence (or absence) of grazers was also noted; however, these organisms were very rare in the samples (see below). Aliquots for flow cytometry were analyzed to enumerate all picoplankton (e.g., picophytoplankton and nonphotosynthetic microbes $< 3 \mu\text{m}$). Cells were stained with 1X Sybr Gold DNA stain (Molecular Probes, Invitrogen), and counts were performed on an Influx flow cytometer (Becton Dickinson). Fluorescence of the Sybr Gold stain was used to delineate and count all cells.

2.6. In-Lake Monitoring

[20] Chl *a* fluorescence profiles at the Index Station were monitored using a Seabird fluorometer before (12 and 22 June 2007) and after (27 June and 24 July 2007) the Angora Fire began, with a dynamic range of 0.03–75 $\mu\text{g L}^{-1}$. In situ chl *a* concentration profile measurements were made on 22 and 27 June and 24 July following Jassby et al. [1999], with a detection limit of 0.05 $\mu\text{g L}^{-1}$. Primary productivity was measured during the fire using ^{14}C uptake experiments as described previously [Goldman, 1988], with a detection limit of 0.01 $\text{mg C m}^{-3} \text{ h}^{-1}$. This method has been used continuously by the Tahoe Environmental Research Center since the 1970s to monitor primary productivity, so the changes we report over time cannot be attributed to method dependent artifacts.

3. Results

3.1. Atmospheric Aerosol Additions

[21] The mean total suspended particle (TSP) load for samples collected between November 2005 and August 2006 was $17.8 \pm 1.3 \mu\text{g m}^{-3}$. Mean soluble nutrient concentrations in the TSP samples were $1.99 \pm 0.18 \text{ nmol N m}^{-3}$ air for NO_3^- , $3.49 \pm 0.49 \text{ nmol N m}^{-3}$ air for NH_4^+ , and $0.073 \pm 0.01 \text{ nmol P m}^{-3}$ air for SRP. Table 1 shows the range of values for each of these parameters, as well as the individual values for aerosols 1 and 2 used in the incubation. The molar ratio of N:P was calculated from the extracted soluble nutrient concentrations and the data are shown in Table 1 and Figure 1. The mean ratio of combined $\text{NO}_3^- + \text{NH}_4^+$ to SRP was 192 ± 26 , with values ranging from 49 to 702. On average NH_4^+ contributed more soluble N than did NO_3^- .

[22] To compare the amount of N and P in aerosols generated during the Angora Fire to the nonfire period, the atmospheric aerosol nutrient content was normalized to the mass of particles for each of the samples. On a per mass basis, both atmospheric aerosol types (fire and nonfire) shared similar concentrations of SRP; however, NO_3^- and NH_4^+ were both

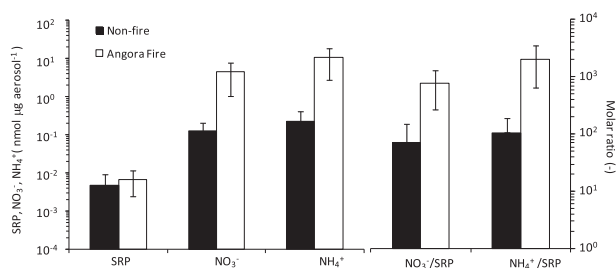


Figure 1. Comparison of nutrient contents and ratios of NO_3^-/SRP and NH_4^+/SRP in aerosols collected during the Angora Fire (25–28 June 2007) and nonfire period (November 2005 to August 2006). Error bars show standard deviation. Note that a log scale is used.

~100-fold higher in aerosols collected during the Angora Fire (Figure 1).

[23] To explore variability in aerosol composition in the region over a longer time frame, we used the Bliss State Park (BSP) data and applied empirical orthogonal function (EOF) analysis. EOF analysis decomposes a data set into a set of mathematically independent structures that efficiently explain the variance in a data set. We performed an EOF analysis on the IMPROVE BSP $\text{PM}_{2.5}$ data for the period 2000–2011. After normalizing the data matrix, we used a singular value decomposition (SVD in Matlab) to decompose the data into the eigenvectors (EOFs) and eigenvalues. We projected the eigenvectors onto the original data to get the principal components (PCs). In this case, the EOFs represent patterns in IMPROVE aerosol composition, and the PCs represent the time dimension. The PCs denote the relative strength of each composition pattern at each time. The first two significant EOFs explain > 85% of the variability in aerosol composition at this site (62% and 24%, respectively; Figures 2a and 2b). The first EOF (Figure 2a, Pattern A) suggests an aerosol source rich in organic matter and secondary sulfate. The second EOF (Figure 2b, Pattern B) suggests a source rich in secondary sulfate as well as mineral dust. Aerosol composition in December 2005 (aerosol 2) was most similar to Pattern A (Figure 2c), and the composition in May 2006 (aerosol 1) was most similar to Pattern B.

[24] Seasonal differences in aerosol chemistry were observed during the two sampling periods. The December 2005 pattern is consistent with biomass burning smoke mixed with other anthropogenic aerosols. The PC associated with this pattern (Pattern A) is very large during the 2007 Angora Fire. In contrast, Pattern B shows higher coarse aerosol content (PM_{10}) during the May 2006 period, indicative of higher dust content. Asian dust transport during the spring significantly impacts aerosol concentrations over the western U.S. [Fischer et al., 2009]; however, locally generated Sierra Cascade soil dust is also observed at IMPROVE sites during spring. Figures 2g and 2h present the average vertical transport for each period. Strong descent characterized the December 2005 (aerosol 2) sample period, but the air arriving at BSP during the May 2006 period (aerosol 1) spent a significant amount of time in the California boundary layer. Thus, we cannot rule out a Cascade soil dust source for this air mass.

[25] We calculated backward trajectories to establish the transport history of the air masses impacting BSP during both periods. Figures 2i and 2j present a summary of the hourly

endpoints from the 3 day backward HYSPLIT trajectories for each period of interest. The December 2005 air mass originated from the west over the Pacific Ocean, whereas the May 2006 air mass followed the continental margin. These figures represent 36 trajectories for the December 2005 aerosol sample and 42 trajectories for the May 2006 aerosol sample. The density plots were created by counting the number of hourly trajectory points within 200 km of each latitude and longitude point. Our goal is to highlight the largest differences in horizontal transport between the two periods of interest so the counts were mapped using a log scale. All trajectories were run for the same amount of time, so trajectories crossing longer distances represent faster speeds.

