Interbasin flow of geothermally modified ground water stabilizes stream exports of biologically important solutes against variation in precipitation

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Abstract: Geothermally modified ground water (GMG) in tectonically active areas can be an important source of stream nutrients, and the relative importance of GMG inflows is likely to change with shifts in precipitation that are predicted to occur in response to climate change. However, few studies have quantified the influence of GMG inflows on export of biologically important solutes from watersheds across years differing in precipitation. We quantified N, soluble reactive P (SRP), and dissolved organic C (DOC) export during a year with high precipitation (6550 mm rain) and a year with average precipitation (4033 mm rain) in 2 gauged tropical streams at La Selva Biological Station in lowland Costa Rica. One stream receives extensive inputs of regional GMG, whereas the other is fed entirely by local runoff. In the stream fed only by local runoff, a 62% increase in precipitation from the dry year to the wet year led to a 68% increase in stream discharge, a 67% increase in export of SRP, DOC, dissolved organic N (DON), and NH_4^+, and a 91% increase in NO_3^- export. In contrast, in an adjacent stream where >⅓ of discharge consists of GMG, the same increase in precipitation from dry year to wet year led to a 14% increase in discharge, a 14 to 31% increase in export of NO_3^-, NH_4^+, DON, and DOC, and only a 2% increase in SRP export. We are unaware of an SRP export rate from a natural system that is higher than the export from the stream receiving interbasin flow of GMG (19 kg ha^{-1} y^{-1}). Our results illustrate that regional ground water, geothermally modified or not, can stabilize stream export of biologically relevant solutes and water across a varying precipitation regime.

Key words: stream, geothermal, ground water, nutrient, nitrogen, phosphorus, DOC, flux, precipitation, stoichiometry, climate change, tropical

Groundwater inflows can contribute a significant fraction of stream solute loads (Maxey 1968, Güler and Thyne 2006). Groundwater inflows that alter concentrations and exports of biologically relevant solutes, such as P, N, and dissolved organic C (DOC), can influence community composition and ecosystem process rates (Pringle and Triska 1991). Different types of geothermally modified ground water (GMG) have been characterized based on concentrations of major cations and anions (Henley and Ellis 1983), some of which contribute to relatively high (i.e., biologically relevant) levels of nutrients, such as dissolved P (Pringle and Triska 1991, Pringle et al. 1993) and N (Hoellein et al. 2012) in surface waters. Tectonically active areas are common worldwide (Fig. 1A) and nutrient concentrations may be high (e.g., Pringle et al. 1993, Valentino et al. 1999, Ramos-Escobedo and Vázquez 2001), but exports of biologically important solutes in GMG-influenced surface waters have been quantified in relatively few locations, e.g., New Zealand (White and Downes 1977, Burger et al. 2008, Hoellein et al. 2012),

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DOI: 10.1086/679739. Received 11 December 2014; Accepted 5 October 2014; Published online 18 December 2014.
Freshwater Science. 2015. 34(1):276–286.

