Biogeochemistry (2005) 76: 421–440
DOI 10.1007/s10533-005-6997-7

Nitrogen transport and retention in an arid land watershed: influence of storm characteristics on terrestrial–aquatic linkages

JILL R. WELTER*, STUART G. FISHER and NANCY B. GRIMM
*School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501; *Author for correspondence (Department of Integrative Biology, University of California, Berkeley, 3040 Valley Life Sciences Building, Berkeley, CA 94720-3140; phone: +1-707-984-6653; e-mail: jwelter@berkeley.edu)*

Received 2 November 2004; accepted in revised form 9 May 2005

Key words: Desert, Nitrogen cycling, Precipitation pulse, Runoff, Terrestrial–aquatic linkage

Abstract. Arid ecosystems experience prolonged dry periods, as well as storms that vary in size, intensity and frequency. As a result, nitrogen (N) retention and export patterns may be a function of individual storm characteristics. Our objective was to determine how seasonal patterns in rainfall as well as individual storm characteristics influence N transport and retention on terrestrial hill slopes in a Sonoran Desert watershed. Regression models indicated that variation in runoff ammonium (NH_4^+) was best explained by antecedent conditions (cumulative seasonal rainfall, days since last storm) while variation in runoff nitrate (NO_3^-) was best explained by single storm characteristics, primarily rain NO_3^-. Increases in runoff NO_3^- along overland surface flowpaths were balanced by decreases in NH_4^+ during summer, with no change in dissolved inorganic nitrogen (DIN) concentration; a pattern consistent with nitrification. Nitrate increases along flowpaths were not as strong during winter storms. Results indicate that NH_4^+ is transported from hillslopes to other parts of the catchment, including streams, and that nitrification occurs along surface flowpaths, particularly during summer storms. These findings suggest that the extent to which a receiving patch is supplied with NH_4^+ or NO_3^- depends on the distance runoff has traveled (flowpath length) and the length of the antecedent dry period. The extent and configuration of fluvial reconnection amongst patches in the landscape following long drought periods likely determines the fate of available N, whether N is processed and retained in the terrestrial or in the aquatic component of the watershed, and the mechanisms involved. The nature of this fluvial reconnection is driven by the size, intensity and sequence of storms in space and time.

Introduction

In arid ecosystems, incoming rain serves as a ‘switch’, stimulating pulses of biological activity (Noy-Meir 1973). These pulses include rapid plant responses to single precipitation events (Sala and Lauenroth 1982; BassiriRad et al. 1999; Ivans et al. 2003), as well as nitrogen (N) transformations in soil, such as mineralization (Fisher et al. 1987; Cui and Caldwell 1997; Austin et al. 2004), microbial immobilization (Gallardo and Schlesinger 1995) and gaseous loss of N (Virginia et al. 1982; Davidson et al. 1993; Mummey et al. 1994; Smart et al. 1999; Hartley and Schlesinger 2000). Pulses are often short-lived and biological activity limited during extended dry periods. Storms also generate runoff and lead to hydrologic redistribution and export of materials, including N (Tongway and Ludwig 1997; Schlesinger et al. 2000; Belnap et al. 2005). Given that arid ecosystems experience prolonged dry periods, as well as storms that vary in size, intensity and frequency, N retention and export patterns may be a function of individual storm characteristics. Our objective was to determine how seasonal patterns in rainfall as well as individual storm characteristics (storm size, intensity, and frequency) influence N transport and retention on terrestrial hillslopes in a Sonoran Desert watershed.

This work was largely motivated by observations made from previous research conducted in Sycamore Creek, a fourth-order perennial stream in Central Arizona. In the Sycamore Creek watershed, on average only 8% of annual rainfall supplied to the catchment exits as stream flow (Grimm 1993). Thus, if N retention is similar to water, this watershed is highly retentive of N. Yet, it is unknown where and under what conditions N retention occurs. In addition, inorganic N concentration in Sycamore Creek floodwater is high, but temporally variable. Peak nitrate (NO_3^-) concentration occurs in floodwater following multiple years of low rainfall (small storms, generating little runoff) and NO_3^- concentration decreases with increasing flood frequency (Grimm and Fisher 1992). These observations suggest that NO_3^- derived from rainfall accumulates within the terrestrial component of the catchment during periods of low runoff and high evaporation. Large infrequent precipitation events then wash accumulated NO_3^- salts from upland soils and export them downstream.

A number of other potential mechanisms may lead to N accumulation, including dry deposition (Fenn et al. 2003), as well as photodegradation (Moorhead and Callaghan 1994; Zepp et al. 1995) and mineralization of organic matter on the soil surface during extended dry periods. Results from Fisher et al. (1987) indicate that mineralization enhances N availability during periods of infrequent rainfall. Davidson et al. (1993) report significant increases in soil ammonium (NH_4^+) upon wetting seasonally dry tropical soils. Pulses in mineralization upon wetting dry soil may be followed by high rates of nitrification, once constraints on NH_4^+ diffusion are alleviated by rainfall (Davidson et al. 1990; Stark and Firestone 1995). These studies also indicate that the length of the antecedent dry period influences the magnitude of N accumulation, as well as the dominant mechanisms of transformation and retention. Length of dry period may also influence patterns in N transport and redistribution in the catchment. Large storms following long dry periods could facilitate rapid fluvial reconnection with the aquatic component of the watershed and export high-N runoff water into streams. In this case, N concentration in hillslope-runoff water would peak following long drought periods (as discussed by Hornung and Reynolds 1995). Furthermore, where (terrestrial or aquatic) and how N is retained in the watershed would be dependent on the magnitude and sequence of rainstorms.

The Sonoran Desert experiences two seasons of rain, receiving frontal storms from the Pacific during the winter months (October–April) and convective monsoon storms in summer (May–September). The nature of rainfall varies dramatically between the two seasons, providing an opportunity to explore the role of both seasonal rainfall patterns and event-based variation in storm size, intensity and frequency (time between events) in nutrient export in Sonoran Desert ecosystems. Winter storms are typically large in spatial extent, low in intensity, and may persist for several days. In contrast, summer monsoon storms build rapidly as a result of convective heating of moisture-laden air from the Gulf of Mexico, producing short, high intensity storms (Sellers and Hill 1974; Sheppard et al. 2002).

In order to explain the pattern in floodwater NO_3^- observed in perennial streams draining the catchment, patterns of inorganic N accumulation and transport on upland hillslopes in the Sycamore Creek Watershed were monitored over the course of both summer and winter seasons. We asked the following questions: (1) Does N accumulate on terrestrial hillslopes during periods of low rainfall and, if so, what is the mechanism and form of accumulated inorganic N (NH_4^+ or NO_3^-)? and, (2) how do individual storm characteristics influence transport, transformation, and retention of accumulated N in both terrestrial (pre-channel hillslopes) and aquatic (intermittent and perennial streams) components of the catchment?