3.2. Nutrient Drawdown

[26] Nutrient concentrations in the incubation water were monitored during the experiment to quantify nutrient drawdown. The background NO_3^- level in the incubation water was $0.15 \mu\text{mol L}^{-1}$. Increases in NO_3^- concentration were observed immediately after aerosol additions were made for both aerosol 1 ($0.37 \mu\text{mol L}^{-1}$) and aerosol 2 ($0.32 \mu\text{mol L}^{-1}$) (Figure 3a). This atmospheric aerosol derived NO_3^- was drawn down by $0.2\text{--}0.3 \mu\text{mol L}^{-1}$ over the course of the experiment, similar to samples receiving inorganic NO_3^- or $\text{NO}_3^- + \text{PO}_4^{3-}$.

[27] The background NH_4^+ concentration was $0.7 \mu\text{mol L}^{-1}$. Samples amended with aerosol 1 began the experiment with $9.6 \mu\text{mol L}^{-1}$ NH_4^+ , while the concentration in samples amended with aerosol 2 was $1.3 \mu\text{mol L}^{-1}$ NH_4^+ . The variability in NH_4^+ content observed for bottles treated with aerosol 1 is typical of an incubation study using natural aerosol samples and is due to natural variability in the size and composition of the aerosol particles [Cahill and Wakabayashi, 1993; Mackey et al., 2010]. For both aerosol treatments, NH_4^+ was drawn down to levels similar to the control by the end of the experiment (Figure 3b). In samples receiving NH_4^+ or $\text{NH}_4^+ + \text{PO}_4^{3-}$, the NH_4^+ concentration was drawn down by approximately $1 \mu\text{mol L}^{-1}$ over the 3 day incubation period.

[28] The background SRP concentration at the start of the experiment was $\sim 0.04 \mu\text{mol L}^{-1}$. SRP drawdown of $0.16 \mu\text{mol L}^{-1}$ was observed in samples receiving inorganic PO_4^{3-} alone. About threefold less SRP drawdown occurred in samples treated with $\text{NH}_4^+ + \text{PO}_4^{3-}$ or $\text{NO}_3^- + \text{PO}_4^{3-}$, in which SRP levels only decreased by $\sim 0.05 \mu\text{mol L}^{-1}$ over the 3 days of incubation (Figure 3c). No significant SRP drawdown was observed for treatments receiving only NO_3^- or NH_4^+ , for which SRP levels remained similar to the control throughout the experiment. Aerosol addition did not contribute measurably to SRP (Figure 3c).

3.3. Chlorophyll

[29] The initial chl *a* concentration in the composite water sample used in the experiment was 0.33 mg m^{-3} . Statistical analysis of chl *a* concentrations on the final day of the experiment included a one-way analysis of variance (ANOVA) followed by Dunnett's test to determine which treatments changed significantly relative to the control. After 3 days of incubation, chl *a* increased significantly ($p < 0.05$) in all treatments except the control, PO_4^{3-} alone, and aerosol 2 (Figure 4a). In all other treatments, chl *a* increased significantly relative to baseline, and the range of chl *a* values was between 0.48 and 0.55 mg m^{-3} (Figure 4a). Addition of PO_4^{3-} together