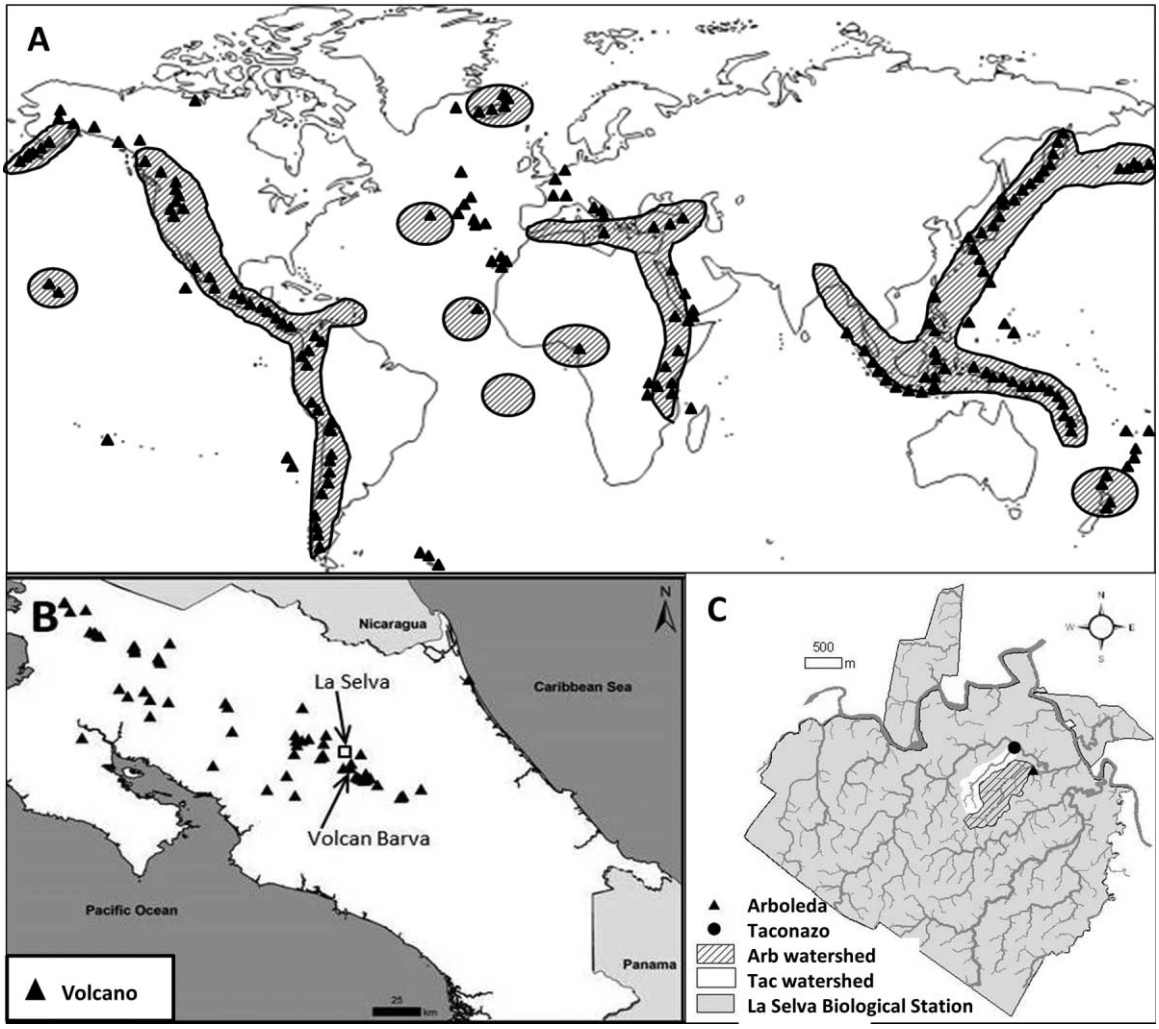

Figure 1. A.—Geothermally active areas of the world; black square in Central America indicates the region enlarged in panel B (modified from: http://vulcan.wr.usgs.gov/Glossary/PlateTectonics/Maps/map_plate_tectonics_world.html). B.—Map of Costa Rica's volcanoes and La Selva Biological Station (modified from Alvarado et al. 1981). C.—La Selva's watersheds include the Arboleda, which received regional geothermally modified and local ground water, and Taconazo, which receives only local ground water.

the western USA (McCleskey et al. 2007), and Costa Rica (Triska et al. 2006, Genereux et al. 2013).

Groundwater inflows also can help minimize seasonal and interannual variability in stream discharge. The constancy of groundwater inflows might become more important as climate change causes global shifts in precipitation regimes. Few investigators have measured the effects of GMG inputs on the stability of stream chemistry. However, some have observed variation in seasonal and interannual contributions from GMG (White and Downes 1977, McCleskey et al. 2007), and Triska et al. (2006) found that concentration and export of GMG-derived P varied with annual precipitation.

Central America is a tectonically active area that has been designated as a region of global priority for predicting and mitigating effects of climate change (Hannah et al. 2013). Climate models for the region indicate that overall precipitation may decrease (Giorgi 2006, Neelin et al. 2006, Rauscher et al. 2008) while extreme precipitation events may increase (Min et al. 2011), which could potentially increase the importance of regional groundwater contributions to in-stream export of water and biologically important solutes.

We asked how GMG inflows affected stream export of biologically important solutes during 2 years that differed in precipitation. We compared stream-water concentrations and watershed stream export of soluble reactive P (SRP), N, and DOC between a high precipitation year and an average precipitation year in a pair of adjacent lowland rainforest watersheds in Costa Rica. One the watersheds receives interbasin flows of GMG, and the other does not.

METHODS

Site description

Our 2 study watersheds are within La Selva Biological Station (lat 10°26 N, long 84°01 W) on the Caribbean slope of Costa Rica in the lower foothills of the Cordillera Central where it merges with the coastal plain. The region around La Selva has received extensive hydrologic and biogeochemical study since the identification of significant effects of regional interbasin groundwater flow on stream chemistry in the area (Pringle et al. 1990, Pringle 1991, Pringle and Triska 1991). This regional ground water is geothermally modified along flow paths in volcanic bedrock as it flows down through the Cordillera Central. The ground water emerges as NaCl-HCO_3^- springs and spatially distributed low-elevation discharge at La Selva Biological Station and is responsible for significant water and solute inputs to lowland rainforest streams and wetlands of La Selva (Pringle and Triska 1991, Pringle et al. 1993, Genereux and Pringle 1997, Genereux and Jordan 2006). Regional ground water is recharged by precipitation at higher elevations in the Cordillera Central (probably on Volcán Barva; Fig. 1B) and is much older (~3000 y; Genereux et al. 2009) and higher in many solute concentrations than the shallower, younger local ground water that is recharged by precipitation at La Selva (Pringle et al. 1993). This solute-rich regional ground water is an ecologically significant source of P to many streams (Pringle et al. 1990, 1993). Regional ground water also buffers streams draining La Selva against seasonal changes in pH (Small et al. 2012, Ardón et al. 2013) and has a significant effect on watershed-scale C fluxes and budgets (Genereux et al. 2013).