In this paper, we describe seasonal patterns in rainfall and runoff inorganic N chemistry. We also evaluate the relationship between individual storm characteristics and nitrogen accumulation and export patterns in the Sycamore Creek watershed. Five variables were included in our analysis: storm size (total event precipitation), rain chemistry (focusing on NH_4^+ and NO_3^-), season (summer vs. winter), cumulative seasonal rainfall (CSR), and days since last storm (length of dry period between storms). Storm size and rain chemistry are individual storm variables, while CSR and days since last storm pertain to the influence of antecedent effects on N transport.

Site description

The Sycamore Creek watershed is located in Central Arizona, approximately 32 km northeast of Phoenix. The entire watershed encompasses an area of 505 km^2, ranging in elevation from 427 to 2164 m; however, this work was completed in a small sub-catchment at an elevation of ~650 m. Vegetation is typical of Sonoran Desert scrub and dominated by palo verde (*Parkinsonia microphyllum*) and mesquite (*Prosopis* sp.). Other common plants include jojoba (*Simmondsia chinensis*), turpentine bush (*Haplopappus laricifolius*), prickly pear (*Opuntia* sp.), buckhorn cholla (*Opuntia acanthocarpa*), and saguaro (*Carnegiea gigantea*) cactus. During the dry months much of the interplant spaces are bare and devoid of plant growth; however, during wet periods, annual grasses can be prevalent.

The lower areas of the watershed are underlain by poorly consolidated alluvial deposits, which consist of Tertiary sandstone, siltstone, and conglomerate. These deposits overlie granite and related crystalline rocks, which are overlain by basaltic lava flows in some areas of the catchment (Thomsen and Schumann 1968). The soil surface is highly dissected and channel density is high throughout the lower watershed. The consolidated alluvium contains large amounts of firmly cemented, fine-grained material and has a low permeability. As a result, runoff tends to flow overland and is quickly channelized. The majority of hillslope flowpaths are shorter than 10 m, before runoff enters a small rill or rivulet.

Methods

Rainfall

Rainfall amounts were measured at four stations in the lower Sycamore Creek watershed (elevation ~650 m) for all storms that occurred from January 1992 to July 2001. Bulk precipitation samples were also collected during the same period and were analyzed for NH_4^+, NO_3^- and chloride (Cl^-) concentration. For all analyses, rainfall was divided into two seasons: summer (May–September) and winter (October–April), based on seasonality of rainfall and source of precipitation. Rain samples were typically collected within 12 h of an event, transported to the laboratory on ice, filtered (0.7 μm pore size, Whatman glass-fiber filter) and analyzed for NH_4^+ and NO_3^- within 24 h. When analysis was delayed, samples were filtered and stored at 4 °C prior to analysis. From 1992 to 1998, Cl^- and NO_3^- analyses were completed on a Bran and Luebbe TRAACS 800 Autoanalyzer, while NH_4^+ concentrations were determined manually using the phenolhypochlorite method (Solorzano 1969). From 1999 to 2001, all analyses were completed using a Lachat QC8000 Flow-Injection Autoanalyser. All values of NO_3^-, NH_4^+, and dissolved inorganic nitrogen (DIN) concentration are reported as N; i.e., mg N/l.

Runoff – Sheetflow

Sheetflow collectors were used to characterize inorganic N concentration in overland flow contributed by upland slopes of differing flowpath lengths (ranging from 4 to 15 m), allowing for direct comparison of rainfall and runoff chemistry. From 1999–2001, runoff was collected using five sheetflow collectors that captured overland flow. These collectors were placed in different topographic positions within approximately 20 m of the rainfall collection site. Sheetflow collectors were constructed using V-shaped metal flashing, with a piece of tubing inserted at the point of the ‘V’. Collectors were inserted into the soil surface (to approximately 2 cm depth) with the point of the ‘V’ facing downslope. Runoff was collected in 4 l sampling containers at the outlet. Runoff samples were analyzed for NH_4^+, NO_3^- and Cl^- concentrations as above. Average values of the five collectors for each individual storm were used in our statistical analyses.

Multiple regression analysis

To evaluate the relationship between seasonal and event-based rainfall characteristics and runoff NH_4^+ and NO_3^- concentrations, multiple-regression analyses were conducted for summer and winter separately and for the two seasons combined. Five rainfall variables were considered: storm size (total event precipitation in cm) and rain N concentration (either NH_4^+ or NO_3^-, mg/l), both single storm features, as well as cumulative seasonal rainfall (CSR), rain season, and days since last storm (length of dry period between storms), variables which pertain to antecedent conditions. For all analyses, multiple regressions were considered using all five variables, as well as all possible sub-sets of variables using SAS (Version 8, SAS Institute Inc.). Partial *F*-tests were used to identify variables that contributed significantly to the explanatory power of each model. Variables were transformed when necessary to meet assumptions of constant variance and normality. All other statistical analyses were completed using SYSTAT (Version 10, SPSS Inc.)

Results

Rainfall

Storms were more intense during summer than winter ($p < 0.0001$; Table 1). Unfortunately, since we obtained storm intensity information for only a limited number of events, we were unable to include it as a variable in our multiple-regression analysis of runoff N; however, it differs considerably between seasons ($p < 0.0001$; Table 1), and may be an important explanatory variable. Individual winter storms were on average larger than summer storms ($p = 0.03$; Table 1), while the number of storms occurring in each season, as well as the time between storms did not differ significantly between winter and summer. As a result, total seasonal rainfall was significantly higher during winter ($p = 0.014$; Table 1). Considerable variation was observed in both rainfall amounts associated with individual storms and the length of dry periods between storms. Storm size ranged from trace amounts (< 0.10 cm) up to 14 cm. Dry periods between storm events ranged from a single day up to 122 days (Table 1).

While rainwater Cl^- concentration did not differ between seasons, NO_3^- ($p < 0.0001$; Table 1) and NH_4^+ ($p < 0.0001$; Table 1) concentrations were significantly higher in summer monsoon rainfall than winter storms. Despite the increase in inorganic N concentration, total DIN input did not significantly

Table 1. Rainfall characteristics and precipitation chemistry, Sycamore Creek watershed, Arizona.

