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Nutrient hot spots in some sierra Nevada forest soils

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Abstract Re-examination of data distributions from several forested sites in the eastern Sierra Nevada Mountains shows consistent, positive outliers and skew for NH_4^+, NO_3^-, and mineral N in resin lysimeters and resin capsules, indicating that most values were low but hotspots of high N flux were present in most cases. Exact causes of these N flux hotspots is not known, but could include water flux hotspots (e.g., preferential flowpaths), microbial hotspots, and possibly the entry of N-enriched O horizon interflow. Soil and resin stake (PRS probe) data from one site (North Lake Tahoe) also showed consistent, positive outliers and skew for NH_4^+, NO_3^-, and mineral N, suggesting the presence of microbially produced hotspots. Bicarbonate-P data from soils and *ortho*-P data from PRS probes also showed highly positive skew and extreme outliers, but Bray (HCl/NH_4F-extractable) P in soils did not. Other measured nutrients (extractable Mg^{2+}, K^+, SO_4^{2-}, and Ca^{2+}) also showed positive skew and outliers, but less so than NH_4^+, NO_3^-, and mineral N. Calcium stood out among measured nutrients as the most abundant nutrient with the least outliers and the lowest (sometimes negative) skew. The differences in distributions of NH_4^+, NO_3^-, and mineral N and those of Ca^{2+} may reflect relative abundance: the most abundant ion, Ca^{2+}, shows little evidence of hotspots whereas the much less abundant ions, NH_4^+, NO_3^- consistently show evidence of hotspots. We hypothesize that the differing distributions of N and Ca reflect the relative biological competition for these nutrients and that positively-skewed distributions and hotspots will be characteristic of any other nutrient when it is in limited supply relative to biological demand.

Keywords Nutrients · Soils · Hotspots · Ammonium · Nitrate · Calcium · *Ortho*-P · Magnesium · Sulfate · Potassium Sierra Nevada Mountains

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Introduction

Many biogeochemical studies are conducted on a kg ha^{-1} scale, where the plot or even watershed is considered the basic unit of study and the replicate for treatment evaluations (Cole and Rapp 1981; Likens et al. 1977; Swank and Crossley 1987; Johnson and Lindberg 1991). To this end, and to save money and reduce unwanted variability, soils are often composited by plot. The potential loss of valuable information by compositing soils is highlighted in a recent paper of Schimel and Bennett (2004), who review the well-recognized importance of soil microsites. Schimel and Bennett (2004) pose a new paradigm for plant-microbial competition where trees can effectively compete with soil microbes by invading N-rich microsites that exist at least temporarily even under relatively N-limited conditions. The definitions of McClain et al. (2003) provide a useful background here; they define biogeochemical hotspots as: "areas (or patches) that show disproportionately high reaction rates relative to the surrounding area (or matrix)," and they define hot moments as "short periods of time that show disproportionately high reaction rates relative to longer intervening time periods" (p. 302). Roots, along with their mycorrhizal symbionats, can presumably tap into hot spots during hot moments with their elongated structure and exploratory habit, thereby allowing plants to, as Schimel and Bennett (2004) put it, "'win' competition events [with soil microbes] when viewed at a macro scale or whole-soil level" (p. 594), and thereby might effectively mine the soil for N over time. This mechanism might explain how trees appear to be able to mine soil N, especially under the influence of elevated CO_2 where root growth is often disproportionately stimulated (Johnson 2006).

The Sierra Nevada montane ecosystems of Nevada and California differ from those considered by Schimel and Bennett (2004) in that rooting is often entirely absent in the O horizons because of extreme summer drought. Thus, decomposition and vegetation uptake processes are spatially discoupled and the intense competition for N between roots and decomposers that characterizes the more humid forest soils is absent in these systems (Stark 1973; Johnson et al. 2009). Because of this vertical discoupling, nutrients released during decomposition in O horizons are not immediately taken up and can be solubilized by rain or snowmelt, creating the solutions with very high inorganic N and P concentrations (Miller et al. 2005, 2006).

As a prelude to initiating some studies specifically designed to search for nutrient hotspots and their causes in these ecosystems, we re-examined data sets from several previous studies for the presence of nutrient hotspots. Although these studies were designed for different purposes (mostly harvesting and fire effects), many of the point sampling techniques are amenable for such a post-hoc investigation.