The focal watersheds in our study are the Arboleda and Taconazo (Fig. 1C), 2 small (Arboleda: 46.1 ha, Taconazo: 27.9 ha; Zanon et al. 2013) adjacent watersheds that are similar in terms of rainfall, temperature, soils, vegetation, and topography. V-notch weirs in both streams have operated nearly continuously since 1998, allowing accurate measurement of discharge.

Soils in both watersheds are ultisols developed on Quaternary volcanic rocks with interbedded mudflow and ash deposits (Bourgeois et al. 1972, Castillo-Muñoz 1983, Foster et al. 1985, Parker et al. 1988, Alvardo Induni 1990). The youngest rocks are 1.2 mybp, with older Pleistocene lava flows of uncertain age (Alvardo Induni 1990). Vegetation is classified as tropical wet forest in the Holdridge Life Zone system, with high species diversity, biomass, and stature (McDade et al. 1994). Annual rainfall averaged 4260 mm from 1958–2004 (http://www.ots.ac.cr/meteoro), and the driest months were February, March, and April.

In a previous budget study of water and non-nutrient ions, Genereux et al. (2005) showed that 75% of the Arboleda's stream flow consists of interbasin groundwater flow and ~½ of that (34% of total stream flow) consists of regional GMG, which is naturally high in SRP (>200 μg/L) and major ions (Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, SO_4^{2-}). In contrast, stream flow in the adjacent Taconazo watershed is entirely locally generated (i.e., derived from precipitation falling within the watershed boundaries) and is low in SRP (<10 μg/L) and major ions. From the perspective of the solute exports presented here, it is critical that the Arboleda receives GMG and the Taconazo does not, and that this GMG enters the Arboleda watershed from outside, i.e., it represents interbasin groundwater flow beneath the topographically defined boundary of the watershed. In this sense, the Arboleda is like many lowland watersheds worldwide (e.g., Genereux et al. 2005 and references therein) in collecting or receiving regional groundwater flow from outside the topographically defined watershed boundaries.

Sampling regime and chemical analysis

We collected samples for water-quality analysis weekly at the 2 gauging stations from 1 October 2001 to 30 May 2004, with additional samples taken during a period of high flows during June–July 2002. We analyzed solute chemistry at Guacimo Spring, the highest-solute water in the area and taken to be representative of the regional GMG source to La Selva streams, monthly. We filtered samples shortly after collection through precombusted glass-fiber filters (Whatman GF/F, 425°C for 6 h) and stored them frozen in acid-washed high-density polyethylene (HDPE) bottles prior to analysis. We measured NH_4^+, NO_3^-, and SRP by flow-injection analysis (Lachat QuikChem Advanced Edition; Lachat, Loveland, Colorado) with the phenol hypochlorite, Cd reduction, and ammonium molybdate methods, respectively. We analyzed DOC as nonpurgeable organic C using high-temperature Pt-catalyzed combustion on a Shimadzu C analyzer (TOC-V or TOC 5000; Shimadzu, Kyoto, Japan) with chemiluminescent detection of total N (Shimadzu TOC-V or Antek 721; Antek, North Arlington, New Jersey) to determine total dissolved N (TDN) concentrations (Merriam et al. 1996). We calculated dissolved organic N (DON) as the difference between TDN and the sum of NH_4^+ and NO_3^-. Rainfall was estimated from daily readings of the field station's tipping-bucket rain gauge. Precipitation was 6550 mm in water year 2002 (1 October 2001–30 September 2002) and 4033 mm in water year 2003 (1 October 2002–30 September 2003).

Calculation of export

We calculated annual export rates for water years 2002 and 2003 as the product of concentration and stream discharge summed over a given time interval. We evaluated concentration–discharge relationships in both streams based on r^2 values following the approach of Mc-

Dowell and Asbury (1994). Because of the large number of data points, many of the concentration–discharge relationships could be considered statistically significant ($p < 0.05$) but had low predictive value ($r^2 < 0.10$). Therefore, we used only those relationships with $r^2 > 0.10$. We tested multiple functional forms for the concentration–discharge relationship of each solute in each stream and, in each case, selected the best-fitting equation if it had $r^2 > 0.10$ (McDowell and Asbury 1994). A relationship with $r^2 = 0.10$ would be a poor predictor of the stream concentration at a given time interval, but this method is adequate for calculation of annual export. As long as the discharge–concentration relationships are unbiased (i.e., error is evenly distributed), overestimates and underestimates are offsetting.