	Rainfall characteristics							Rain chemistry			
	Storm intensity (cm/h)	Storm size (cm)	Limits (cm)	No. of storms	Time between storms (days)	Limits (days)	Total rain (cm)	Cl (mg/l)	NO_3-N (mg/l)	NH_4-N (mg/l)	Total DIN input (mg/m^2)
Summer	1.24 (0.31)	1.2 (0.21)		9.89 (1.32)	18 (3)	1–122	11.91 (2.54)	3.83 (0.70)	0.97 (0.12)	0.87 (0.08)	133.42 (21.89)
May		0.6 (0.26)	tr – 3.6	1.0 (0.55)	30 (10)	1–50	0.85 (0.68)	10.57	0.68 (0.14)	0.58 (0.06)	8.92 (8.03)
June		1.2 (0.34)	0.30–2.0	0.3 (0.24)	27 (18)	8–82	0.35 (0.23)	1.49	1.24 (0.21)	1.20 (0.19)	7.57 (5.07)
July		1.1 (0.25)	tr – 4.8	2.1 (0.48)	36 (8)	1–117	2.55 (0.93)	3.51 (1.07)	1.16 (0.23)	1.00 (0.12)	41.74 (11.44)
August		1.7 (0.73)	tr – 14.0	4.3 (0.83)	14 (5)	1–122	6.28 (1.64)	3.17 (0.56)	1.02 (0.17)	0.82 (0.14)	59.18 (11.83)
September		1.2 (0.38)	tr – 3.3	2.1 (0.65)	11 (3)	1–25	1.89 (0.52)	4.19 (1.86)	0.63 (0.14)	0.71 (0.15)	17.00 (4.94)
Winter	0.22 (0.67)	2.1 (0.29)		13.3 (1.58)	17 (2)	1–109	27.57 (4.93)	2.55 (0.46)	0.32 (0.06)	0.38 (0.04)	96.95 (11.32)
October		2.0 (0.29)	tr – 7.2	2.0 (0.82)	36 (8)	1–66	3.01 (1.71)	2.20 (0.92)	0.35 (0.13)	0.43 (0.08)	9.92 (2.82)
November		1.8 (0.66)	tr – 9.8	2.3 (0.36)	20 (7)	1–109	2.70 (1.13)	1.84 (0.43)	0.49 (0.09)	0.52 (0.10)	12.38 (2.50)
December		2.1 (0.56)	tr – 6.2	2.8 (0.49)	18 (5)	1–57	3.81 (1.63)	1.58 (0.36)	0.2 (0.06)	0.51 (0.30)	10.65 (4.64)
January		1.9 (0.66)	tr – 14.0	2.7 (0.75)	32 (11)	1–100	6.38 (2.71)	3.47 (1.07)	0.58 (0.20)	0.58 (0.12)	20.04 (3.93)
February		2.0 (0.34)	tr – 5.4	2.4 (0.48)	17 (3)	1–77	5.02 (1.46)	3.26 (1.49)	0.27 (0.06)	0.36 (0.08)	21.20 (6.12)
March		2.0 (0.41)	tr – 6.6	2.8 (0.66)	14 (4)	1–40	5.49 (1.30)	3.07 (1.51)	0.21 (0.05)	0.35 (0.06)	18.20 (4.00)
April		1.8 (0.38)	tr – 7.6	1.2 (0.36)	17 (5)	2–38	2.10 (0.72)	1.59 (0.44)	0.26 (0.06)	0.38 (0.05)	9.81 (4.50)
Season											
p	< 0.0001	0.03		0.12	0.65		0.01	0.14	< 0.0001	< 0.0001	0.15

tr = trace.

Values are means (standard error in parentheses) or limits (min–max) for the period indicated. Storm intensity values are means of all storms that occurred during summer (n = 22 storms) and winter (n = 14 storms) seasons between 2000 and 2002. All remaining means are based on rainfall data collected between 1992 and 2001 for both summer (n = 9 seasons) and winter rain seasons (n = 10 seasons).

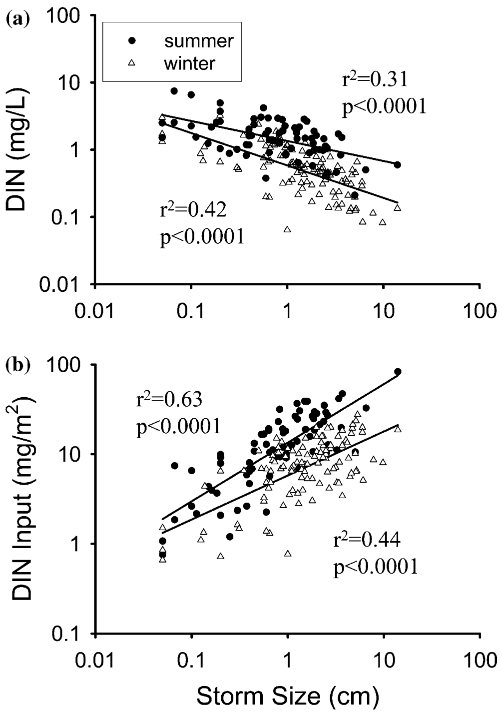

Figure 1. Relationship between storm size and (a) rainfall DIN concentration (mg/l) and (b) total DIN Input (mg/m^2) for summer vs. winter rain events.

differ among seasons ($p = 0.15$; Table 1). While there was no difference in DIN load between the two seasons, there was monthly variation, with 40% of the annual DIN load (mg/m^2) occurring during July and August alone (Table 1).

Storm–rainfall relationships

N concentration in rainwater varied as a function of storm size and exhibited greatest variation for small storms. NH_4^+ concentration ranged from 0.1 to 4.2 mg N/l, while NO_3^- ranged from 0.16 to 6.0 mg N/l for storms smaller than 1 cm. There were significant negative relationships between storm size and both NH_4^+ (summer: $r^2 = 0.16$, $p < 0.0001$, winter: $r^2 = 0.23$, $p < 0.0001$) and NO_3^- concentration (summer; $r^2 = 0.32$, $p < 0.0001$, winter: $r^2 = 0.14$, $p < 0.0001$) during summer and winter seasons, indicating that DIN was diluted in rainwater (Figure 1a) as storm size increased. However, DIN load (mg/m^2) exhibited a significant positive relationship with storm size during both seasons (Figure 1b), with storm size explaining 63% of the variation in DIN input (mg

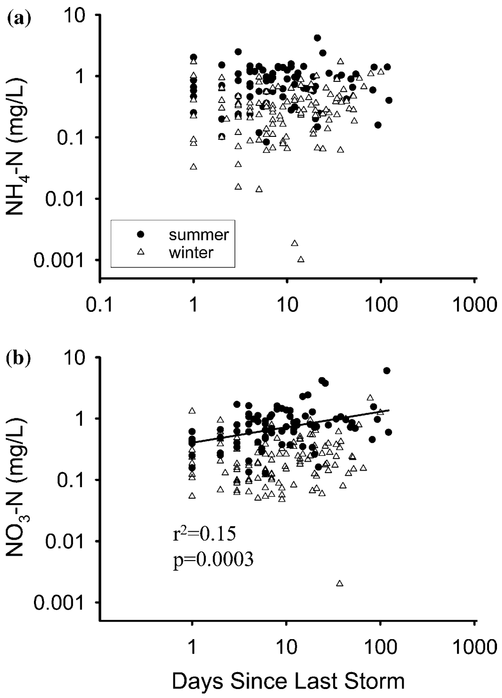

Figure 2. Relationship between length of dry period between storms and (a) rainfall NH_4-N and (b) NO_3-N concentration (mg/l) for summer vs. winter rain events.

N/m^2) during the summer monsoons and 44% during winter rains. Thus, despite the dilution of N with increasing storm size, larger storms had larger DIN loads.

Days since last storm explained little variation in inorganic nitrogen concentration in rainfall. There was a weak positive relationship between NO_3^- concentration and days since last storm during summer ($r^2 = 0.15$, $p = 0.003$; Figure 2b); however, there were no significant relationships between days since last storm and NH_4^+ concentration in either season (Figure 2a) or with NO_3^- during winter (Figure 2b).