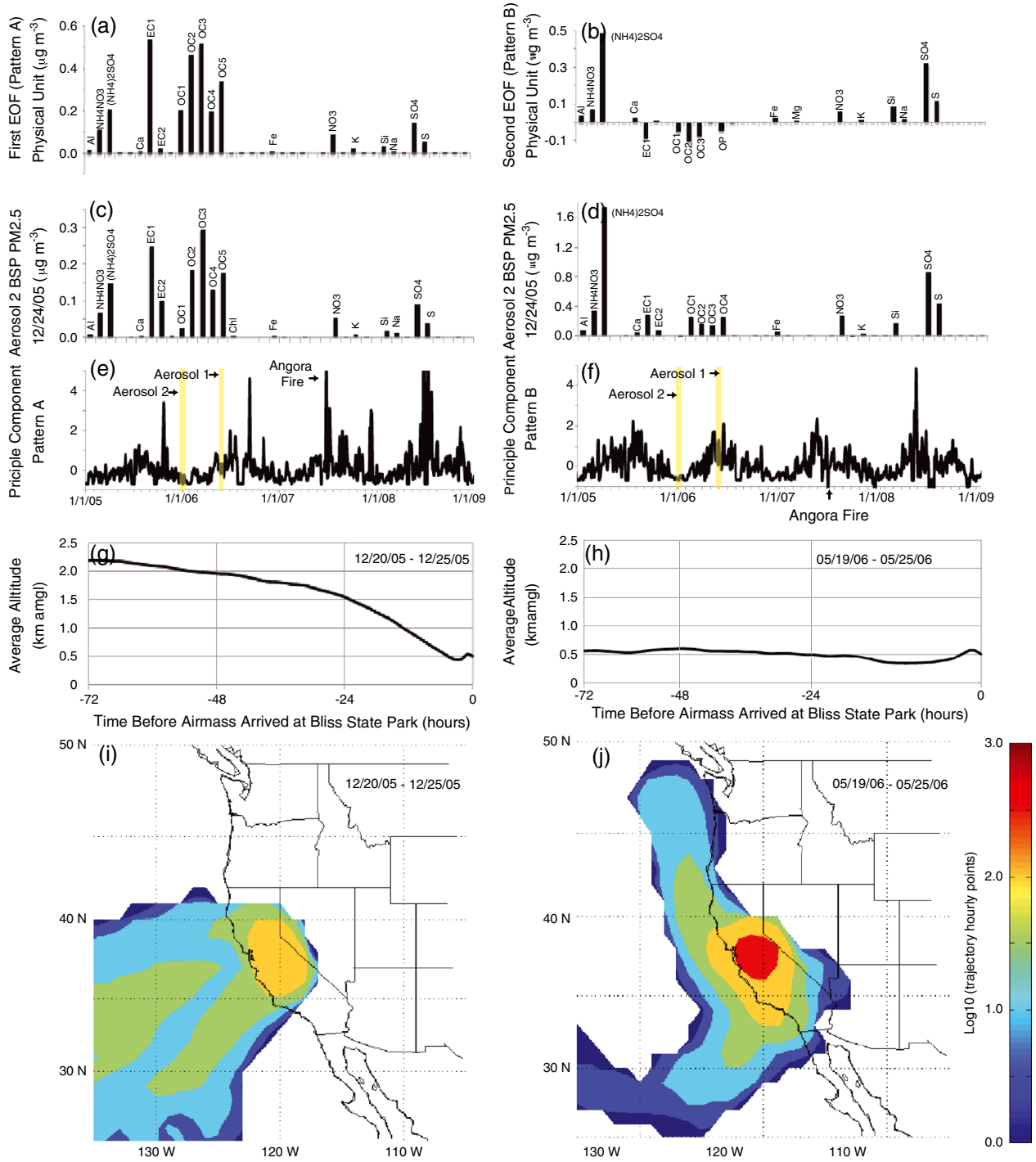


Figure 2. (a) First significant EOF for the IMPROVE Bliss State Park (BSP) PM_{2.5} data. (b) Second significant EOF for the BSP PM_{2.5} data. (c) BSP PM_{2.5} aerosol composition for 24 December 2005. (d) BSP PM_{2.5} aerosol composition for 20 May 2006. (e) Principle component associated with the first significant EOF for the BSP PM_{2.5} data. (f) Principle component associated with the second significant EOF for the BSP PM_{2.5} data. (g) Average vertical air mass transport to BSP during the period 20–25 December 2005. Vertical scale is meters above model ground level (m amgl). (h) Average vertical air mass transport to BSP during the period 19–25 May 2006. (i) Horizontal distribution of air mass transport to BSP during the period 20–25 December 2005. These maps were created from 3 day HYSPLIT backward trajectories initialized from BSP 4 times daily. The colors represent the number of points within a 200 km radius of each latitude and longitude point. Note the common log scale. (j) As in Figure 2i but for 19–25 May 2006. Yellow shading in Figures 2e and 2f indicates the sampling periods 20–25 December 2005 and 19–25 May 2006.

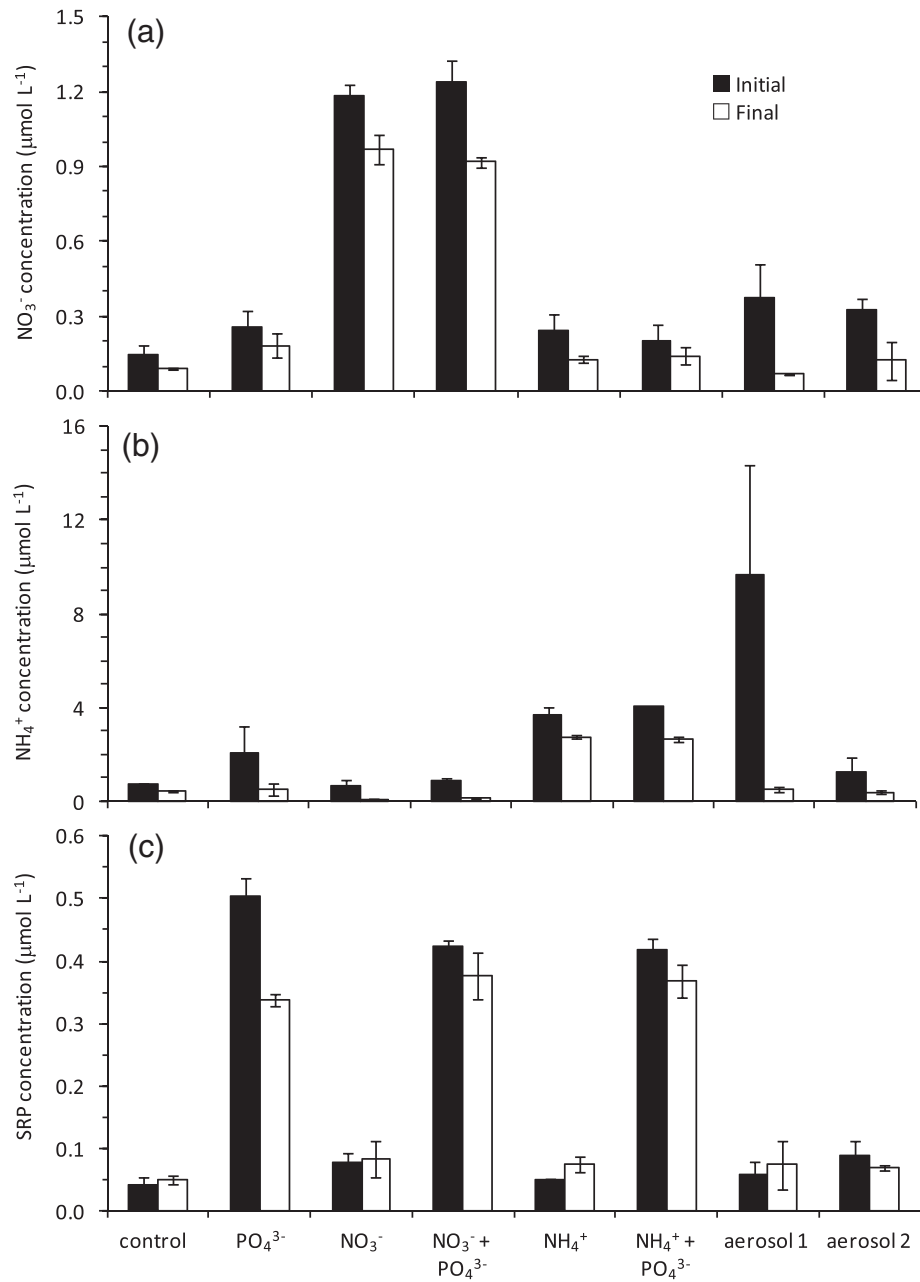


Figure 3. Initial (black) and final (white) concentrations of (a) NO_3^- , (b) NH_4^+ , and (c) SRP in the incubation experiment water. Error bars show standard error of three replicates.

with N did not induce higher chl *a* levels than for N alone, indicating that phytoplankton were primarily N limited rather than colimited for N and P at the time of our experiment.

