Carbon and Nitrogen Losses by Surface Runoff following Changes in Vegetation

Noah G. Fierer* and Emmanuel J. Gabet

ABSTRACT

Rainfall simulation experiments were conducted on annual grassland and coastal sage scrub hillslopes to determine the quantities of C and N removed by surface runoff in sediment and solution. Undisturbed coastal sage scrub soils have very high infiltration capacities (>140 mm h^{-1}), preventing the generation of surface runoff. Trampling disturbance to the sage scrub plots dramatically reduced infiltration capacities, increasing the potential for surface runoff and associated nutrient loss. Infiltration capacities in the grassland plots (30–50 mm h^{-1}) were lower than in the sage scrub plots. Loss rates of dissolved C and N in surface runoff from grasslands were 0.5 and 0.025 mg m^{-2} s^{-1} respectively, with organic N accounting for more than 50% of the dissolved N. Total dissolved losses with simulated rainfall were higher than losses in simulations with just surface runoff, demonstrating the importance of raindrop impact in transferring solutes into the flow. Experimental data were incorporated into a numerical model of runoff and sediment transport to estimate hillslope-scale sediment-bound nutrient losses from grasslands. According to the model results, sediment-bound nutrient losses are sensitive to the density of vegetation cover and rainfall intensity. The model estimates annual losses in surface runoff of 0.2 and 0.02 g m^{-2} for sediment-bound C and N, respectively. The results of this study suggest that conversion of coastal sage scrub to annual grasslands increases hillslope nutrient losses and may affect stream water quality in the region.

The Mediterranean climate of the Central Coast of California commonly produces rainfall events that are episodic in nature and of relatively short duration with very high intensities. These rainstorms often generate substantial surface runoff with the potential for accompanying soil and nutrient losses (Wells, 1982). On an annual basis, the flux of dissolved and particulate nutrients from hillslopes by overland flow is often of greater magnitude than nutrient transport by subsurface flow (Owens et al., 1991; Viney, 2000). Surface runoff can remove large quantities of nutrients from the soil in both dissolved and sediment-bound forms (Gifford and Busby, 1973; Lowrance and Williams, 1988). However, the high degree of temporal and spatial variability in the distribution of surface runoff makes it difficult to conduct studies on nutrient transport by this process. An adequate understanding of nutrient transport by surface runoff is necessary if we want to understand the watershed biogeochemistry of the Central Coast region of California and similar areas.

The role of surface runoff in nutrient dynamics becomes particularly important in light of global climate change scenarios. Predictions from climate change models for continental North America include the "repackaging" of total annual rainfall into fewer, more intense rainfall events (Easterling, 1990; Houghton et al., 1990). These changes in rainfall patterns and intensities may result in greater amounts of overland flow and a concomitant increase in the quantities of C and N removed from hillslopes (Edwards and Owens, 1991). Over time, any increase in nutrient removal from soil may have long-term consequences for soil quality and ecosystem productivity (Pimentel and Kounang, 1998). Furthermore, an increase in hillslope nutrient losses may reduce the quality of regional stream waters (Crosson, 1985).

In the Central Coast region of California, the rate of nutrient transport by surface runoff may be strongly controlled by vegetation type. The hillslopes of the study area are generally vegetated by either coastal sage scrub or annual grassland communities, with little mixing of the vegetation types (Mooney, 1977). In recent years, land cover changes associated with these plant communities have become increasingly important. There has been considerable loss of sage scrub habitat due to the combined pressures of development, agriculture, and conversion to nonnative annual grasslands for grazing (Davis et al., 1994). Throughout California, the area of sage scrub habitat has been reduced to 10 to 15% of its former extent (Westman, 1981), but few studies have examined the potential impacts of this loss of sage scrub habitat on nutrient export from hillslopes.

Rainfall simulation experiments allow us to study the factors controlling the quantity and forms of nutrients lost from hillslopes via overland flow. With a rainfall simulator, we can apply rainfall with realistic raindrop sizes and velocities to small hillslope plots and quantify both the discharge from overland flow and the rates of sediment transported from the plot in the runoff. We can then estimate plot-level nutrient losses via overland flow by analyzing the nutrient contents of the runoff water and suspended sediments. By conducting a series of rainfall simulations with varied rainfall intensities on plots with different characteristics, we can begin to predict hillslope-scale nutrient losses under natural rainfall conditions.