Runoff

Seasonal patterns in surface runoff were similar to rainfall, including considerable variation in the number of runoff events that occurred during any given month (ranging from 0 to 6) and number of days between runoff events (ranging from 1 to 96 days; Table 2). Once again, NO_3^- ($p = 0.002$) and NH_4^+ ($p = 0.005$) concentrations (mg N/l) were higher during summer than winter (Table 2). There was no significant difference between seasons in the

Table 2. Sheetflow characteristics and sheetflow chemistry, Sycamore Creek watershed, Arizona.

	Sheetflow characteristics				Sheetflow chemistry		
	No. of runoff events	Limits	Time since last runoff (days)	Limits (days)	Cl (mg/l)	NO_3-N (mg/l)	NH_4-N (mg/l)
Summer	8.5 (0.5)	8–9	19 (7)	1–96	2.50 (0.38)	1.30 (0.28)	0.79 (0.16)
May	0	0–0					
June	1.0 (1.0)	0–2	46 (38)	8–84	4.15	1.55 (0.40)	1.40 (0.51)
July	2.5 (1.5)	1–4	28 (18)	2–96	2.09 (0.05)	0.94 (0.28)	0.82 (0.41)
August	4.5 (1.5)	3–6	7 (2)	1–16	2.21 (0.33)	1.47 (0.51)	0.66 (0.18)
September	0.5 (0.5)	0–1	24	24–24	1.82	0.74	0.42
Winter	13.0 (7.0)	6–20	14 (5)	1–100	2.09 (0.59)	0.48 (0.11)	0.27 (0.07)
October	2.0 (2.0)	0–4	4 (1)	3–5	2.26 (0.73)	0.25 (0.07)	0.07 (0.01)
November	1.5 (1.5)	0–3	6 (3)	2–11	1.69 (0.32)	1.67 (0.36)	0.20 (0.01)
December	0	0–0					
January	3.5 (2.5)	0–6	22 (13)	1–100	2.40 (1.07)	0.42 (0.08)	0.27 (0.14)
February	1.5 (0.6)	1–2	27 (12)	14–51	2.19 (0.64)	0.47 (0.12)	0.48 (0.32)
March	3.0 (1.0)	2–4	8 (3)	1–21	1.02 (0.27)	0.19 (0.05)	0.26 (0.11)
April	1.5 (1.5)	0–3	5	5–5			
Season							
p	0.59		0.58		0.62	0.002	0.005

Values are means (standard error in parentheses) and limits (min–max) for all storms that occurred during summer (n = 17. storms) and winter (n = 26 storms) rain seasons between 2000 and 2002.

Table 3. Regression parameters for ammonium and nitrate concentration (mg N/l) in runoff during both seasons combined, summer, and winter, as a function of seasonal and event-based rainfall characteristics.

Predictor variable	Seasons combined		Summer		Winter	
	NH_4	NO_3	NH_4	NO_3	NH_4[a]	NO_3
Intercept	1.813 (0.261)***	0.550 (0.472)***	−0.930 (0.266)**	−0.802 (0.174)***	0.677 (0.047)***	
ln cumulative seasonal rainfall	−0.579 (0.076)***				−0.194 (0.014)***	
Season	−1.055 (0.158)***	−0.888 (0.222)***				
ln storm size	−0.417 (0.114)***	−0.582 (0.136)***	−0.694 (0.182)**		−0.106 (0.018)***	−0.585 (0.172)**
Rain NO_3		0.842 (0.270)**		1.151 (0.198)***		0.493 (0.165)** [b]
ln days since last storm			0.375 (0.108)**		0.054 (0.011)***	
Model r^2 (d.f.)	0.872*** (3,28)	0.792*** (3,28)	0.832*** (2,10)	0.754*** (1,11)	0.977*** (3,15)	0.692*** (2,16)

Variables included in the model selection process were storm size (total event precipitation in cm), cumulative seasonal rainfall (cm), season (summer vs. winter), days since last rainfall (length of dry period) and rain N concentration (ammonium or nitrate, mg N/l). Parameter values are listed with standard error in parenthesis and *p*-value as superscript (***$p<0.001$; **$p<0.01$). Blank cells indicate non-significant predictor variable or intercept.

[a]Runoff NH_4 and NO_3 were natural log transformed in all models with the exception of winter NH_4.

[b]Rain NO_3 was natural log transformed in the winter NO_3 model.

average number of days between runoff events or the average number of runoff events.

Storm–runoff relationships

In multiple-regression analyses with seasons combined, runoff NH_4^+ concentration (mg N/l) was best explained by cumulative seasonal rainfall (CSR; partial $F = 57.81$), season (partial $F = 44.62$), and storm size (partial $F = 13.33$) (model $r^2 = 0.872$, $p < 0.0001$; Table 3). Runoff NH_4^+ concentration was high when CSR was low and storm size was small, and was higher during summer. Partial *F*-values indicated that CSR contributed most strongly to this model and when considered in isolation (in a single variable model), CSR explained 65% of the variation in runoff NH_4^+ concentration. In contrast, NO_3^- concentration was best explained by storm size (partial $F = 18.34$), season (partial $F = 16.08$) and rain NO_3^- (partial $F = 9.73$) (model $r^2 = 0.792$, $p < 0.0001$; Table 3), with storm size contributing most explanatory power to the three-variable model. Runoff NO_3^- concentration was high when rain NO_3^- was also high and storm size was small, and was higher during summer. Thus, across seasons, variation in runoff NH_4^+ was best explained by antecedent conditions (CSR) while variation in NO_3^- was best explained by individual storm characteristics (storm size and rain NO_3^-).

In both models, season was a significant variable, indicating that summer and winter seasons behaved differently. As a result, analyses were also completed for winter and summer individually; however, results were similar to those for seasons combined. Variation in summer runoff NH_4^+ was best explained by storm size (partial $F = 14.56$) and days since last storm (partial $F = 12.22$) (model $r^2 = 0.832$, $p < 0.0001$; Table 3), while variation in winter NH_4^+ was best explained by CSR (partial $F = 187$), storm size (partial $F = 34$), and days since last rain (partial $F = 24.3$) (model $r^2 = 0.962$, $p < 0.0001$; Table 3), with CSR contributing strongly to the explanatory power of the model. Cumulative seasonal rainfall and days since last storm were more strongly correlated with each other in summer ($r = 0.48$) than in winter ($r = 0.31$), which likely contributed to the difference between these two models. In addition, there was a significant positive relationship between the $NH_4^+ : NO_3^-$ ratio in surface runoff and days since last storm during summer ($r^2 = 0.732$, $p < 0.0001$; Figure 3), but not during winter (Figure 3). In summary, runoff NH_4^+ was high when CSR was low during the winter season, and for both seasons when storm size was small and length of the dry period was long. Based on the results of this analysis, antecedent conditions have a strong influence on runoff NH_4^+ concentration.