3.4. Flow Cytometry

[30] Picoplankton (e.g., picocyanobacteria, picoeukaryotes, and nonphotosynthetic cells $< 3 \mu\text{m}$) were enumerated by flow cytometry. Statistical analysis included a one-way ANOVA followed by Dunnett's test to determine which treatments changed significantly relative to the control. The incubation water at the start of the experiment contained 320×10^3 small cells mL^{-1} . The concentration did not change significantly by the end of the experiment in the control or in samples treated with NO_3^- , $\text{NO}_3^- + \text{PO}_4^{3-}$, PO_4^{3-} , $\text{NH}_4^+ + \text{PO}_4^{3-}$, or aerosol

2 ($p < 0.05$; Figure 4b). In contrast, the concentration of picoplankton increased significantly ($p < 0.05$) in samples treated with NH_4^+ alone (430×10^3 cells mL^{-1}) or aerosol 1 (390×10^3 cells mL^{-1}).

3.5. Cell Counts

[31] The initial nanophytoplankton population in the incubation water was dominated by diatoms (350×10^3 cells mL^{-1}), the two most abundant species being *Achnanthes microcephala* and *Cyclotella gordonensis* (Figure 6). *Cyclotella glomerata* was not detected at the start of the experiment, but reached low but detectable levels (5 cells mL^{-1}) in all bottles treated with aerosol 1. It was not present above detection in any of the other treatments.

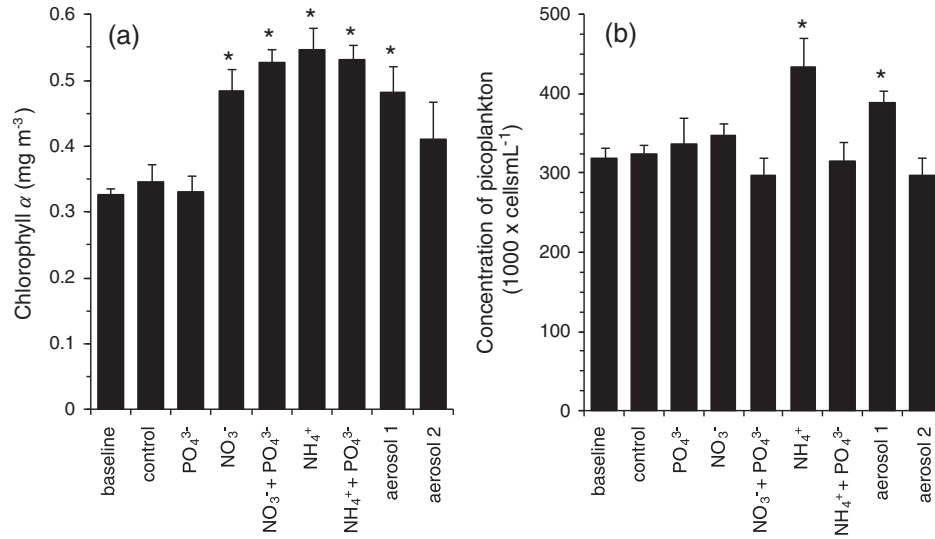


Figure 4. (a) Chl a and (b) concentration of picoplankton cells $< 3 \mu\text{m}$ in the incubation experiment. Error bars show standard error of three replicates. Asterisk indicates the treatment is statistically different from the control ($p < 0.05$).

[32] About an order of magnitude less abundant than the diatoms were the chlorophytes ($4.0 \times 10^3 \text{ cells mL}^{-1}$), which were dominated by the species *Ankistrodesmus spiralis* and *Planktonema lauterbornii* (Figure 6) and the chrysophytes ($4.8 \times 10^3 \text{ cells mL}^{-1}$). The cell concentrations of these three populations remained relatively stable for all treatments over the course of the experiment (Figures 5a–5c). One exception was for the $\text{NO}_3^- + \text{PO}_4^{3-}$ treatment, in which chlorophytes were approximately twofold more abundant than in other samples. Like the other samples, *Ankistrodesmus spiralis* and *Planktonema lauterbornii* were abundant in the $\text{NO}_3^- + \text{PO}_4^{3-}$ treatment, but the species *Oocystis parva* also contributed significantly to the abundance of chlorophytes in these samples.

[33] Cyanobacteria $> 3 \mu\text{m}$ were rare in the initial nanophytoplankton population at the start of the experiment. Water samples taken before experimental treatments were made indicated that these larger cyanobacteria cells were present at concentrations of $< 1 \text{ cell mL}^{-1}$

(Figure 5d). The abundance of cyanobacteria increased in all treatments over the course of the experiment. The greatest increases in cyanobacteria, however, were observed in samples treated with aerosol 1. In these samples, cyanobacteria concentrations reached $3.6 \times 10^3 \text{ cells mL}^{-1}$, approximately 1–2 orders of magnitude higher than for the other treatments (Figure 5d).

[34] The composition of the cyanobacterial population (cells $> 3 \mu\text{m}$) also differed between treatments. In nonaerosol treatments the cyanobacteria population comprised *Chroococcus limneticus* (Figure 6b) and *Leptolyngbya* sp. (Figure 6c) in similar abundances. However, in the aerosol treatment, *Leptolyngbya* sp. outnumbered *Chroococcus limneticus* by > 2 orders of magnitude.

[35] The presence of grazers was also noted during the cell count procedure, though the numbers were not high enough for quantitative comparison. No ciliates were observed in any of the samples, consistent with the observation that these organisms are more commonly observed in the spring during periods of high runoff and not in the summer when our water

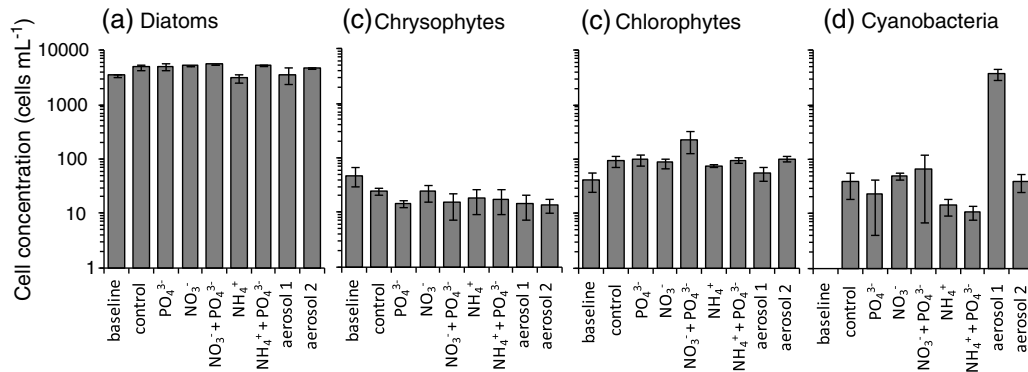


Figure 5. Abundances of (a) diatoms, (b) chrysophytes, (c) chlorophytes, and (d) cyanobacteria present in samples from the incubation experiment. Note that a log scale is used. Error bars show standard error of three replicates, except for PO_4^{3-} , NO_3^- , and $\text{NO}_3^- + \text{PO}_4^{3-}$, where only duplicate samples were analyzed. For these treatments, error bars show the minimum and maximum values.