Sites and methods

Sites

A listing of climate, soils, parent material and major vegetation for the sites used in this study are given in Table 1. In all cases, snow accounts for >50% of annual precipitation. The North Lake Tahoe and Truckee sites were initiated to study the combined effects of thinning and understory removal with prescribed fire (Glass, 2006; Murphy et al. 2006a; Johnson et al. 2008). Only data obtained before treatment were used in the current analysis. The Gondola site was also originally designed as a thinning and prescribed fire study, but a wild fire broke out and burned nine of the 16 plots, converting the study to one of wildfire effects. Again, only pre-fire data were used in this analysis. The Little Valley site was burned in a wildfire in 1981 and subjected to nutrient budget analyses during the 1997–2001 period during which the former fire, now dominated by an N-fixing shrub (*Ceanothus velutinus*), was compared

Table 1 Location, climatic conditions, soils, parent material and vegetation of the Sierran forest sites

Site name	Location	MAT (°C)	MAP (cm)	Parent material	Soil type	Dominant vegetation
Truckee	13 km north of Truckee, California	4.8	94	Andesite	Ultic Haploxeralfs	*Pinus jeffreyii*
North Lake Tahoe	6 km north of Tahoe City, California	6.7	81	Basalt	Typic Cryoboralfs	*Abies concolor, Pinus jeffreyii, Calocedrus decurrans, Pinuus labertiana, Abies magnifica*
Little Valley	46 km south of Reno, NV	5.0	45	Granite	Typic Xeropsamments	*Pinus jeffreyii*
Gondola	1 km south of Stateline, NV	8.0	87	Granite	Typic Cryopsamments	*Pinus jeffreyii, Abies balsamea*

to an adjacent forested stand (Johnson et al. 2005; Stein 2006). In this case, only data from the adjacent forested site was used.

Methods

North Lake Tahoe

Details on the experimental design, sampling methods and effects of treatments on soils have been reported previously (Glass 2006; Loupe et al. 2009); only a brief summary of collections relevant to the current analysis are given here. Five 0.04 ha sampling plots were established in each of four treatments ($n = 20$), and five subsampling points randomly distributed within each sampling plot ($n = 100$ sample points). Depth-proportional soil samples (0–10 cm) were taken with a trowel at each point immediately before the fire.

All soil samples were oven dried at 55°C for 48 h (lower temperatures now recommended in order to avoid NH_4^+ volatilization in an email exchange with the forest soils community; forsoils@u.washington.edu), sieved to 2 mm, and analyzed for nutrients. Subsamples were sent to Oklahoma State University Soil, Water and Forage Laboratory (SWAFL). At SWAFL, total C and N were analyzed using a dry combustion C and N analyzer (LECO, St. Joseph, Missouri, USA). For soil NH_4^+ and NO_3^-, 10 g of oven-dried, ground soil were shaken with 20 ml of 1 M KCl for 30 min followed by analysis on a Lachat 8000 flow-injection analyzer (Hach Co., Loveland, Colorado, USA). Another set of subsamples was sent to A&L Western Agricultural Laboratories, Modesto, California, USA for Bray-extractable P (2 g soil in 0.5 M HCl plus 1 M NH_4F), Olsen (bicarbonate-extractable) P (2 g soil in 50 ml 0.05 M $NaHCO_3^-$) using a Jarrell Ash ion coupled plasma spectrophotometer (ICP; Thermo Jarrell Ash Corp., Franklin, Massachusetts, USA), exchangeable Ca^{2+}, K^+, and Mg^{2+} and extractable SO_4^{2-} (10 g soil in 50 ml 1 N ammonium acetate (pH 7) followed by ICP analyses).

At each of the five subsampling locations within each plot, Western Agricultural Innovations Plant Root Simulator (PRS) probes and WESCA-UNIBEST PST-1 resin capsules were used to monitor nutrient changes in the system. Both resin devices were installed in the O horizon and exposed over the winter snow season prior to and after burn treatments. (Capsules were installed at the bottom of the O horizon, PRS probes, being more elongated, were exposed to a 10 cm depth of O horizon from the bottom.). After retrieval, the resin capsules were washed with distilled water to remove adhering soil and then extracted with three sequential 20 ml solutions of 2 M KCl on a platform shaker for 20 min each. The combined extractant solution (60 ml) was analyzed at SWAFL as described above for NH_4^+ and NO_3^-. Values were expressed at μmol N cm^{-2} of resin area (which for two sides of the capsule is 11.4 cm^2). After retrieval, the PRS probes were washed with distilled water to remove adhering soil and sent to Western Ag Innovations, Saskatoon, Canada for extraction. At Western Ag, the probes were extracted with 17.5 ml of 0.5 N HCl for 1 h in a zip lock bag, and the extractant was analyzed for NH_4^+ and NO_3^- colorimetrically using a Technicon Autoanlyzer II (Seal Analytical, Mequon, Wisconsin). The remaining nutrients were analyzed with the use of inductively-coupled plasma emission spectroscopy (Perkin Elmer Optima 3000-DV ICP; Perkin Elmer, Inc. Shelton, CT). The values for both the probes were reported in units of 10 μmol cm^{-2} of resin surface, and these were converted to μg cm^{-2} in this study for the purpose of comparing to the resin capsules.