The model that best described summer runoff NO_3^- contained only rain NO_3^- (model $r^2 = 0.754$, $p < 0.0001$; Table 3). In winter, NO_3^- was best described by storm size (partial $F = 11.57$) and rain NO_3^- (partial $F = 8.94$) (model $r^2 = 0.692$, $p < 0.0001$; Table 3), with both variables contributing fairly

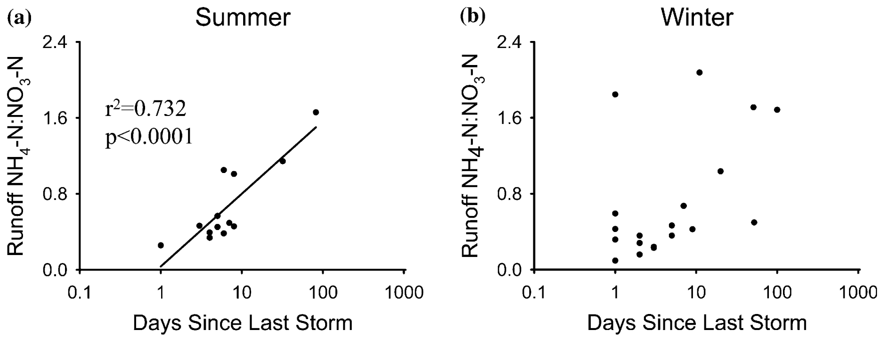

Figure 3. Relationship between runoff NH_4-N (mg/l) to NO_3-N (mg/l) ratio and days since last storm for (a) summer and (b) winter seasons.

equally to the explanatory power of the model. In contrast to the models describing variation in runoff NH_4^+, models for NO_3^- were dominated by single storm characteristics, primarily rain NO_3^-.

Finally, to determine whether NH_4^+ and NO_3^- changed as a function of distance traveled along surface flowpaths, N concentrations were compared among three runoff collectors, placed at 4.5, 11.7 and 14.5 m along a single hillslope flowpath. As a result of limited sample size, there were insufficient degrees of freedom to conduct a repeated measures analysis of variance; therefore, paired *t*-tests were conducted for all combinations of the three flowpath lengths for individual storms over the course of summer and winter seasons. Alpha values were Bonferroni-adjusted to take multiple comparisons into account. During summer, increases in NO_3^- along the surface flowpath (14.5 m > 4.5 m, $p = 0.008$; df = 8; Figure 4a) were balanced by decreases in NH_4^+ (14.5 m < 11.7 m, $p = 0.025$; 14.5 m < 4.5 m, $p = 0.016$) with no change in DIN concentration (Figure 4a), a pattern consistent with nitrification. During winter, both DIN (14.5 m > 4.5 m, $p = 0.001$; 11.7 m > 4.5 m; $p = 0.01$; df = 12; Figure 4b) and NO_3^- concentrations increased (14.5 m > 4.5 m, $p = 0.001$; 11.7 m > 4.5 m, $p = 0.002$) along the flowpath, while NH_4^+ concentration decreased (14.5 m < 4.5 m; $p = 0.002$).

Discussion

The nine-year rainfall record (1992–2001) indicates that summer storms are more intense and deposit more DIN than winter storms, while winter storms on average are larger and supply more rain (Table 1). The observed difference in inorganic N concentration in rain and runoff between summer and winter is likely related to differences in storm intensity among seasons, as well as N input associated with dust storms, lightning fixation of N_2 during summer monsoons (Ridley et al. 1996), or photochemical smog that moves into the study area

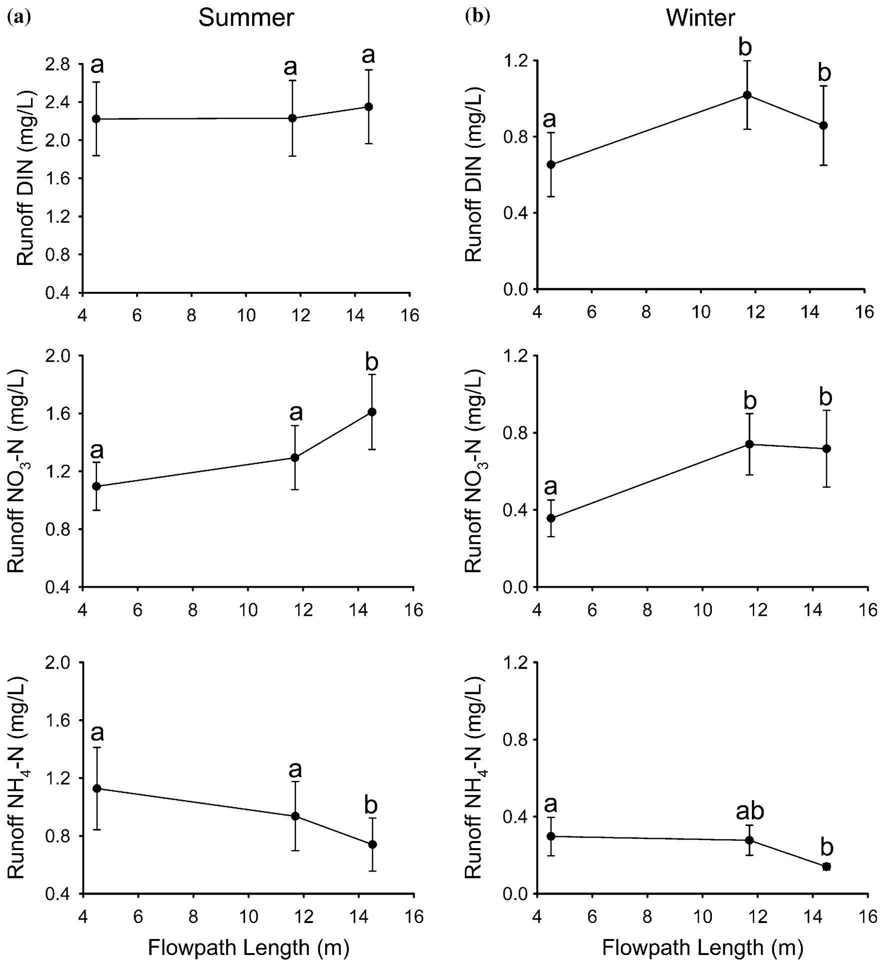

Figure 4. Changes in surface runoff NH_4-N, NO_3-N and DIN concentration (mg/l) along a hillslope flowpath during both (a) summer and (b) winter seasons. Lower-case letters indicate significant differences in paired *t*-test comparisons between points along the flowpath.

from the Phoenix metropolitan area (Ellis et al. 2000; Fernando et al. 2001; Fenn et al. 2003; Lee et al. 2003). Summer storms are more likely to generate rapid overland flow (Canton et al. 2001; Michaelides and Wainwright 2002) and facilitate fluvial export of N to the aquatic component of the watershed. Storm intensity likely contributed to the explanatory power of season in multiple regression models, but other key variables include soil temperature and evaporation rate, both of which are higher during summer.