For solutes that were poorly predicted by discharge (DOC and DON in both streams, NH_4^+ and SRP in the Taconazo), we estimated solute export as the product of the flow-weighted average annual concentration and total runoff for the year (i.e., the method referred to as M4 by Walling and Webb 1985, Hope et al. 1997, Birgand et al. 2010). For other solutes (SRP and NH_4^+ in the Arboleda, and NO_3^- in both streams), we used the regression equation describing the concentration–discharge relationship of the solute and the 15-min stream discharge record to predict solute concentration every 15 min (e.g., McDowell and Asbury 1994, Malmer 1996, Stoorvogel et al. 1997, Salmon et al. 2001, Genereux et al. 2005). We then calculated solute export at 15-min intervals from the predicted solute concentrations and stream discharge values measured every 15 min.

The 15-min record of discharge was not complete because of occasional equipment malfunction or backflooding of the weirs. Therefore, we were forced to estimate discharge for ~7% of the total record. Backflooding occurs when the Puerto Viejo River rises rapidly, backing up the La Selva streams that drain into the Puerto Viejo. This situation temporarily results in either no stream flow or reversed, upstream flow in the Arboleda and Taconazo. In these cases, we reasoned that stream discharge was effectively 0 because the rising river water prevented stream discharge at the weir, and we assigned a value of 0 for discharge at those times. When gaps resulted from equipment malfunction, we used either a linear interpolation between measured stream discharge values for gaps <0.5 d or a regression between Arboleda and Taconazo stream discharge ($r^2 = 0.96$) to estimate the missing discharge values wherever possible. When neither gauge was functioning, we used regression-based rainfall–runoff relationships ($r^2 = 0.62$–0.89) to estimate discharge (Jordan 2003).

When solute fluxes are based on high-frequency stream discharge data (15-min in our study) and much lower frequency solute concentration data (weekly in our study), uncertainty in the fluxes is difficult to estimate. If a well-defined concentration–discharge relationship for the solute does not exist, no reliable way exists to know what the flux might have been during the times between solute concentration measurements. A new approach based on subsampling very high-frequency chemical data from in situ chemical probes offers the most promising approach to the question of the uncertainty in solute flux (Birgand et al. 2010, 2011a, b), but the method has been applied to relatively few watersheds thus far. Birgand et al. (2011a) estimated that uncertainties in annual watershed export for 2 coastal plain watersheds in North Carolina, USA, were 5 to 19% for NO_3^-, 41 to 76% for NH_4^+, 19 to 31% for P, and 11 to 21% for DOC, when the chemical sampling was done on a weekly basis and the stream discharge was continuous. We lack the very high frequency chemical data needed to directly apply this approach at La Selva, but we viewed the uncertainty estimates by Birgand et al. (2011a) as reasonable (possibly, the best available) indices of uncertainties in solute export for sampling situations similar to that in our study. The exception was uncertainty estimated for NH_4^+. Birgand et al. (2011a) suggested that the large uncertainty they reported for this solute was the result of some unusually large spikes (10–20× baseflow values) in NH_4^+ concentration, which did not occur in our data set.

RESULTS

SRP concentration at Guacimo Spring was 232 μg/L. SRP concentration was 26× higher in the Arboleda, which receives GMG inflows, than in the Taconazo, which is fed only by local water from surrounding hill slopes (165.7 vs 6.3 μg/L). In contrast, stream N and DOC concentrations were similar between the watersheds (Table 1). High SRP concentrations resulted in a lower dissolved inorganic molar N : P ratio in the Arboleda (2.6) than in the Taconazo (57.3). DOC concentrations in both streams exceeded DOC concentration in the regional ground water, which averaged 730 μg/L, but NO_3^-, NH_4^+, and DON were similar between the 2 streams and Guacimo Spring (Table 1).

Discharge was an order of magnitude lower in the Taconazo than in the Arboleda (Fig. 2A, B). In the Arboleda, SRP concentrations were inversely related to discharge ($r^2 = 0.78$, $p < 0.0001$; Fig. 3A) with declines in SRP concentration of ~80% during periods of high flow, whereas NO_3^- and NH_4^+ concentrations were positively related to discharge ($r^2 = 0.33$, $p < 0.0001$ and $r^2 = 0.22$, $p < 0.0001$, respectively; Fig. 3B, C). DOC and DON were not related to discharge in the Arboleda (Fig. 3D, E). In the Taconazo, NO_3^- concentration was positively correlated to stream discharge and was the only solute that had a robust concentration–discharge relationship ($r^2 = 0.46$, $p < 0.0001$; Fig. 3F–J). A series of high-flow events during the wet season of 2002 showed these patterns over short time

Table 1. Mean (±1 SD) concentrations of solutes and N:P ratios in the Taconazo (local nongeothermal ground water) and Arboleda (regional geothermally modified ground water) streams and the regional groundwater source for the Arboleda. Stream data are averages from weekly and storm samples taken October 2001 to May 2004. SRP = soluble reactive P, DON = dissolved organic N, DOC = dissolved organic C.