Truckee

At the Truckee site, soil samples were bulked by plot and thus are not appropriate for the current analysis. However, resin lysimeters according to the design of Susfalk and Johnson (2002) were deployed in the treatment plots (15 cm depth in mineral soil) and were analyzed individually (Murphy et al. 2006a). The resin lysimeters consisted of 5.5 cm long, 4 cm inside diameter PVC pipe within which ten g of Rexyn® I-300 (H–OH) resin is trapped between two Nitex® nylon sheets. Twenty gram of moist, washed silica sand is placed on each end of the lysimeter to make contact with the soil. The resin lysimeters were installed by digging a small pit, creating a small tunnel parallel to the surface, and placing the lysimeter in the tunnel, seated against an undisturbed soil profile above it. Resin lysimeters were installed late summer/early fall and taken out the following spring for two seasons before the fire and three seasons after the fire; the two pre-fire data sets from the unharvested treatment (four randomly placed lysimeters per plot in eight plots) will be examined here. Once the lysimeters were removed from the field, the resins were extracted by shaking in 100 ml of 1 M KCl for one hour and analyzed for NH_4^+ and NO_3^- at SWAFL as described above.

Little valley

Vegetation, detritus and soils from the former fire and the adjacent forested site were sampled and reported on previously (Johnson et al. 2005). In this analysis, we used the resin lysimeter and resin capsule data from the forested site only, where 12 randomly-located replicates were in place at 15 cm depth in the mineral soil during two consecutive years (Stein 2006).

Gondola wildfire

Sixteen 0.045 ha plots were established in order to conduct a study on the effects of thinning and prescribed fire at this site. Before the treatments could be implemented, a wildfire broke out in July 2002, burning all but seven of the plots, most of which had been previously sampled. In this analysis, we used resin lysimeter data from the unburned plots (four randomly placed replicates per plot, 15 cm depth in mineral soil); (Murphy et al. 2006b).

Statistics

Each data set was analyzed for the presence of outliers, extreme outliers, and for skewness using DataDesk software (Velleman 1997). The value for positive extreme outliers was determined by the equation:

$$x > Q3 + 3IQR \quad (1)$$

where: x = The value, Q3 = the third quartile value (75th percentile), and IQR = interquartile range (range from 25th to 75th percentile)

The equation for a negative extreme outlier is:

$$x < Q1 - 3IQR \quad (2)$$

where Q1 = the first quartile (25th percentile).

The respective equations for moderate positive and negative outliers are:

$$x > Q3 + 1.5IQR \quad (3)$$

$$x < Q1 - 1.5IQR \quad (4)$$

Values for Skewness (skw) are:

$$skw = M_3/M_2^{3/2} \quad (5)$$

where

$$M_2 = \sum (yi - \bar{y})^2 \Big/ n \quad (6)$$

$$M_3 = \sum (yi - \bar{y})^3 \Big/ n \quad (7)$$

A value for skewness is considered significant if twice the standard error does not overlap zero (Brown 1997). The standard error of skewness (SES) is approximated by (Brown 1997)

$$SES = (6/n)^{0.5} \quad (8)$$

Results and discussion

Figure 1 shows box plots of NH_4^+, NO_3^-, and mineral N fluxes measured by resin lysimeters in the Truckee, Gondola, and Little Valley fire sites and Table 2 gives the values for skewness for these data sets. Without exception, resin lysimeter data in all three sites show one or more positive outliers (both moderate and extreme), no negative outliers, and significant positive skewness. Thus, the majority of NH_4^+, NO_3^-, and mineral N fluxes in these data sets were low, but a few high outliers (hotspots) were present in all data sets. Similarly, resin capsule and resin PRS probe data for the North Lake Tahoe site (where the soil was too rocky to install resin lysimeters) show several positive outliers, no negative outliers, and significant positive skew for NH_4^+, NO_3^-, and mineral N (Fig. 3 and Table 2). Resin capsules and PRS probes absorb nutrients that are leached to them, but, in contrast to resin lysimeters, they are in direct contact with the soil and therefore include diffusional inputs as well. (Resins in resin lysimeters are isolated physically from contact with the soil by the pvc walls and layers of sand on top and bottom Susfalk and Johnson 2002.) The resin capsule data for the Little Valley site shows positive skew for NH_4^+, NO_3^-, and mineral N, but skew is significant only for NO_3^-. There are no extreme outliers for resin capsules at the Little Valley site (not shown). Figure 2

Two factors contribute to the variation in resin lysimeter flux, water flux and nutrient concentration in