Storm size was consistently retained as a significant variable in runoff models for both NO_3^- and NH_4^+ (Table 3). This result is not surprising since small precipitation events concentrate material, leading to a higher concentration of

N in runoff, while larger storms are diluted in inorganic N (Figure 1). On the other hand, there were fundamental differences between NO_3^- and NH_4^+ in the remaining variables that explained variation in runoff. Runoff NO_3^- was driven by individual-event variation in rain NO_3^- and not by antecedent conditions. In contrast, runoff NH_4^+ was a function of days since last storm and CSR, suggesting that antecedent conditions result in large pulses of NH_4^+ in surface runoff following long dry periods. Others have observed accumulation and/or pulses of NH_4^+ following dry periods in arid ecosystems (Austin et al. 2004) and attributed them to N mineralization during the dry period (Fisher et al. 1987) or upon rewetting (Davidson et al. 1993). Photodegradation of surface litter (Zepp et al. 1995, 1998), as well as bacterial cell lysis (Marumoto et al. 1982; Bottner 1985; Van Gestel et al. 1993) and/or release of intracellular solutes (Kieft et al. 1987; Halverson et al. 2000) upon rewetting, may also contribute to this pulse. Soil organic matter may also become more accessible as a result of drying-rewetting cycles (Appel 1998), adding to increased availability of substrate for decomposition following storms.

While numerous studies indicate that precipitation stimulates microbial activity in the terrestrial component of the watershed (Davidson et al. 1990, 1993; Mummey et al. 1994; Hartley and Schlesinger 2000; Austin et al. 2004), our results suggest accumulated N may also run off and be transported from

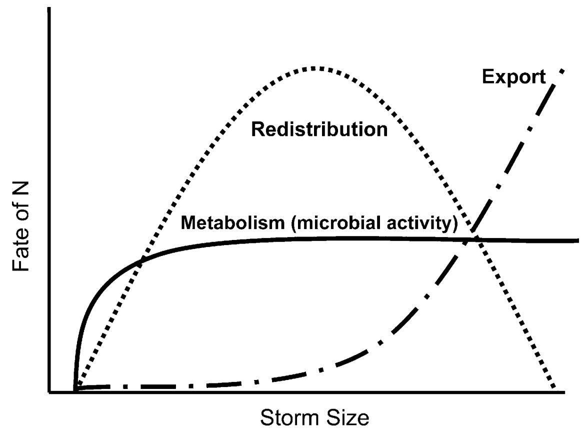

Figure 5. Conceptual model describing possible fates of accumulated N during dry periods on terrestrial hillslopes. Rainstorms may stimulate microbial activity upon wetting, leading to N retention within the terrestrial component of the watershed. This scenario would be most likely to occur during small storms that 'activate' microbial activity and plant uptake, but do not lead to appreciable overland flow. As storm size increases, N may be redistributed in the landscape. Depending on storm intensity, surface material may infiltrate vertically and accumulate as storage in deep soils, or be transported horizontally as overland flow into small rills and rivulets, and topographic depressions. However, rare large storms will result in rapid horizontal transport and flooding in large streams. During these events, N will be exported from the terrestrial component of the watershed and delivered to stream-riparian systems, fueling metabolism and retention in the aquatic component of the watershed.

hillslopes to other parts of the catchment, including streams (Hornung and Reynolds 1995). Thus, the magnitude and sequence of rainstorms will influence N availability in different parts of the catchment and where and how N is transformed and retained. Fluvial connection between terrestrial hillslopes and stream networks are often excluded from consideration of ecological processes in arid lands (Grimm et al. 2003), but may be an important component of biogeochemical cycling, and contribute to low N availability in terrestrial systems (Austin et al. 2004).

The fate of pulses of available N following drought periods is also influenced by storm size and intensity (Figure 5), which determine runoff N concentration and thus resource availability to receiving patches. Storm features determine whether material is transported vertically, infiltrating hillslope soils, horizontally to other hillslope patches (Tongway and Ludwig 1997; Puigdefabregas et al. 1998), or into stream networks (Grimm and Fisher 1992; Grimm 1993; Puigdefabregas et al. 1999; Belnap et al. 2005). This relationship is depicted in a conceptual model (Figure 5) representing how storms of different size interact with the landscape. Small storms wet upland soil, and stimulate local biological activity (Figure 5). Thus, in the case of small, low intensity events, catchment N retention would occur primarily in shallow terrestrial soils. As storm size increases, material may be redistributed in the landscape either vertically (deep seepage) or horizontally (overland flow), depending on storm intensity (Loik et al. 2004). Walvoord et al. (2003) found large accumulations of NO_3^- in deep soils of southwestern deserts, suggesting that infiltration and vertical leaching can result in storage of N in arid land ecosystems. With increases in storm intensity, however, material may be redistributed in the landscape as a result of overland transport (Figure 5) (Fletcher et al. 1978). If the storm is large enough and exceeds infiltration rate, rapid fluvial reconnection between the terrestrial and aquatic components of the watershed may serve to export accumulated material from hillslopes to large stream-riparian systems. Based on characteristics of individual rain events, this conceptual model describes how accumulated N may be transported in catchments, and where hot spots for N retention (sensu McClain et al. 2003) are likely to occur (also discussed in Belnap et al. 2005).

This conceptual model is supported by subtle differences between runoff NH_4^+ models for each season. Days since last storm was a significant variable in both summer and winter models; however, the coefficient changed dramatically from 0.375 for summer to 0.054 for winter (weakest in model, Table 3), suggesting slower accumulation of NH_4^+ in winter (since runoff NH_4^+ was natural log transformed in the summer model, the direct comparison of these two parameter values is conservative). Winter storms are larger and less intense than summer storms (Table 1). Thus, they may more effectively infiltrate upland soils, generating less surface runoff (Bowyer-Bower 1993; Howes and Abrahams 2003). Furthermore, as a result of lower evaporation rates, soils likely remain wet longer during the winter season, increasing plant production (Reynolds et al. 2004; Schwinning and Sala 2004) and enhancing opportunity for plant uptake, as well as microbial immobilization of inorganic N (Gallardo and Schlesinger 1995). As a result, more available N would be retained and processed in the terrestrial part of the watershed during winter, weakening the relationship with days since last storm.

Our results also indicate that nitrification occurs along surface flowpaths (Figure 4), particularly during summer storms. Nitrification is suggested by the observation that increases in NO_3^- were balanced by decreases in NH_4^+, with no change in DIN concentration (Figure 4a). Rapid nitrification has been observed upon wetting dry soil (Davidson et al. 1993). Furthermore, Holmes et al. (1994) observed an increase in nitrate along hydrologic flowpaths in an arid stream of similar magnitude to changes along a surface flowpath reported here (Figure 4a). Thus, nitrification rates can be high enough to account for the patterns observed here. Nitrification may be constrained during dry periods due to limited diffusion of NH_4^+ in dry soil (Davidson et al. 1990; Stark and Firestone 1995). In addition, the water repellent nature of xeric soils following persistent dry periods limits the extent of infiltration upon initial re-wetting (DeBano 1971; Burch et al. 1989). Low infiltration limits delivery of NH_4^+ to the soil microbial community, further constraining nitrification and may explain temporal shifts in runoff NH_4^+: NO_3^- in relation to time since the last storm. However, this substrate limitation would be alleviated by subsequent rainfall, generating high nitrification rates (Davidson et al. 1993), resulting in increases in NO_3^- along hydrologic flowpaths. Nitrate increased along the flowpath during winter storms as well (Figure 4b), but relationships were not as strong and both NO_3^- and DIN concentrations increased, indicating that either dissolution of NO_3^-salts or coupled mineralization-nitrification may have occurred along the flowpath. These results suggest that the ratio of available NH_4^+ to NO_3^- decreases as a function of distance along surface flowpaths and varies on a seasonal basis, possibly as a result of differences in storm intensity and evaporation rate among seasons.