Mean concentration (μg/L)	Taconazo	Arboleda	Regional ground water
SRP	6.3 ± 9.6	165.7 ± 56.8	232 ± 45
Flow-weighted average	6.9	160.5	–
n	90	101	34
NO_3-N	133.3 ± 29.0	173.7 ± 26.8	147 ± 33
Flow-weighted average	139.9	174.0	–
n	136	135	14
NH_4-N	29.8 ± 11.3	22.0 ± 8.6	24 ± 31
Flow-weighted average	27.3	22.5	–
n	137	135	14
DON	46 ± 36	49 ± 46	60 ± 50
Flow-weighted average	43	43	–
n	125	117	14
DOC	1350 ± 750	1280 ± 1070	730 ± 670
Flow-weighted average	1375	1283	–
n	137	137	14
N : P	57.3	2.6	1.6

periods (Fig. 4A–D). The stream flows sampled for chemical analyses bracketed the full range of flows occurring during the 2 water years, and thus, the concentration–discharge relationships are suitable for calculating fluxes.

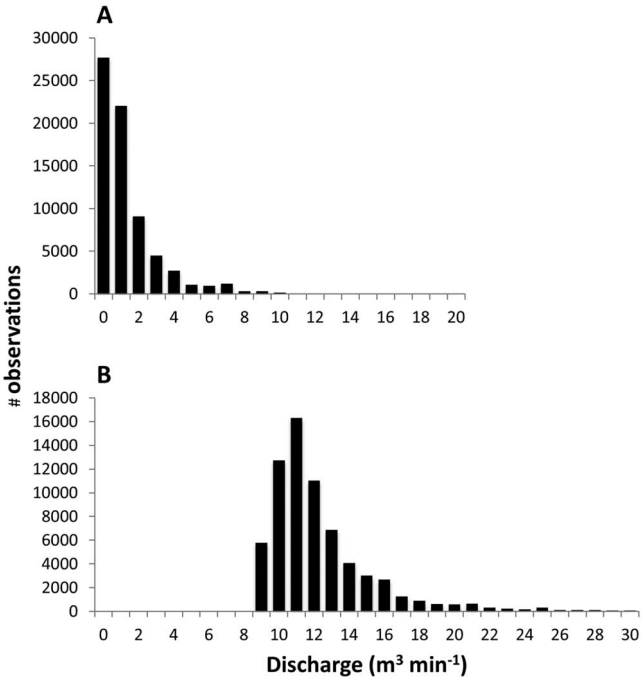

Figure 2. Histograms of discharge for the Arboleda (A) and Taconazo (B) streams during the study periods.

No seasonal variability in solute concentrations was evident in our data set.

Export of water, dissolved N, and DOC from the Arboleda were ~3× higher on an areal basis (using topographically defined watershed boundaries) than export from the Taconazo (Table 2) as a result of interbasin groundwater inflows to the Arboleda, even though the concentrations of dissolved N and DOC were not elevated relative to the Taconazo (Table 1). SRP export in the Arboleda was especially elevated because of high SRP concentrations in the GMG, with >50× higher export (19.03–19.49 kg ha^{-1} y^{-1}) than the Taconazo (0.18–0.30 kg ha^{-1} y^{-1}). Arboleda stream discharge was 3.4 and 5.0× higher than Taconazo stream discharge for water years 2002 and 2003, respectively, when normalized by watershed area. Mean discharge in the Arboleda and Taconazo was 0.211 m^3/s and 0.032 m^3/s, respectively.

Precipitation during water year 2002 (6550 mm rainfall) was 62% greater than during water year 2003 (4033 mm rainfall). Rainfall in the January to April dry season varied by only 0.35% between years, but wet-season rainfall was 77% higher in water year 2002 in large part because of 3 extremely wet months: 901 mm rain in November 2001, 1080 mm in December 2001, and 890 mm in May 2002.

The response of annual export of biologically important solutes to this change in annual precipitation varied markedly between the 2 streams. In the Taconazo, the 62% increase in annual precipitation led to a 68% increase in annual runoff, an ~67% increase in SRP, NH_4^+,