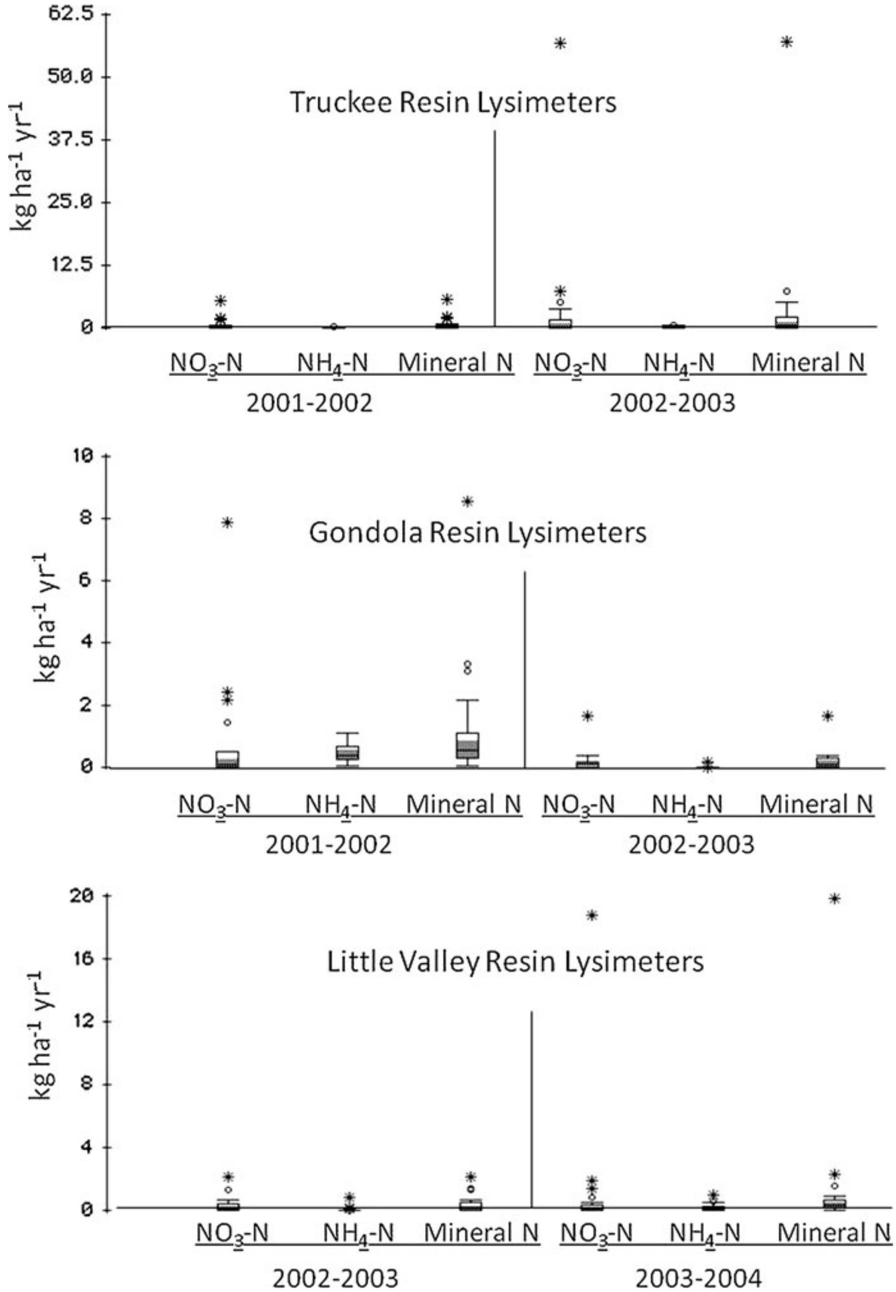

Fig. 1 Box plots of NH_4^+, NO_3^-, and mineral N flux in resin lysimeters for water years 2001–2002 and 2002–2003 at the Truckee and Gondola sites, and 2002–2003 and 2003–2004 water years at the Little Valley site. The *horizontal middle line* indicates the median; the *lower* and *upper* edges of the box indicate the 25 and 75% points, respectively; the whiskers indicate the main body of the data (not including outliers), *shaded intervals* are for comparing medians and defined by ±1.58 (high hinge–low hinge)/$\sqrt{n}$, *circles* indicate outliers and *stars* indicate extreme outliers. See "Methods" for definitions of outliers

water. Thus, an N flux hotspot might be due simply to a hotspot of high water flux, an N hotspot in the soil, or both. If high water flux is the dominant cause of N flux hotspots, soil physical factors would have the most influence, especially those affecting preferential flowpaths (hydrophobicity, macroporosity, variations in texture and structure) which are known to occur in these soils (Burcar et al. 1994). If soil N hotspots are the primary cause of N flux hotspots, then variations in microbial activity and root uptake would have the most influence. It is not possible to estimate the relative importance of these two factors with the present data.

One possible cause of the N flux hotspots is the entry of N-rich O horizon interflow into mineral soils. Miller et al. (2005, 2006) and Loupe et al. (2009) have documented the occurrence of very high concentrations NH_4^+ and NO_3^- in waters flowing through the O horizons (O horizon interflow). Such