We also observed a significant increase in NH_4^+: NO_3^- in runoff water during summer storms with increasing length of the dry period (Figure 3a). Since NO_3^- concentration increases along surface flowpaths, we would expect accumulated NH_4^+ in runoff from early season monsoon storms to be converted to NO_3^- as water moves downhill. This potential mechanism explains floodwater pulses of NO_3^- observed by Grimm and Fisher (1992) following low rainfall periods. These findings also suggest that the extent to which a receiving patch is supplied with NH_4^+ or NO_3^- depends on the distance runoff has traveled (flowpath length) (Figure 4) as well as the length of the dry period (Figure 3a) and thus, the mechanism of retention may shift spatially and temporally depending on the predominant form of N supplied. The vast majority of storms generated runoff; however, many storms do not result in hydrologic linkage between the terrestrial upland and large perennial streams. Instead, they redistribute material on hillslopes and within intermittent drainage networks, such that NO_3^- produced along intermittent hydrologic flowpaths accumulates in the catchment as evaporites during rapid drying following small storms, contributing to large floodwater NO_3^- peaks when surface runoff eventually reaches large streams.

In summary, the nature of fluvial reconnection among patches in the landscape following long drought periods likely determines whether N is processed and retained in the terrestrial or aquatic component of the watershed, as well as the retention mechanism. The nature of this reconnection is driven by the size, intensity and sequence of storms in space and time. If small storms precede large storms, material may be retained (plant uptake, microbial immobilization) or lost (gaseous loss) by biological mechanisms in shallow terrestrial soils or upland deep storage. Conversely, if large storms precede small storms, material may be redistributed into the stream network, shifting ecosystem N retention from the terrestrial to the aquatic component of the watershed. Of course, the magnitude and spatial location of material transport and retention will depend on the extent of the accumulation (duration of dry period) and the frequency and sequence of storms, while the mechanism of retention may vary spatially depending on the predominant form of available N (NH_4^+ vs. NO_3^-). Climatic decoupling of N accumulation and biological consumption (Ulrich 1983; Hornung and Reynolds 1995) may become more prevalent given predicted shifts in precipitation regimes and more extensive drought as a result of climate change (West et al. 1994; Gregory et al. 1997; Karl and Trenberth 2003). Knowledge of the role of rainfall patterns in N transformations and retention rates, as well as the effect of N transport on both terrestrial and aquatic ecosystems, will provide us with a better understanding of the spatial and temporal dynamics involved in N retention at the watershed scale.

Acknowledgements

We would like to thank past and present members of the stream lab at Arizona State University for assistance with collection of precipitation samples and laboratory analysis, especially Shero Holland, Tom Colella, Cathy Kochert and Jennifer Zachary. We also thank two anonymous reviewers for helpful comments on the manuscript. This research was supported by National Science Foundation grants DEB-0075650 to S.G. Fisher and DEB-9615358 to N.B. Grimm and S.G. Fisher.

References

Appel T. 1998. Non-biomass soil organic N – the substrate for N mineralization flushes following soil drying-rewetting and for organic-N rendered $CaCl_2$-extractable upon soil drying. Soil Biol. Biochem. 30: 1445–1456.

Austin A.T., Yahdjian L., Stark J.M., Belnap J., Porporato A., Norton U., Ravetta D.A. and Schaeffer S.M. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141: 221–235.

BassiriRad H., Tremmel D.C., Virginia R.A., Reynolds J.F., de Soyza A.G. and Brunell M.H. 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecol. 145: 27–36.

Belnap J., Welter J.R., Grimm N.B., Barger N. and Ludwig J.A. 2005. Linkages between microbial and hydrologic processes in arid and semi-arid watersheds. Ecology 86: 298–307.

Bottner P. 1985. Response of microbial biomass to alternate moist and dry conditions in a soil incubated with ^{14}C- and ^{15}N-labelled plant material. Soil Biol. Biochem. 17: 329–337.

Bowyer-Bower T.A.S. 1993. Effects of rainfall intensity and antecedent moisture on the steady-state infiltration rate in a semi-arid region. Soil Use Manage. 9: 69–76.

Burch G.J., Moore I.D. and Burns J. 1989. Soil hydrophobic effects on infiltration and catchment runoff. Hydrol. Process. 3: 211–222.

Canton Y., Domingo F., Sole-Benet A. and Puigdefabregas J. 2001. Hydrological and erosion response of a badlands system in semiarid SE Spain. J. Hydrol. 252: 65–84.

Cui M. and Caldwell M.M. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. Plant Soil 191: 291–299.

Davidson E.A., Matson P.A., Vitousek P.M., Riley R., Dunkin K., Garcia-Mendez G. and Maass J.M. 1993. Processes regulating soil emissions of NO and N_2O in a seasonally dry tropical forest. Ecology 74: 130–139.

Davidson E.A., Stark J.M. and Firestone M.K. 1990. Microbial production and consumption of nitrate in an annual grassland. Ecology 71: 1968–1975.

DeBano L.F. 1971. The effect of hydrophobic substances on water movement in soil during infiltration. Proc. Soil Sci. Soc. Am. 35: 340–343.

Ellis A.W., Hildebrandt M.L., Thomas W.M. and Fernando H.J.S. 2000. Analysis of the climatic mechanisms contributing to the summertime transport of lower atmospheric ozone across metropolitan Phoenix, Arizona, USA. Climate Res. 15: 13–31.

Fenn M.E., Haeuber R., Tonnesen G.S., Baron J.S., Grossman-Clarke S., Hope D., Jaffe D.A., Copeland S., Geiser L., Rueth H.M. and Sickman J.O. 2003. Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience 53: 391–403.

Fernando H.J.S., Lee S.M., Anderson J., Princevac M., Pardyjak E. and Grossman-Clarke S. 2001. Urban fluid mechanics: air circulation and contaminant dispersion in cities. Environ. Fluid Mech. 1: 107–164.

Fisher F.M., Parker L.W., Anderson J.P. and Whitford W.G. 1987. Nitrogen mineralization in a desert soil: interacting effects of soil moisture and nitrogen fertilizer. Soil Sci. Soc. America J. 51: 1033–1041.

Fletcher J.E., Sorensen D.L. and Porcella D.B. 1978. Erosional transfer of nitrogen in desert ecosystems. In: West N.E. and Skujins J.J. (eds), Desert Ecosystems. Dowden Hutchinson and Ross, Stroudsburg, PA pp.171–181.

Gallardo A. and Schlesinger W.H. 1995. Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry 28: 55–68.

Gregory J.M., Mitchell J.F.B. and Brady A.J. 1997. Summer drought in northern mid-latitudes in a time-dependent CO_2 climate experiment. J. Climate 10: 662–686.