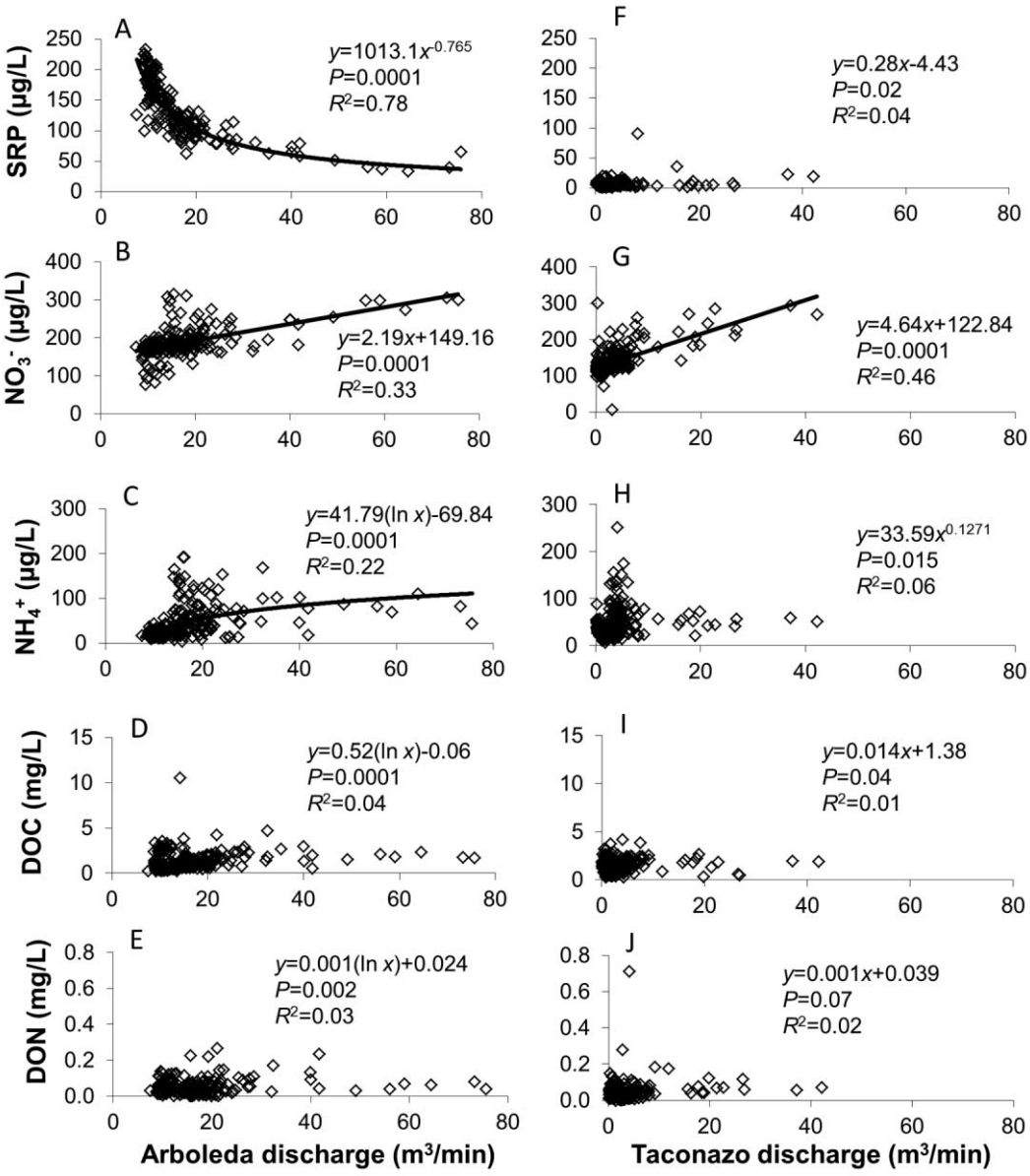

Figure 3. Effects of discharge (m^3/min) on soluble reactive P (SRP) (A, F), NO_3^- (B, G), NH_4^+ (C, H), dissolved organic C (DOC) (D, I), and dissolved organic N (DON) (E, J) concentrations in Arboleda (regional geothermal groundwater input) (A–E) and Taconazo (local nongeothermal ground water) (F–J) watersheds at La Selva Biological Station from 2001 to 2004. Regression lines are shown for significant ($r^2 > 0.10$) relationships.

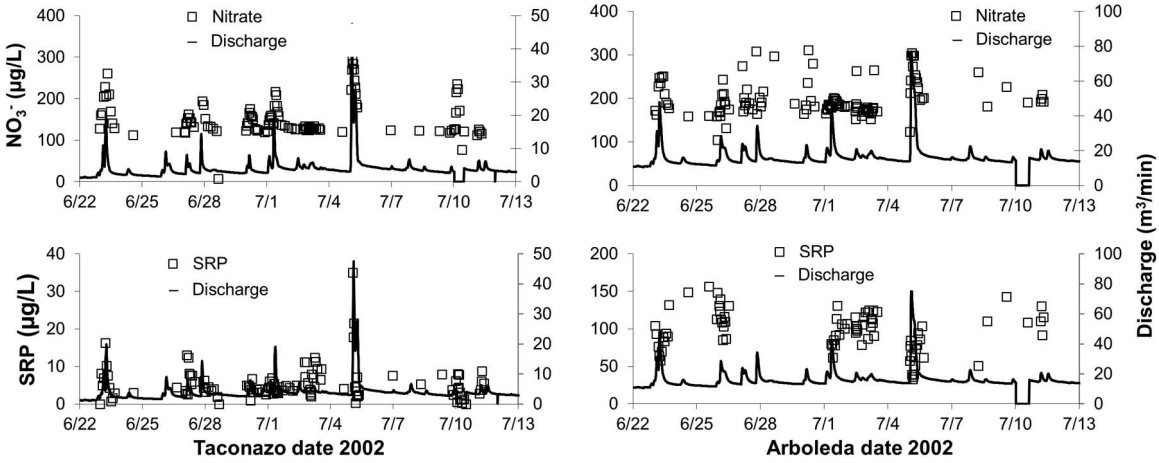

Figure 4. Relationships between discharge and NO_3^- (A, B) and soluble reactive P (SRP) (C, D) in the Taconazo (local nongeothermal ground water) (A, C) and Arboleda (regional geothermal groundwater input) (B, D) during a 4-wk storm series in June–July 2002.