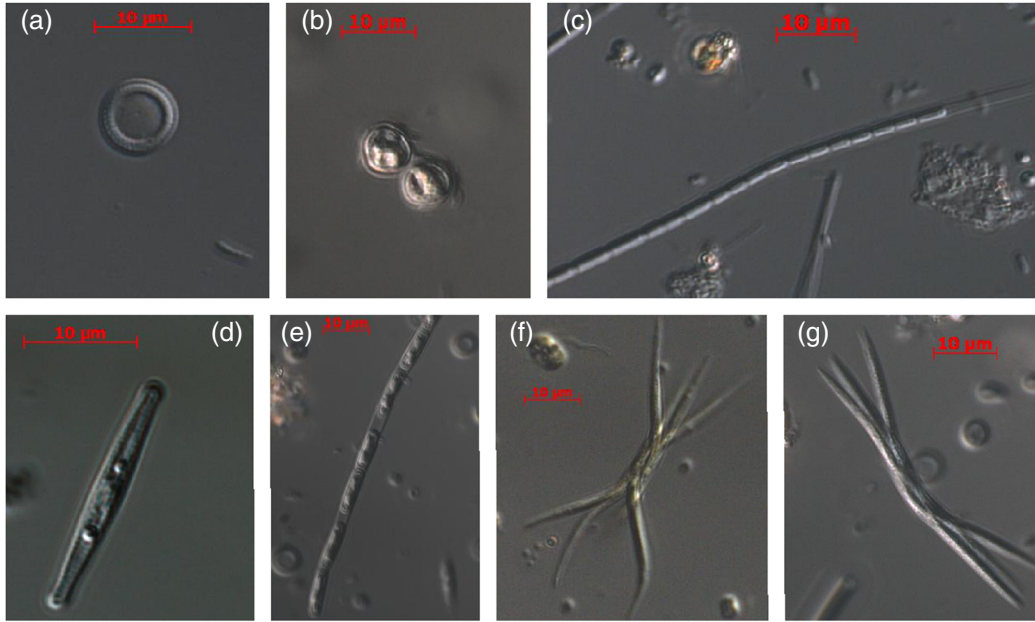


Figure 6. Micrographs (630X) of phytoplankton cells present in samples from the incubation experiment, including (a) diatom *Cyclotella gordonensis*; (b) cyanobacteria *Chroococcus limneticus*, two cells; (c) cyanobacteria *Leptolyngbya* sp., filament, numerous cells; (d) diatom *Achnanthes microcephala*; (e) chlorophyte *Planktonema lauterbornii*, filament, numerous cells; and (f, g) chlorophyte *Ankistrodesmus spiralis*.

was collected. Small flagellates ($<5 \mu\text{m}$) were present in low numbers (their counts are included in the chrysophytes, Figure 5b), and these cells can become mixotrophic during parts of their life cycle. It is possible that other small protozoan grazers were also present; however, these organisms are not identified as part of the routine cell counting for the long-term monitoring program at Lake Tahoe, and in our samples, they were not abundant enough to be quantitatively enumerated. No intact zooplankton were observed in any of our incubation samples. The lack of zooplankton grazers is consistent with the fact that the incubation water was prefiltered to remove grazers and that the incubation water was collected in the morning, whereas copepod zooplankton

migrate to the surface to feed at night and then return to depth in the morning.

3.6. Angora Fire

[36] Chl *a* concentration, chl *a* fluorescence, and primary productivity profiles were monitored before and after the start of the Angora fire (Figure 7). Chl *a* concentration and fluorescence showed no strong changes over the sampling dates, particularly in surface waters that were directly influenced by deposition from the fire. In contrast, primary productivity doubled in surface waters within 3 weeks of the start of the fire (Figure 7c).

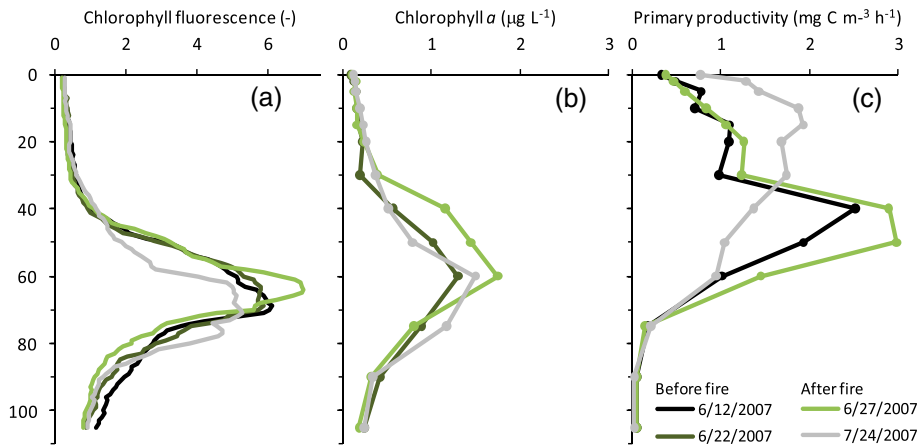


Figure 7. Depth transects showing (a) chl *a* fluorescence, (b) chl *a* concentration, and (c) primary productivity in June–July 2007 before and after the onset of the Angora Fire (legend for all panels as in Figure 7c). The Angora Fire began on 24 June 2007. Primary productivity doubled in the mixed layer (top ~20 m) following the fire, whereas chl *a* concentration and fluorescence remained stable in the surface.