Grimm N.B. 1993. Implications of climate change for stream communities. In: Kareiva P., Kingsolover J. and Huey R. (eds), Biotic Interactions and Global Change. Sinauer Associates Inc, Sunderland, pp. 293–314.

Grimm N.B. and Fisher S.G. 1992. Responses of arid land streams to changing climate. In: Firth P. and Fisher S.G. (eds), Climate Change and Freshwater Ecosystems. Springer-Verlag, New York, New York.

Grimm N.B., Gergel S.E., McDowell W.H., Boyer E.W., Dent C.L., Groffman P., Hart S.C., Harvey J., Johnston C., Mayorga E., McClain M.E. and Pinay G. 2003. Merging aquatic and terrestrial perspectives of nutrient biogeochemistry. Oecologia 137: 485–501.

Halverson L.J., Jones T.M. and Firestone M.K. 2000. Release of intracellular solutes by four soil bacteria exposed to dilution stress. Soil Sci. Soc. Am. J. 64: 1630–1637.

Hartley A.E. and Schlesinger W.H. 2000. Environmental controls on nitric oxide emission from northern Chihuahuan desert soils. Biogeochemistry 50: 279–300.

Holmes R.M., Fisher S.G. and Grimm N.B. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. J. North Am. Benthol. Soc. 13: 468–478.
Hornung M. and Reynolds B. 1995. The effects of natural and anthropogenic environmental changes on ecosystem processes at the catchment scale. Trends Ecol. Evol. 10: 443–449.
Howes D.A. and Abrahams A.D. 2003. Modeling runoff and runon in a desert shrubland ecosystem, Jornada Basin, New Mexico. Geomorphology 53: 45–73.
Ivans C.Y., Leffler A.J., Spaulding U., Stark J.M., Ryel R.J. and Caldwell M.M. 2003. Root responses and nitrogen acquisition by *Artemisia tridentata* and *Agropyron desertorum* following small summer rainfall events. Oecologia 134: 317–324.
Karl T.R. and Trenberth K.E. 2003. Modern global climate change. Science 302: 1719–1723.
Kieft T.L., Soroker E. and Firestone M.K. 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. 19: 119–126.
Lee S.M., Fernando H.J.S., Princevac M., Zajic D., Sinesi M., McCulley J.L. and Anderson J. 2003. Transport and diffusion of ozone in the nocturnal and morning planetary boundary layer of the Phoenix valley. Environ. Fluid Mech. 3: 331–362.
Loik M.E., Breshears D.D., Lauenroth W.K. and Belnap J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141: 269–281.
Marumoto T., Anderson J.P.E. and Domsch K.H. 1982. Mineralization of nutrients from soil microbial biomass. Soil Biol. Biochem. 14: 469–475.
McClain M.E., Boyer E.W., Dent C.L., Gergel S.E., Grimm N.B., Groffman P.M., Hart S.C., Harvey J.W., Johnston C.A., Mayorga E., McDowell W.H. and Pinay G. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6: 301–312.
Michaelides K. and Wainwright J. 2002. Modelling the effects of hillslope-channel coupling on catchment hydrological response. Earth Surf Process. Landforms 27: 1441–1457.
Moorhead D.L. and Callaghan T. 1994. Effects of increasing ultraviolet B radiation on decomposition and soil organic matter dynamics: a synthesis and modelling study. Biol. Fertility Soils 18: 19–26.
Mummey D.L., Smith J.L. and Bolton H. 1994. Nitrous oxide flux from a shrub-steppe ecosystem: sources and regulation. Soil Biol. Biochem. 26: 279–286.
Noy-Meir I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4: 25–52.
Puigdefabregas J., del Barrio G., Boer M.M., Gutierrez L. and Sole A. 1998. Differential responses of hillslope and channel elements to rainfall events in a semi-arid area. Geomorphology 23: 337–351.
Puigdefabregas J., Sole A., Gutierrez L., del Barrio G. and Boer M. 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. Earth Sci. Rev. 48: 39–70.
Reynolds J.F., Kemp P.R., Ogle K. and Fernandez R.J. 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141: 194–210.
Ridley B.A., Dye J.E., Walega J.G., Zheng J., Grahek F.E. and Rison W. 1996. On the production of active nitrogen by thunderstorms over New Mexico. J. Geophys. Res. Atmos. 101: 20985–21005.
Sala O.E. and Lauenroth W.K. 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia 53: 301–304.
Schlesinger W.H., Ward T.J. and Anderson J. 2000. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. Biogeochemistry 49: 69–86.
Schwinning S. and Sala O.E. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141: 211–220.
Sellers W.D. and Hill R. 1974. Arizona Climate. University of Arizona Press, Tucson.
Sheppard P.R., Comrie A.C., Packin G.D., Angersbach K. and Hughes M. 2002. The climate of the US Southwest. Climate Res. 21: 219–238.

Smart D.R., Stark J.M. and Diego V. 1999. Resource limitations to nitric oxide emissions from a sagebrush-steppe ecosystem. Biogeochemistry 47: 63–86.

Solorzano L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

Stark J.M. and Firestone M.K. 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. Appl. Environ. Microbiol. 61: 218–221.

Thomsen B.W. and Schumann H.H. 1968. The Sycamore Creek Watershed, Maricopa County, Arizona. Geological Survey Water-Supply Paper, Vol. 1861, pp. 1–53.

Tongway D.J. and Ludwig J. 1997. The conservation of water and nutrients within landscapes. In: Ludwig J., Tongway D., Freudenberger D., Noble J. and Hodgkinson K. (eds), Landscape Ecology: Function and Management. CSIRO, Australia.

Ulrich B. 1983. A concept of forest ecosystem stability and of acid deposition as driving force for destabilization. In: Ulrich B. and Pankrath J. (eds), in Effects of Accumulation of Air Pollutants in Forest Ecosystems. D. Reidel Pub. Co, Hingham, MA pp. 1–29.

Van Gestel M., Merckx R. and Vlassak K. 1993. Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soil from different climates. Soil Biol. Biochem. 25: 109–123.

Virginia R.A., Jarrell W.M. and Franco-Vizcaino E. 1982. Direct measurement of denitrification in a *Prosopis* (mesquite) dominated Sonoran desert ecosystem. Oecologia 53: 120–122.

Walvoord M.A., Phillips F.M., Stonestrom D.A., Evans R.D., Hartsough P.C., Newman B.D. and Striegl R.G. 2003. A reservoir of nitrate beneath desert soils. Science 302: 1021–1024.

West N.E., Stark J.M., Johnson D.W., Abrams M.M., Wight J.R., Heggem D. and Peck S. 1994. Effects of climatic change on the edaphic features of arid and semiarid lands of western North America. Arid Soil Res. Rehab. 8: 307–351.

Zepp R.G., Callaghan T. and Erickson D. 1995. Effects of increased solar ultraviolet radiation on biogeochemical cycles. Ambio 24: 181–187.

Zepp R.G., Callaghan T.V. and Erickson D.J. 1998. Effects of enhanced solar ultraviolet radiation on biogeochemical cycles. J. Photochem. Photobiol. B: Biol. 46: 69–82.