DON, and DOC export, and a 91% increase in NO_3^- export (Table 2). In contrast, in the Arboleda, the 62% increase in annual precipitation led to a 14% increase in annual runoff, a 2% increase in SRP export, a 31% increase in NH_4^+ export, a 14% increase in DOC and DON export, and a 17% increase in NO_3^- export (Table 2).

DISCUSSION

Our results show that geothermally modified interbasin groundwater flow greatly stabilized the export of biologically relevant solutes across 2 years that varied widely in precipitation. The relatively constant inflow of GMG into the Arboleda is important to water (Genereux et al. 2005) and SRP export (Table 2) and buffers export of SRP, N, and DOC against changes in local runoff throughout the year. In both watersheds, NO_3^- concentrations increased with discharge, making NO_3^- export highly sensitive to seasonal and interannual changes in precipitation and runoff. In the Taconazo, NO_3^- export was 91% higher in the wet year than in the average precipitation year, but in the Arboleda, NO_3^- export increased only 17% during the wet year because of the stabilizing effect of interbasin groundwater flow. The stabilizing effect of GMG inputs on stream solute export is magnified for solutes that occur in high concentrations in GMG, as illustrated by the SRP export that increased only 2% in the Arboleda between normal and wet years, compared to a 67% increase in SRP export in the Taconazo.

Triska et al. (2006) hypothesized that the large increase in SRP export from the lower reach of the Salto River at La Selva during a severe 1998–1999 El Niño Southern Oscillation (ENSO) event was caused by release of sorbed P resulting from changes in sediment redox

Table 2. Annual fluxes of solutes (kg ha^{-1} y^{-1}) and N:P ratios in the Taconazo (local nongeothermal ground water) and Arboleda (regional geothermal ground water) streams during wet year 2002 (October 2001–September 2002) and dry year 2003 (October 2002–September 2003), and the ratios of the fluxes between the 2 years. SRP = soluble reactive P, DON = dissolved organic N, DOC = dissolved organic C.

	Taconazo			Arboleda		
Variable	Wet year	Dry year	Wet year : dry year	Wet year	Dry year	Wet year : dry year
Discharge (mm)	4514	2681	1.68	15365	13513	1.14
SRP (kg ha^{-1} y^{-1})	0.30	0.18	1.67	19.49	19.03	1.02
NO_3-N (kg ha^{-1} y^{-1})	7.54	3.94	1.91	26.42	22.53	1.17
NH_4^+-N (kg ha^{-1} y^{-1})	2.18	1.30	1.68	6.34	4.85	1.31
DON (kg ha^{-1} y^{-1})	2.33	1.38	1.69	7.09	6.24	1.14
DOC (kg ha^{-1} y^{-1})	66.21	39.32	1.68	186.37	163.91	1.14

conditions. Also, a short-term (3 h) experimental acidification of a tributary of the Arboleda receiving GMG inflows showed SRP release in response to a decrease in pH (Ardón et al. 2013). These findings show that stream sediments receiving SRP-rich GMG inflows can store a large pool of P, and that changes in redox or pH can potentially lead to P releases that alter stream SRP concentrations, N : P ratios, and SRP export. In effect, changes in sediment P storage may destabilize stream SRP concentrations episodically despite the overall stabilizing effects of GMG inputs on solute export in streams like the Arboleda.

Solute exports in the Arboleda are comparable to or higher than those published for other geothermal systems. SRP export in the Arboleda is an order of magnitude higher than that recorded for geothermal sites in New Zealand (up to 1.8 kg ha^{-1} y^{-1}; White and Downes 1977), and Arboleda dissolved inorganic N (DIN) export also is higher than that recorded by White and Downes (1977) (3.1–9.1 kg ha^{-1} y^{-1}). We are unaware of any published studies in which DOC export in streams receiving GMG have been documented other than the study by Genereux et al. (2013) and our study.

A comparison of other export studies shows that P export in the Arboleda is the highest recorded in any *natural* system. It is 2 orders of magnitude higher than values reported from nongeothermal stream sites (0.02–0.79 kg P ha^{-1} y^{-1}; Yanai 1992, Liu et al. 2003) and comparable to export from intensively fertilized agricultural plots (up to 18.6 kg P ha^{-1} y^{-1}; Reckhow et al. 1980, Lin 2004). In fact, the magnitude of SRP export in the Arboleda is surpassed only by streams draining feedlots and manure storage facilities (up to 795 kg P ha^{-1}/y^{-1}; Reckhow et al. 1980, Lin 2004). NO_3^- export from the Arboleda also is higher than that of most nongeothermal natural systems (0.10–6.10 kg NO_3-N ha^{-1} y^{-1}; McDowell and Asbury 1994, Markewitz et al. 2006) because of the high volume of water/watershed area, which is a consequence of the magnitude of regional interbasin groundwater flow. Arboleda DOC export also is among the highest values recorded for natural systems except for streams draining peatlands (217–431 kg DOC ha^{-1} y^{-1}; Alkhatib et al. 2007, Baum et al. 2007).