4. Discussion

4.1. Growth Responses of Phytoplankton and Picoplankton

[37] Our incubation experiment suggests that aerosols can contribute to the trophic shift that has been observed in Lake Tahoe by selectively supporting the growth of picoplankton (Figure 4b) and larger (nonpicoplankton) cyanobacteria (Figure 5d) in surface waters. Nonpicoplankton cyanobacteria cells were rare (<1 cell mL^{-1}) in our initial sample water but bloomed quickly over the course of the experiment (Figure 5d), possibly due in part to the removal of grazing pressure. However, nonpicoplankton cyanobacteria growth was much stronger in the aerosol 1 treatment, where cyanobacteria were up to 100 times more abundant than for nonaerosol treatments. Within the nonpicoplankton cyanobacteria, aerosol additions favored growth of the genus *Leptolyngbya* sp. over the more common *Chroococcus limneticus* observed in nonaerosol treatments. *Chroococcus* sp. are planktonic cells, typically common in stable surface waters with populations reaching a maximum during the summer months. In contrast, *Leptolyngbya* sp. are not common in Tahoe's planktonic community and likely arrived at the Index Station via discharge from the nearby Blackwood Creek. Their preferred habitat is associated with the periphyton or attached communities in riparian streams that flow into the lake, and they are known to inhabit P-limited mat communities in tropical wetlands [Rejmánková and Komárková, 2000]. The growth of *Leptolyngbya* sp. is representative of areas receiving riparian influence and is not likely to occur across the lake. However, the enhancement of *Leptolyngbya* sp. following aerosol fertilization demonstrates the ability of aerosols to exert influence on microbial community composition by supporting the growth of opportunistic, rare cell types that are less competitive under the typical nutrient regime in Lake Tahoe, but that thrive when nutrients and/or trace metals from aerosols are provided. The growth of *Leptolyngbya* sp. in response to aerosol 1 addition was not due to the high NH_4^+ in the aerosol, because NH_4^+ addition did not stimulate their growth above control levels (Figure 5d). It is possible that the aerosol 1 treatment relieved trace metal limitation of these cells or provided favorable organic nutrients; however, more work is needed to determine the specific component in aerosol 1 that caused the strong growth response of these cyanobacteria, as well as the role of grazing in controlling their growth.

[38] Picoplankton concentrations also increased in response to aerosol additions in the incubation experiment. Picoplankton growth was strongest for the NH_4^+ treatment. Aerosol 1 (the aerosol with higher NH_4^+ content, Table 1 and Figure 3b) also caused increased growth in this group. In contrast, aerosol 2 treatment did not induce growth that differed significantly from the control. The significant picoplankton growth responses following aerosol 1 addition indicates that picoplankton cells can respond to aerosol additions rapidly, on the order of days (Figure 4b). However, the lack of response in aerosol 2 demonstrates the variability in responses to aerosols with different chemical compositions.

[39] Long-term monitoring of natural and nutrient enriched lakes has suggested that cyanobacteria may be favored when N:P ratios are low [Smith, 1983; Schindler et al., 2008]. This is because many cyanobacteria species are able

to fix nitrogen, a strategy that allows them to survive and outcompete other algae when N is scarce. However, these studies have relied on conventional microscopy to enumerate cells and do not account for smaller picocyanobacteria that may not employ a diazotrophic growth strategy. For this reason, Blomqvist et al. [1994] argue that considering different types of cyanobacteria (e.g., nitrogen fixing versus non-nitrogen fixing) as separate groups is warranted when studying the effects of nutrient availability on lake ecology.

[40] Picoplankton, including picocyanobacteria, may have different responses to nutrient additions compared to larger cyanobacteria. Indeed, shifts in microbial populations toward picoplankton have been observed in lakes in response to N additions and following eutrophication. Picoplankton such as the cyanobacteria *Synechococcus* tend to dominate lakes with higher N:P ratios [Stockner and Shortreed, 1988; Suttle and Harrison, 1988; Takamura and Nojiri, 1994], particularly when P concentrations are very low [Wehr, 1989, 1991]. Similar responses have been observed during nutrient enrichment experiments in oligotrophic Kennedy Lake [Stockner and Shortreed, 1988]. In these experiments the nanophytoplankton *Anabaena circinalis* dominated the phytoplankton community when N:P ratios ranged from 10:1 to 15:1, whereas *Synechococcus* dominated once the N:P ratio was increased to 35:1.

[41] The strong response of picoplankton to inorganic NH_4^+ as well as to aerosols with a high NH_4^+ :P content in our incubation experiment is consistent with these prior findings of increased picoplankton abundance. Dissolved P levels were very low ($\sim 0.05 \mu\text{mol L}^{-1}$) in the incubation water at the start of the experiment; thus, addition of NH_4^+ alone or aerosols with high NH_4^+ :P content would have favored the growth of small picoplankton cells. In contrast, addition of PO_4^{3-} together with NH_4^+ , which provided a lower NH_4^+ :P ratio, led to a relative decline in picoplankton concentrations (Figure 4b). Thus, the high ratio of NH_4^+ to P in atmospheric aerosols has the potential to cause shifts in the microbial community toward smaller cells, as has been observed in other lakes following anthropogenic eutrophication caused by nutrient inputs from nonatmospheric sources. Low N:P ratios did not favor the growth of larger nitrogen-fixing cyanobacteria as has been previously proposed [Smith and Schindler, 2009]. This could be due to the low numbers of cells of these species in the lake water at the time of our incubation (Figure 5d), where very low P levels may have inhibited their growth despite their ability to fix N.

[42] In contrast to cells in the NH_4^+ treatment, picoplankton growth in response to NO_3^- addition was smaller, and the increase was not statistically different from the control (Figure 4b). While the cause of this different response to NH_4^+ versus NO_3^- is not known, it could suggest that recycled forms of N like NH_4^+ are preferred by picoplankton in Lake Tahoe. For example, it has been shown that enrichment with NH_4^+ (as opposed to NO_3^-) causes selective stimulation of non-nitrogen-fixing cyanobacteria in lake communities [Blomqvist et al., 1994] consistent with our observations of increased picoplankton abundance (in which picocyanobacteria are included). Together, these results suggest that while the N:P ratio clearly influences microbial community composition, the response is modulated by the nutrient chemistry as well as the unique nutrient preferences of each species.