Our primary objective was to determine the magnitude of solute and sediment C and N loss occurring by overland flow from coastal sage scrub and grassland hillslopes. We also looked at the short-term effects of cattle trampling on nutrient losses from sage scrub hillslopes. With plots of both vegetation types, we focused particular attention on hillslope sediment-bound nutrient losses, which are inherently difficult to measure (Lowrance and Williams, 1988) and often ignored in similar studies. Simulations were performed with and without raindrop impact to study the processes associated with nutrient transport by overland flow. The transfer of solutes from the soil to surface runoff were of specific interest because they are so poorly understood (Walton et al., 2000). The results from the rainfall simulations conducted on

Noah G. Fierer, Dep. of Ecology, Evolution, and Marine Biology, and Emmanuel J. Gabet, Dep. of Geological Sciences, Univ. of California, Santa Barbara, CA 93106. Received 5 Aug. 2001. *Corresponding author (fierer@lifesci.ucsb.edu).

Published in J. Environ. Qual. 31:1207–1213 (2002).

Table 1. Plot and rainfall characteristics of the rainfall simulation experiments.

Plot number	Vegetation type	Range of vegetation cover (C_v)	Hillslope angle	Range of applied rainfall intensities
			degrees	mm h^{-1}
1	Annual grass	0.94–0.88	10	60–120
2	Annual grass	0.73–0.71	17	60–120
3	Annual grass	0.70–0.57	14	60–120
4	Annual grass	0.98	4	50–60
5	Annual grass	0.82–0.66	17	50–70
6	Annual grass	0.70–0.56	13	40–120
7	Annual grass	0.74–0.64	9	70–110
8	Annual grass	0.64–0.34	13	70–120
9	Annual grass	0.86–0.46	5	70–130
10	Sage scrub	0	11	130–140
11	Sage scrub	0	11	120–130
12	Sage scrub	0.85–0.00	15	70–110
13	Sage scrub	0.80–0.00	16	130–140
14	Sage scrub	0	15	80–130
15	Sage scrub	0	25	80–110

annual grassland plots were incorporated into a numerical model of sediment removal by overland flow, allowing us to scale-up from the plot level and investigate the controls on sediment-bound nutrient losses for entire hillslopes.

METHODS

Study Area

All rainfall simulations were conducted on hillslopes located in Sedgwick Ranch, a University of California Natural Reserve in the Santa Ynez Valley near Santa Barbara, California. The soils are generally silty clay loams with smectitic-type clays; further details of the soils can be found in Gessler et al. (2000) and Shipman (1972).

Rainfall simulations were conducted on a total of nine annual grassland plots and six sage scrub plots (Table 1). Sage scrub habitats are dominated primarily by the perennials California sage (*Artemisia californica* Less.) and purple sage (*Salvia leucophylla* Greene). Annual grassland habitats are dominated by grasses such as brome grass (*Bromus* spp.) and Mediterranean barley (*Hordeum murinum* L.). The grassland plots, like most of the annual grasslands in the region, have been historically grazed by cattle. The coastal sage scrub plots were ungrazed. Hillslope angles in both sage scrub and grass plots ranged from 4 to 25 degrees (Table 1). Vegetation cover density on each plot was measured with a pin frame at 10-cm intervals.

The history of vegetation conversion in the study area is unclear, but the earliest aerial photos from Sedgwick Ranch suggest that the present distribution of vegetation was established before the 1930s. Hamilton (1997) speculates that most annual grasslands in the area were formerly dominated by coastal sage scrub. In addition, larger diameter root fragments typical of California sage have been found in soil pits excavated on annual grassland slopes in the study area (Gabet, unpublished data, 2000), indicating that these slopes were once covered by sage scrub vegetation.

Rainfall Simulations

We constructed a rainfall simulator capable of sprinkling a 6- × 2.5-m plot with realistic raindrop sizes and terminal velocities (Dunne et al., 1991; Gabet and Dunne, 2002). Water was obtained from a nearby deep well and transported to the site in a stainless steel tank. Applied rainfall intensities varied from 40 to 140 mm h^{-1} and simulated rain events were 20 to 60 min in duration. Surface runoff was collected in a trough on the downhill side of the plot, with discharge determined by timed volumetric sampling. A total of 49 rainfall simulations were conducted on grassland plots and 15 on sage scrub plots. These rainfall simulations were done during the dry season, July and August of 1999 and 2000. On each plot, the rainfall simulations were conducted consecutively within a one-week period. The infiltration capacities of the plots remained constant between rainfall simulations, regardless of antecedent soil moisture. Between rainfall simulations, vegetation cover was experimentally reduced on each plot by clipping vegetation and carefully removing ground litter. Two rainfall simulations were conducted on grassland plots during the wet season, February 2000, to determine if there were any seasonal effects on nutrient loss rates. No wet season rainfall simulations were conducted on sage scrub plots.

Flow Simulations

To investigate the importance of raindrop impact on the transfer of nutrients from the soil to the surface runoff as solutes, we performed nine flow simulations without rainfall on four grassland plots. Flow simulations were conducted by introducing water from the top of the plot through a perforated pipe installed at ground level. Discharges were adjusted to approximate discharges from the rainfall simulations.