The DOC export values in our study are consistent with those reported by Genereux et al. (2013) for the same streams as part of a comparison of watershed C budgets. Our results highlight the high interannual variability in DOC export in the Taconazo (the stream not receiving inputs of GMG). However, stream export is a relatively small pathway in the Taconazo watershed C budget, with C loss to stream degassing of CO_2 potentially higher (Genereux et al. 2013). Stream DOC export represents at most 0.39% of total above- and below-ground net primary production (Russell et al. 2010) and 0.63% of C flux via terrestrial respiration (Schwendenmann and Veldkamp 2006). Thus, variation in DOC export caused by precipitation regimes may have little direct effect on the watershed C budget.

Stream N export from La Selva watersheds also is relatively minor when compared to the magnitude of terrestrial N cycling. NO_3^- accounted for ~⅔ of N export in both watersheds. These areal NO_3^- export values correspond to up to 3.8% of detrital N production and 3.2% of total plant N uptake (Russell and Raich 2012) and are similar to background N atmospheric deposition values (Eklund et al. 1997).

P-rich GMG inputs can affect stream nutrient dynamics at both small and large spatial and temporal scales (Triska et al. 2006). Stream N : P can be altered at the local level (Pringle et al. 1993). For example, N : P ratios similar to that of the Arboleda (2.6) were found at 2 New Zealand geothermal streams (1.26 and 5.27) by White and Downes (1977). Nutrient inputs from ground water also can have effects at the landscape scale by contributing to nutrient loading downstream. For example, GMG inputs contribute to eutrophication in New Zealand's Lake Rotoiti, where geothermal inputs represent 0.17% of water inflow but 46.6% of NH_4^+ input (Hoellein et al. 2012). Geothermal tributaries of Lake Rotorua contribute a small proportion of water inflow but have high NH_4^+ and SRP export (Burger et al. 2008). High N export from NH_4^+-rich geothermal tributaries also occurs along the Gibbon River in Yellowstone National Park (McCleskey et al. 2007).

Previous investigators focused on the role of some geothermal systems in buffering streams against effects of temperature shifts subsequent to climate change (O'Gorman et al. 2014), but our work demonstrates the importance of geothermal systems in buffering against changes in stream flow and nutrient export. Inflows from groundwater sources can stabilize fluxes against seasonal and interannual variability in local precipitation (e.g., Tague et al. 2008), and this effect is amplified by the magnitude of interbasin flow of GMG at our study site in Costa Rica. This interbasin flow of regional ground water stabilizes export of water and biologically important solutes. In contrast, export of water and biologically important solutes in streams fed only by local ground water are more closely tied to local precipitation regimes and could significantly decrease with more severe dry seasons or years, leading to lower overall export rates. Therefore, streams receiving interbasin flows of GMG could be important for stabilizing local and regional water and solute budgets in an increasingly dry climate (although presumably, on much longer time scales that depend on the characteristics of the regional groundwater systems, even these deep systems will respond to changing climate and precipitation). Drier conditions in streams receiving interbasin

GMG flows also could lead to decreased N : P ratios as the proportion of flow derived from high-SRP ground water increases. In the Arboleda, SRP concentration increased with lower discharge, a trend similar to those described by Pringle and Triska (1991) and Triska et al. (2006) in other La Selva streams. Higher SRP concentrations potentially could push stream communities toward limitation by other resources, such as light (in the case of algae), DOC, N, or micronutrients.

In conclusion, interbasin flows of GMG can stabilize stream export of water and biologically important solutes at local and landscape scales and should be taken into account in tectonically active areas worldwide. Our results suggest that the effects of climate change on freshwater ecosystems may depend on regional groundwater characteristics as well as altered precipitation patterns.

ACKNOWLEDGEMENTS

We thank Minor Hidalgo and William Ureña for assistance in the field and dedication to field sampling under arduous conditions. Laboratory analyses by Jeff Merriam and Jody Potter of the University of New Hampshire Water Quality Analysis Laboratory are gratefully acknowledged, and we are grateful to Marcia Snyder for assistance with mapping. We also thank Guest Editor Mike Gooseff and 3 anonymous referees for their feedback, which greatly improved this paper. Funding was provided by NSF DEB 0087248 and 0108385 to WHM, NSF DEB 9528434, 0075339, and 0545463 to CMP, and NSF EAR 9800129, 9903243, 0049047, and 0421178 to DPG. Fieldwork was conducted under Costa Rica MINAE permit 0142014SINAC.

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