4.2. Community Dynamics, Grazing, and Implications for Lake Ecology

[43] The response of the microbial community to atmospheric nutrient deposition depends on several factors. First, the chemical composition of the aerosol (which depends on the aerosol source) is important; we found that atmospheric deposition collected locally at Lake Tahoe during nonfire periods has a range of nutrient compositions and N:P ratios (Table 1 and Figure 2), consistent with other studies [Jassby *et al.*, 1994, 1995; Gertler *et al.*, 2006]. The strongest response of picoplankton in the incubation experiment occurred for aerosol 1, which contained a higher concentration of NH_4^+ than aerosol 2 (Table 1 and Figure 3b). Back trajectory modeling indicated that the air mass associated with aerosol 1 spent more time within the California atmospheric boundary layer than the air mass associated with aerosol 2. The higher proportion of NH_4^+ in aerosol 1 may be attributed to several anthropogenic sources in the region. Emissions of ammonia (NH_3) are highly uncertain, but fertilizer use and animal waste are the largest sources. Vehicle exhaust also contains NH_3 , and the relative importance of this source is larger in winter when agricultural emissions are at a minimum [Battye *et al.*, 2003]. NH_3 is also emitted from biomass burning [Akagi *et al.*, 2011]. Fire ash from the Angora Fire was enriched in N, but the overall chemical composition of the leachable components of ash is likely different than that of atmospheric deposition during nonfire periods, and thus the effects on the microbial community would be distinct. Although not quantified in this study, atmospheric material can also contain bioavailable forms of organic N [Peierls and Paerl, 1997].

[44] The response of the microbial community to atmospheric aerosols also depends on the availability of other growth limiting nutrients like P or trace metals, which change in space and time. For example, runoff from the watershed provides ~65% of the total P to Lake Tahoe on an annual basis [Hatch, 1997], and most of this input comes primarily during the wet season when N availability is higher as a result of convective mixing. Atmospheric nutrients may play a more important role in the dry summer season, when N levels become depleted due to stratification and P inputs are also more limited. Indeed, NH_4^+ concentrations in aerosols show a seasonal pattern that peaks during these more nutrient-deplete summer months (Figure 2f). Finally, the presence of different phytoplankton taxa with different nutrient requirements, preferences, and uptake rates will also determine how the community responds to atmospheric aerosol deposition over seasonal cycles.

[45] The incubation experiment generated several results with respect to the potential impact of atmospheric aerosols on phytoplankton dynamics. First, large phytoplankton appear to be better competitors than picoplankton when P is also available and when N:P ratios are low (Figure 4a). This is consistent with prior studies in which community shifts from picoplankton to nanophytoplankton were observed following increased P availability [Wehr, 1989, 1991], and in response to lower N:P ratios [Stockner and Shortreed, 1988]. A decline was likewise observed in surface populations of picocyanobacteria in Lake Tahoe following combined additions of N and P during the stratified summer season [Winder, 2009]. We suggest that nanophytoplankton,

particularly chlorophytes, may have effectively outcompeted picoplankton in our incubation by consuming more of the N when P was also added, resulting in lower picoplankton abundances in the N+P treatments than when N was added alone (Figure 4b).

[46] Our experiments also show that the increase in cell numbers in some treatments is not associated with increase in chl *a* (Figures 4 and 5). The concentration of chl *a* in the incubation experiment was likely influenced more strongly by large eukaryotic phytoplankton that have more chl *a* per cell and can increase their cellular chl *a* content rapidly following nutrient enrichment [Riemann *et al.*, 1989]. Because of this, the increase in picoplankton cell numbers did not affect the chl *a* concentrations strongly (e.g., compare the different responses of chl *a* and picoplankton growth to different treatments shown in Figures 4a and 4b). Due to their high concentrations and growth rates, photosynthetic picophytoplankton can contribute substantially to primary production. However, due to their small size, photosynthetic picoplankton cells do not contribute as much chl *a* or biomass on a per cell basis as larger phytoplankton cells do, and this can cause a decoupling between chl *a* levels, cell numbers, and measured primary productivity rates [Goldman and Carter, 1965; Saunders *et al.*, 1962]. Nonphotosynthetic cells < 2 μm are also included in the picoplankton fraction, and increases in their numbers or metabolic rates could increase respiration and likewise affect productivity measurements while leaving chl *a* concentrations unaffected. Small diatoms 5–15 μm with higher surface to volume ratios, higher nutrient uptake rates, and higher metabolic rates have increased dramatically in Lake Tahoe in recent years [Winder, 2009], yet these cells contribute less biomass on a cellular basis compared to larger phytoplankton cells. We suggest that changes in microbial community composition due in part to atmospheric aerosol deposition could contribute toward a decoupling between chl *a* and primary productivity by selecting for cells with relatively high growth rates but low chl *a* content. Grazing is also likely to affect the relationship between chl *a* and primary productivity.

[47] In the typical model of “top-down” control of phytoplankton in lakes, increased phytoplankton growth supports higher levels of grazers, which in turn keep the phytoplankton biomass at a stable level even as phytoplankton cells divide rapidly. In this way, productivity can increase without leading to increased phytoplankton biomass or chl *a*. While phytoplankton growth in Lake Tahoe is generally considered to be controlled by “bottom-up” processes like nutrient availability [Jassby *et al.*, 1992], it is likely that grazing also helps control phytoplankton growth and community composition. This was evident from the results of the incubation experiment in the present study, where removal of larger grazers led to a measurable increase in chl *a* as phytoplankton grew. Selective feeding by different groups of grazers has been demonstrated in Lake Tahoe [Elser and Goldman, 1991], and the replacement of native cladoceran grazers with larger mysid grazers since the 1960s [Richards *et al.*, 1975] could be another process that contributes to the success of smaller phytoplankton via preferential grazing of mysids on larger phytoplankton. Protozoan grazers (e.g., ciliates, flagellates) would be more likely to prey on picoplankton due to their smaller size [Gonzalez *et al.*, 1990]. However, protozoans are more abundant in the

spring than in the summer when our experiment was conducted, and protozoans were rare in our samples. The rareness of these organisms may be one factor that allowed picoplankton numbers to increase in response to nutrient and aerosol additions in our experiment. The seasonal variation in dominant grazer communities, including protozoans that favor picoplankton as prey, would play an important role in affecting phytoplankton community composition in addition to nutrient concentrations and ratios. More work is needed to characterize the role of grazing in modulating the relationship between chl *a* and productivity in Lake Tahoe.