Nutrient Analyses

The fluxes of C and N in sediments were determined by collecting 1-L runoff samples approximately every 3 to 5 min. These runoff samples were then filtered through a Whatman (Maidstone, UK) #1 paper filter and the sediment was weighed to quantify the sediment load suspended in each runoff sample. The sediments were analyzed for C and N content on a Fisons (Danvers, MA) NA1500 C/N analyzer. There were no measurable quantities of inorganic C in the sediment (as determined by acid digestion), so total C content was assumed to be equivalent to organic C content.

A second set of runoff samples (50 mL) was collected every 3 to 5 min for analysis of dissolved nutrients. These samples were kept on ice in the field and filtered with a Whatman #1 filter to remove particulates, and the flow-through was frozen for later analyses. The NH_4^+ and NO_3^- concentrations in the runoff were determined using a Lachat (Milwaukee, WI) autoanalyzer. Ammonium was analyzed using the diffusion method (Lachat Method #31-107-06-5-A) and NO_3^- was analyzed using Griess–Ilovsay reaction after Cd reduction (Lachat Method #12-107-04-1-B). To estimate dissolved organic C and N concentrations, the samples were digested in an autoclave using a persulfate digestion technique (A.P. Doyle, personal communication, 2000). The digested and undigested samples were then analyzed on a Lachat autoanalyzer for NO_3^- and CO_3^{2-}. The differences in total dissolved C and N concentrations between the digested and undigested samples represent the concentrations of dissolved organic C and N. Generally, less than 5% of total dissolved C was inorganic C, so all of the C measured after digestion was assumed to be organic C. The concentrations of nutrients removed in runoff were obtained by subtracting the nutrient concentrations in the applied water from that in collected runoff.

Runoff and Erosion Modeling

The numerical model, described in detail in Gabet and Dunne (2002), calculates the rate of sediment detachment from raindrop impact. With the field data, the model can be applied to calculate sediment-bound nutrient loss as the product of sediment detachment rate and the percent C and percent N in the sediment.

Rain power is the time derivative of the kinetic energy of rainfall and incorporates rainfall, ground cover, and hillslope angle so that:

$$R = [\rho i v^2 (1 - C_v)\cos\theta]/2 \qquad [1]$$

where R = rain power (W m^{-2}), ρ = density of water (1000 kg m^{-3}), i = rainfall intensity (m s^{-1}), v = raindrop velocity (m s^{-1}), C_v = fraction of plot area covered by vegetation, and θ = hillslope angle (degrees).

Sediment detachment rate can be expressed as a product of rain power and a dimensionless attenuation function that accounts for the dampening of raindrop impact by water on the surface (Gabet and Dunne, 2002):

$$\psi = \alpha R^{\beta} A(h,d) \qquad [2]$$

where ψ = sediment detachment rate (g m^{-2} s^{-1}), α and β = empirically determined constants, $A(\,)$ = attenuation function, h = water depth (mm), and d = raindrop diameter (mm).

Values for α and β were determined with the results from the rainfall simulations and Eq. [2] was found to accurately predict rates of sediment detachment (Gabet and Dunne, 2002). This formulation for calculating detachment rates is coupled to a flow-routing algorithm to calculate flow depths for the attenuation function and can predict sediment loss for entire lengths of hillslopes (Gabet and Dunne, 2002).

Statistical Analyses

The concentrations of dissolved nutrients did not change during steady state runoff so the average values of the collected runoff for each simulation were used for the analyses. All statistical analyses were conducted using Systat 10 for Windows 2000 (SPSS, 2000). Loss rates of nutrients with different experimental treatments or conditions were compared using two sample t tests. The assumptions of equal variance, as required for the t tests, were validated using F tests.

RESULTS AND DISCUSSION

Infiltration Capacities on Sage Scrub Hillslopes

Nutrient loss by overland flow only occurs on hillslopes where surface runoff can be generated. On hillslopes such as those studied here, overland flow occurs when the precipitation is greater than the infiltration capacity (i.e., Horton infiltration excess). Therefore, infiltration capacity is the first-order control on nutrient transport by surface runoff.

Despite applied rainfall intensities of 140 mm h^{-1}, no overland flow was generated on undisturbed sage scrub plots. Even after the removal of all vegetation and surface litter from the plots, rainfall simulations failed to yield any surface runoff. This indicates that the infiltration capacities of the soils in the sage are sufficiently high to absorb natural rainfall, preventing surface runoff and associated nutrient losses. Although no wet season rainfall simulations were conducted on sage scrub plots, there is no evidence for surface runoff during even the most intense winter rainstorms.