Table 2 Skewness for NO_3^-, NH_4^+, and mineral N (NO_3^-, NH_4^+) in soils, resin capsules, resin lysimeters, and resin stakes (PRS probes[TM]) in various sites in the eastern Sierra Nevada Mountains

	n	Skewness		
		NO_3^-	NH_4^+	$NH_4^+ + NO_3^-$
North Lake Tahoe				
Resin capsules	76	4.37 ± 0.56*	4.67 ± 0.56*	3.07 ± 0.56*
PRS probes	77	4.61 ± 0.56*	2.88 ± 0.56*	3.30 ± 0.56
Little Valley				
Resin lysimeters				
2002–2003	24	2.61 ± 1.00*	3.94 ± 1.00*	2.10 ± 1.00*
2003–2004	24	4.47 ± 1.00*	2.15 ± 1.00*	4.47 ± 1.00*
Resin capsules	22	1.10 ± 1.04*	0.70 ± 1.04	0.99 ± 1.04
Truckee				
Resin lysimeters				
2001–2002	31	4.12 ± 0.88*	0.92 ± 0.88*	3.97 ± 0.88*
2002–2003	31	5.07 ± 0.88*	1.19 ± 0.88*	5.07 ± 0.88*
Gondola				
Resin lysimeters				
2001–2002	23	3.39 ± 1.02*	3.40 ± 1.02*	2.58 ± 1.02*
2002–2003	27	13.62 ± 0.94*	4.42 ± 0.94*	3.56 ± 0.94*

Asterisks indicate statistical significance (twice the standard error of skewness [SES] does not overlap zero where SES = $(6/n)^{0.5}$)

O horizon interflow has found to occur regularly in many forests of the Sierra Nevada Mountains, both during summer thunderstorms when mineral soils are hydrophobic and during late winter and early spring snowmelt when mineral soils are saturated. Microbial activity must play the major role in mineral N flux through O horizon interflow; as mentioned earlier, roots are absent in O horizons in these ecosystems and thus root uptake plays no role in O horizon interflow.

Resin-based samplers integrate fluxes at given points on the landscape whereas soil analyses represent snapshots of nutrient pools. As mentioned earlier, soil samples from most of these studies were bulked by

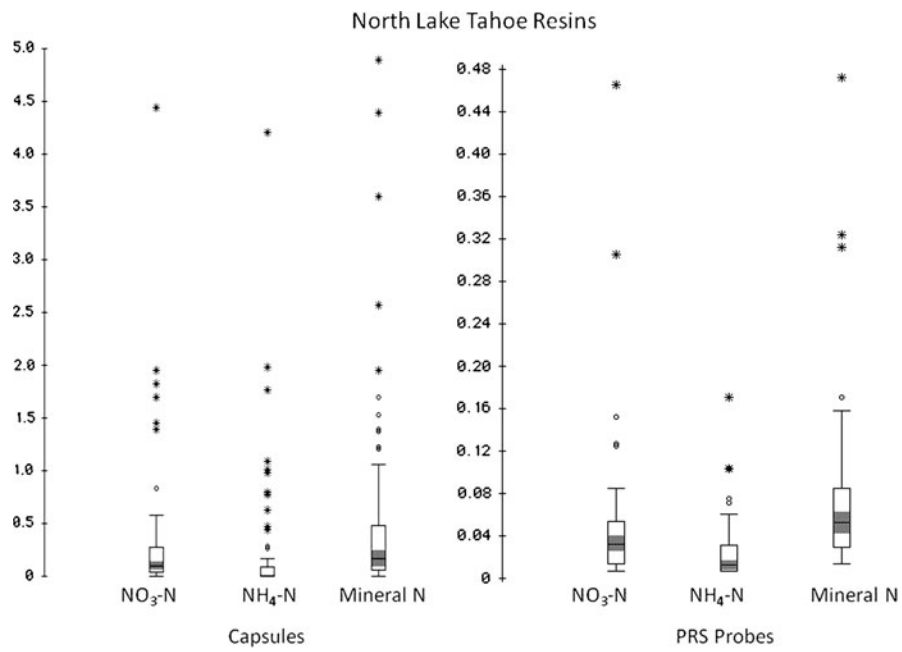

Fig. 2 Box plots of NH_4^+, NO_3^-, and mineral N for resin capsules and resin stakes (PRS probes[TM]) placed within 20 cm of one another at the North Lake Tahoe site (data adapted from Glass 2006). The *horizontal middle line* indicates the median; the *lower* and *upper* edges of the box indicate the 25 and 75% points, respectively; the whiskers indicate the main body of the data (not including outliers), *shaded intervals* are for comparing medians and defined by ±1.58(high hinge–low hinge)/$\sqrt{n}$ *circles* indicate outliers and *stars* indicate extreme outliers. See "Methods" for definitions of outliers

plot, precluding a post-hoc search for hot spots. The exception to this was the North Lake Tahoe site, where Glass (2006) took five replicate soil samples from each of the 20 plots immediately before and immediately after the fire in order to examine direct fire effects on soils. These data also included analyses of more abundant nutrients in these soils (Ca, Mg, K), which can be compared to less abundant nutrients (N, P, and S). In this analysis, we will use only the pre-fire data set.