4.3. Microbial Responses to Atmospheric Deposition From Fires

[48] The observation that atmospheric aerosols can in some cases increase productivity without increasing chl *a* levels is consistent with monitoring observations from large deposition events associated with forest fires in the vicinity of Lake Tahoe. Goldman *et al.* [1990] reported on the effects of the 1985 Wheeler Fire, showing that productivity increased threefold in response to dry deposition from the fire. Similar to the Wheeler Fire, productivity doubled in surface waters following the 2007 Angora Fire (Figure 7c). Unlike primary productivity, chl *a* levels remained relatively unchanged in surface waters following the Angora Fire (Figures 7a and 7b), just as biomass remained constant following the Wheeler Fire [Goldman *et al.*, 1990]. Both of these observations suggest that large phytoplankton either did not grow much or were heavily grazed in response to deposition from the fires, otherwise increased biomass and chl *a* would have been apparent (because large cells contribute more biomass and chl *a* on a per cell basis). Because no appreciable increase in phytoplankton biomass occurred during the Wheeler Fire, Goldman *et al.* suggested that the productivity of individual phytoplankton cells may have increased during the fire due to relief from photoinhibition and that this would explain the increase in primary productivity he observed. However, it is possible that some of the increased productivity observed in the Wheeler and Angora Fires may have been due to aerosol-induced stimulation of the picoplankton community, which is capable of contributing to productivity without causing large increases in biomass or chl *a*. Grazing of microzooplankton on picoplankton is another mechanism by which the biomass and chl *a* concentration could remain low while picoplanktonic primary production rates remain high; however, grazing rates were not measured in this study so this possibility remains unquantified.

[49] Given the incubation results that suggest picoplankton are better competitors under high NH_4^+ and high $\text{NH}_4^+:\text{P}$ conditions, picoplankton would be strongly favored by deposition of ash from fires. For example, atmospheric aerosols during the Angora Fire had ~ 100 -fold more N compared to nonfire aerosols on a per mass basis (Figure 1). The amount of P in these samples was similar to nonfire aerosols, yielding N:P values that were considerably higher during the fire compared to typical values. Moreover, NH_4^+ contributed approximately twice as much N as NO_3^- in these samples, resulting in a mean soluble $\text{NH}_4^+:\text{P}$ ratio of over 2000:1 for the aerosols during the fire (Figure 1). In our incubation experiment, the $\text{NH}_4^+:\text{P}$ ratio was 91:1 in aerosol 1 which stimulated picoplankton growth. Clearly, if NH_4^+ availability and low P (e.g., high $\text{NH}_4^+:\text{P}$ ratio) favor these small cells as the

incubation experiment suggests, then atmospheric aerosol deposition in general (and during fires in particular) also has the potential to support picoplankton growth due to the very high $\text{NH}_4^+:\text{P}$ ratio in these aerosols. Accordingly, based on the high $\text{NH}_4^+:\text{P}$ ratios in atmospheric aerosols collected during the fire and the strong growth response of picoplankton to NH_4^+ -rich aerosol 1 during the incubation experiment, we suggest that picoplankton and possibly other opportunistic phytoplankton were responsible for the increased primary productivity levels during the Wheeler and Angora Fires (Figure 7c) [Goldman *et al.*, 1990]. To our knowledge, no picoplankton monitoring has been conducted during fires at Lake Tahoe, and measurements should be made to evaluate the contribution of these small cells, including picoeukaryotes, and picocyanobacteria, to productivity during future fires.

[50] In a model developed by Swift *et al.* [2006], both chl *a* concentration and suspended particulate material were shown to have a strong effect on Secchi depth. Stimulation of phytoplankton by nutrient loading from atmospheric aerosol deposition therefore has the potential to contribute to Tahoe's loss of clarity by affecting both of these factors. Increased chl *a* from the growth of larger phytoplankton increases the amount of light that gets absorbed in the water, while increased concentrations of small cells contributes more to light scattering. This is because when particle/cell size is small compared to the wavelength, light will scatter more isotropically than for larger particles/cells [Dunn and Richards-Kortum, 1996]. The $\sim 100,000$ cell mL^{-1} increase in picoplankton and cyanobacteria we observed in our incubations is an increase of tenfold compared to typical levels of $\sim 10,000$ particles mL^{-1} for Lake Tahoe [Sunman, 2001]. While grazing would modulate this response in the lake, this is a considerable change. Based on the model by Swift *et al.* [2006] with all other factors being equal, the moderate chl *a* increase observed in our incubation experiment for aerosol 1 would result in a 1–2 m loss of clarity from light absorption. The increased concentration of picoplankton would likewise result in an additional meter of Secchi depth shoaling from light scattering, for a combined clarity loss of ~ 2 –3 m, or $\sim 10\%$ of total Secchi depth if this type of growth was to occur in the lake (T. Swift, personal communication, 2011). This effect would presumably last as long as the cells were still present in the water before senescing or getting consumed by grazers, likely on the order of days to weeks. However, the model is not specifically calibrated to account for the scattering effects of small cells, which have a different refractive index than inorganic particulate materials, and the estimates given here are only meant to provide an approximation of the possible effect of microbial growth on clarity in Lake Tahoe.

5. Conclusions

[51] In this study we have sought to understand if and how aerosol dry deposition impacts the microbial community in Lake Tahoe. Our data indicate that atmospheric aerosols provide nutrients with a high ratio of N:P (and specifically high $\text{NH}_4^+:\text{P}$), consistent with prior studies. Our study also demonstrates that aerosols can support the growth of picoplankton (which are more competitive at high N:P ratios and low P) as well as other opportunistic cyanobacteria;

however, the extent to which aerosol nutrients influence microbial community composition over different seasons remains to be determined. In contrast, larger phytoplankton appear to be better competitors when P is available. Picoplankton cells further affect the Lake's ecology by contributing to productivity without generating large amounts of chl *a* per cell, and their presence, together with shifts in grazing dynamics, may explain the uncoupling of chl *a* concentration and primary productivity rates observed over the past several decades in Lake Tahoe, as well as following fires in the region.

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