Table 3 shows the averages, standard errors, range, and skewness values for NH_4^+, NO_3^-, mineral N, Ca^{2+}, Mg^{2+}, K^+, Bray P, bicarbonate P, and SO_4^{2-} in these soils. Figure 3 shows box plots of the

Table 3 Average, standard error (SE), range, and skewness for NH_4^+, NO_3^-, mineral N, extractable P (Bray and bicarbonate), extractable S (ammonium acetate), and exchangeable Ca^{2+}, Mg^{2+}, and K^+ in surface soils (0–10 cm) at the North Lake Tahoe site (data from Glass 2006)

Nutrient	n	Avg ± SE (mmol kg $^{-1}$)	Range (mmol kg^{-1})	Skewness
NH_4^+	84	4.2 ± 0.2	2.1–14.4	3.04 ± 0.52*
NO_3^-	84	0.30 ± 0.01	0.08–1.10	4.56 ± 0.52*
Mineral N	84	4.5 ± 0.2	2.3–15.0	3.06 ± 0.52*
Ca^{2+}	84	37.9 ± 1.6	14.1–90.2	0.79 ± 0.52*
Mg^{2+}	84	2.6 ± 0.2	0.3–12.5	1.99 ± 0.52*
K^+	84	7.7 ± 0.3	3.5–18.8	1.33 ± 0.52*
Bray P	84	2.2 ± 0.1	0.2–5.4	0.66 ± 0.52*
Bicarb P	84	1.4 ± 0.1	0.4–9.7	4.90 ± 0.52*
SO_4^{2-}	84	0.07 ± 0.01	0.02–0.20	1.26 ± 0.52*

Asterisks indicate statistical significance (twice the standard error of skewness [SES] does not overlap zero where SES = $(6/n)^{0.5}$)

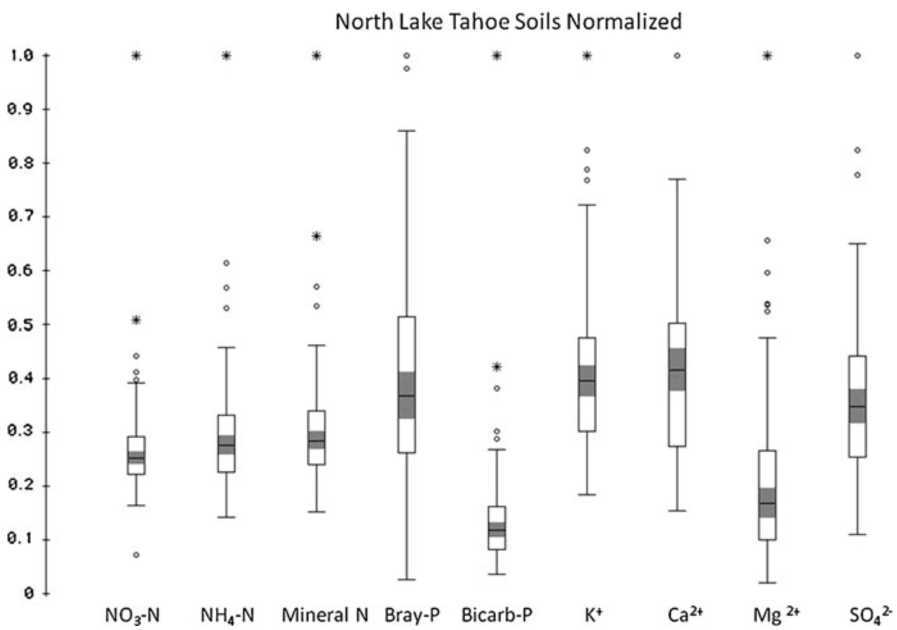

Fig. 3 Box plots of normalized values for NH_4^+, NO_3^-, and mineral N bicarbonate-P, Bray P, K^+, Ca^{2+}, Mg^{2+} and SO_4^{2-} for resin stakes surface soils at the North Lake Tahoe site (D.W. Johnson and D.W. Glass, unpubl. data). The data were normalized to a percentage of the highest measured value for the purposes of scaling. The *horizontal middle line* indicates the median; the *lower* and *upper* edges of the box indicate the 25 and 75% points, respectively; the whiskers indicate the main body of the data (not including outliers), *shaded intervals* are for comparing medians and defined by ±1.58(high hinge–low hinge)/$\sqrt{n}$ *circles* indicate outliers and *stars* indicate extreme outliers. See "Methods" for definitions of outliers

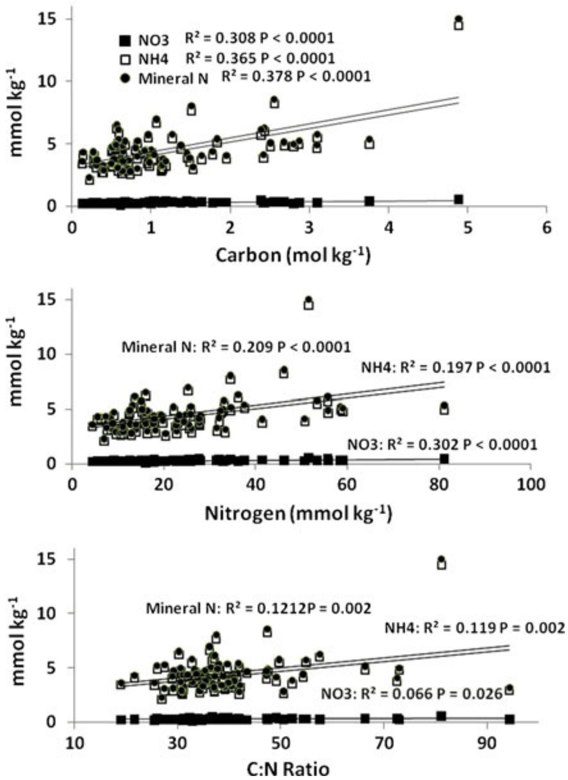

Fig. 4 Plots of total C, total N, and C:N ratio versus NH_4^+, NO_3^-, and mineral N in surface soils at the North Lake Tahoe site (Data adapted from Glass 2006). Correlation coefficients (R^2) and probabilities of regressions are show

normalized data (fraction of highest values, so that scales are comparable and plots of individual ions are visible). All measured nutrients showed one or more positive outliers, none showed negative outliers. Ammonium, NO_3^-, mineral N, bicarbonate-P, K^+, and Mg^{2+} showed one or more extreme outliers whereas Bray-P, Ca^{2+}, and SO_4^{2-} showed none. Calcium showed the fewest outliers (one moderate). Skewness for all measured ions was statistically significant, but was considerably lower for, Ca^{2+}, Mg^{2+}, K^+, SO_4^{2-} (0.66–1.99) and Bray P than for NH_4^+, NO_3^- mineral N, and bicarbonate P (3.04–4.90) (Table 3). Calcium stands out as the nutrient that is most abundant, has the fewest outliers, and the least skew among the measurements made. As noted by Glass (2006), this site was relatively rich in mineral N compared to other sites in the Sierra Nevada that we have investigated.

The differences in bicarbonate and Bray-P distribution are considerable and defy explanation at this time. There are no correlations between Bray- or bicarbonate P and any other measured nutrient that offer clues as to why this difference in distribution occurred. Kuo (1996) notes that the acid fluoride methods promote *ortho*-P desorption from reactive Al by forming Al–F complexes whereas bicarbonate methods decrease the activity of both Ca^{2+} and Al^{3+}. The bicarbonate methods are appropriate for both acid and calcareous soils, whereas acid fluoride methods are not appropriate for calcareous soils because of the neutralization of the acid by $CaCO_3$. Vimpany et al. (1997) report that acid fluoride extractions are less effective at extracting *ortho*-P bound with reactive Fe than bicarbonate extractions are, and thus the ratio of bicarbonate- to Bray-extractable P should increase as reactive Fe increases. Thus, there may have been differences in the nature of Fe and Al hydrous oxides among these samples that could help explain the differences in Bray- and

Table 4 Average, standard error, range, and skewness for NO_3^-, NH_4^+, mineral N, *ortho*-P, SO_4^{2-} Ca^{2+}, Mg^{2+}, and K^+ measured by resin stakes (PRS probes^{TM}) prior to treatment at the North Lake Tahoe site (data from Glass 2006)

Nutrient	n	Avg ± SE (µmol cm^{-2})	Range (µmol cm^{-2})	Skewness
NH_4^+	77	0.024 ± 0.003	0.007–0.171	2.88 ± 0.56*
NO_3^-	77	0.047 ± 0.0.007	0.007–0.466	4.61 ± 0.56*
Mineral N	77	0.071 ± 0.0.008	0.014–0.473	3.30 ± 0.56*
Ca^{2+}	77	4.74 ± 0.15	0.24–8.63	−0.71 ± 0.56*
Mg^{2+}	77	1.14 ± 0.06	0.28–2.68	1.03 ± 0.56*
K^+	77	0.59 ± 0.0.05	0.01–2.02	1.00 ± 0.56*
Ortho-P	77	0.063 ± 0.0.008	0.001–0.513	4.55 ± 0.56*
SO_4^{2-}	77	0.083 ± 0.006	0.022–0.347	2.06 ± 0.56*

Asterisks indicate statistical significance (twice the standard error of skewness [SES] does not overlap zero where SES = $(6/n)^{0.5}$)

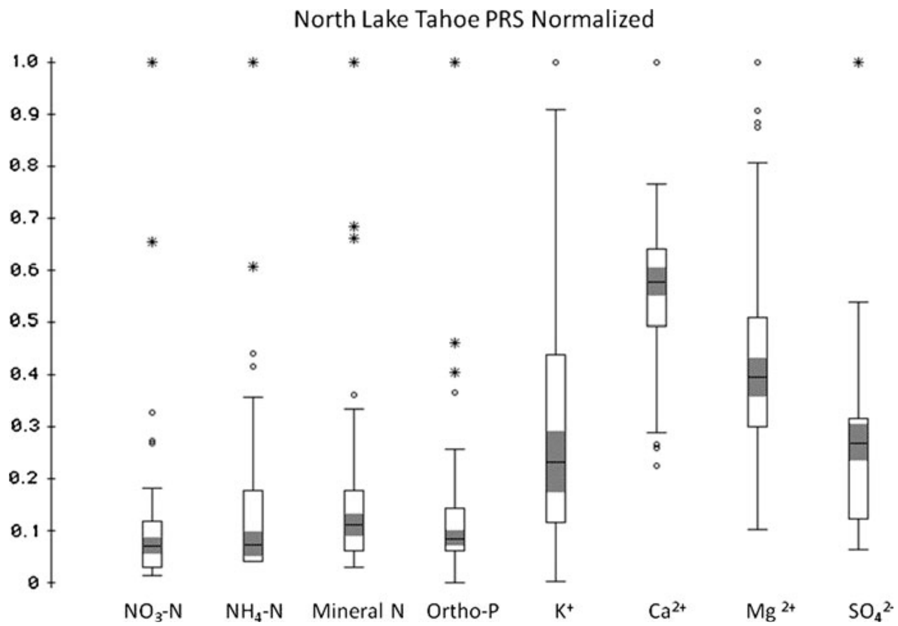

Fig. 5 Box plots of normalized values for NH_4^+, NO_3^-, and mineral N *ortho*-P, K^+, Ca^{2+}, Mg^{2+} and SO_4^{2-} for resin stakes (PRS probes^{TM} at the North Lake Tahoe site (D.W. Johnson and D.W. Glass, unpubl. data). The data were normalized to a percentage of the highest measured value for the purposes of scaling. The *horizontal middle line* indicates the median; the *lower* and *upper* edges of the box indicate the 25 and 75% points, respectively; the whiskers indicate the main body of the data, *shaded intervals* are for comparing medians and defined by ±1.58 (high hinge–low hinge)/$\sqrt{n}$ *circles* indicate outliers and *stars* indicate extreme outliers. See "Methods" for definitions of outliers

bicarbonate P distribution. An investigation of such differences is beyond the scope of this paper.

The soil data also includes total C and N and thus we can test whether mineral N hotspots have any relation to these measurements or to C:N ratio (Carbonates are absent in these soils and thus total C can be equated to organic C). Figure 4 shows plots of total C, total N, and C:N mass ratio against NH_4^+, NO_3^-, and mineral N in soils. Ammonium, NO_3^-, and mineral N are significantly positively correlated with total C, total N, and, surprisingly, C:N ratio. The latter is the exact opposite of the relationship expected based on textbook concepts of the effects of C:N ratio on N availability (Gardiner and Miller 2008). The correlation coefficients are relatively low, however, especially for C:N ratio where only 12% of the variation in mineral N is explained.

Resin stakes also included analyses of *ortho*-P, Mg^{2+}, K^+, SO_4^{2-}, and Ca^{2+} in addition to NH_4^+, NO_3^-, and total mineral N. Table 4 shows the averages, standard errors, range, and skewness values for NH_4^+, NO_3^-, mineral N, Ca^{2+}, Mg^{2+}, K^+, *ortho*-P, and SO_4^{2-} for the PRS probes and Fig. 5 shows box plots of the normalized data (fraction of highest values). Similar to the soils data, *ortho*-P and mineral N had the highest positive skew and Ca^{2+} the lowest (actually a significant negative skew). Calcium had one positive and three negative moderate outliers; Mg^{2+} had four moderate positive outliers, and K^+ had one moderate positive outlier. Thus, the resin stakes generally reflected the same patterns as traditional soil analyses: NH_4^+, NO_3^-, mineral N and *ortho*-P were least abundant, and had the greatest skew and greatest number of positive outliers whereas Ca^{2+} was most abundant and had the lowest skew and fewest numbers of outliers.

Summary and conclusions

Re-examination of data from several forested sites in the eastern Sierra Nevada Mountains shows consistent, positive outliers and significant positive skew for NH_4^+, NO_3^-, and mineral N in resin lysimeter fluxes, resin capsules, PRS probes and soils. This fits well with the definition of McClain et al. (2003) for hotspots as areas (or patches) that show disproportionately high reaction rates relative to the surrounding area (or matrix)". Exact causes of these N hotspots are not known, but must certainly include hotspots of microbial activity. In soils, there are some statistically significant correlations among NH_4^+, NO_3^-, mineral N and total C, total N, and C:N ratio, but the R^2 values are low. In the case of resin lysimeter fluxes, factors could include not only microbial hotspots, but also soil physical factors affecting water flux and possibly also the entry of N-enriched O horizon interflow. Bicarbonate-P data from soils and *ortho*-P data from PRS probes also showed highly positive skew and extreme outliers, but Bray P in soils did not. Calcium stood out among measured nutrients in both soils and PRS probes as the most abundant nutrient with the least outliers and the lowest (sometimes negative) skew.

In sum, we find ample evidence that hotspots exist for NH_4^+, NO_3^-, and mineral N and possibly also for *ortho*-P in soils of the eastern Sierra Nevada mountains. This may reflect the relative scarcity of these nutrients, as the most abundant nutrient, Ca^{2+}, shows little evidence of hotspots. Future research will address the nature of these hotspots and the factors affecting them.

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