Careful inspection of the mineral soil under coastal sage scrub vegetation reveals a laterally extensive and continuous 1- to 2-cm-thick biotic crust, composed primarily of fine roots, moss, and lichens. We hypothesize that the high porosity of this biotic crust layer is responsible for the high infiltration rates in coastal sage scrub soils. Biotic crusts of similar morphology are common in other semiarid sagebrush habitats (Johansen, 1993). West (1990) and Eldridge (1998) have shown that highly porous biotic crusts can dramatically reduce surface runoff volumes by increasing infiltration rates.

The conversion of sage to grasslands for cattle grazing is common in the region, so the effect of trampling on the biotic crust is critical to our understanding of how grazing may affect surface runoff generation and associated nutrient loss. To investigate this, we conducted rainfall simulations on two plots before and after disturbance to the surface soil by trampling. Due to the difficulties inherent in persuading cattle to walk around inside a small plot, we mimicked cattle trampling by affixing cow hooves to the feet of a 90-kg human (carrying an additional 30 kg of weight) who then walked within the confines of the plot for approximately 15 min. We were only able to simulate a maximum trampling pressure of 120 kg hoof^{-1}, whereas, with an average cow weight of 600 kg, the maximum pressure would be 200 kg hoof^{-1}.

The effect of the trampling was considerable. Infiltration capacities decreased from more than 140 mm h^{-1} to a maximum of 60 mm h^{-1}. This dramatic change was most likely due to destruction of the biotic crust and compaction of the top layer of soil. This is supported by an increase in bulk densities of soil samples taken from the top 1 to 2 cm of the soil before and after trampling. Pretrampling samples had bulk densities of 0.62 g cm^{-3} (SE = 0.03) and posttrampling samples had bulk densities of 1.16 g cm^{-3} (SE = 0.23). A similar decrease in soil infiltration capacities after disturbance to biotic crusts has been observed elsewhere (Eldridge, 1998; Belnap, 1995). However, other studies have found no discernible effect of biotic crust cover on soil hydraulic properties (Eldridge et al., 1997; Williams et al., 1999). Regional differences in soil characteristics and crust composition make it difficult to develop a general theory relating biotic crust cover to soil hydrological properties.

Infiltration Capacities on Grassland Hillslopes

Infiltration capacities on the grassland plots were much lower than for sage scrub plots, generally ranging from 30 to 50 mm h^{-1} during the summer dry seasons when the rainfall simulations were conducted for this study. Infiltration capacities were measured on a few grassland plots during the winter and were much lower, ranging from 5 to 10 mm h^{-1}. This substantial seasonal difference is probably due to the swelling of the smectitic clays during the wet winter months. Since approximately 10% of the recorded 1-h rainfall intensities are greater than 5 mm h^{-1} (Figueroa Mountain Ranger Station, National Oceanic and Atmospheric Administration [NOAA], 5 km from site), the generation of overland flow on these hillslopes during the winter is infrequent, but not rare.

Rainfall Intensity and Loss Rates of Dissolved Nutrients

On grassland plots there was no systematic variation in rates of dissolved nutrient losses with respect to hillslope vegetation cover or slope ($r^2 < 0.2$ in all cases, for cover and slope versus NH_4^+, NO_3^-, organic N, and organic C losses). We expected a relationship between rainfall intensity and rates of dissolved nutrient losses since studies have shown that raindrop impact is important in mixing surface runoff with pore water (Ahuja, 1990; Ahuja and Lehman, 1983). Surprisingly, only NO_3^- loss rates (mg N m^{-2} s^{-1}) were influenced by rainfall intensity (Fig. 1) and they can be estimated for different rainfall intensities (i, mm h^{-1}) with:

$$NO_3^- \text{ loss rate} = 10^{-6} i^2 \quad [3]$$

Comparisons of the rates of dissolved nutrient losses with the rainfall simulations and the flow simulations (Fig. 2) conducted on the same plots show that NO_3^-, organic C, and organic N losses are significantly higher with raindrop impact ($P < 0.05$). Rates of NH_4^+ loss are much lower and not affected by raindrop impact ($P = 0.6$). These results suggest that a portion of the dissolved nutrients enter the flow through turbulent mixing of pore water and surface water caused by raindrop impact. This agrees well with laboratory experiments performed by Ahuja and Lehman (1983) and Ahuja (1990), but conflicts with the insensitivity of dissolved losses to rainfall intensity (with the exception of NO_3^-). The simulator reproduces natural rainfall characteristics so that higher intensities are associated with larger raindrops and greater impact velocities. Higher intensities, therefore, would be expected to increase rates of turbulent mixing of pore water and surface water by drop impact and lead to higher rates of dissolved losses. These apparently contradictory results suggest that, with the exception of NO_3^-, any rainfall intensity may cause sufficient turbulent mixing and that the diffusion of solutes from the soil to the pore water is a rate limiting step.

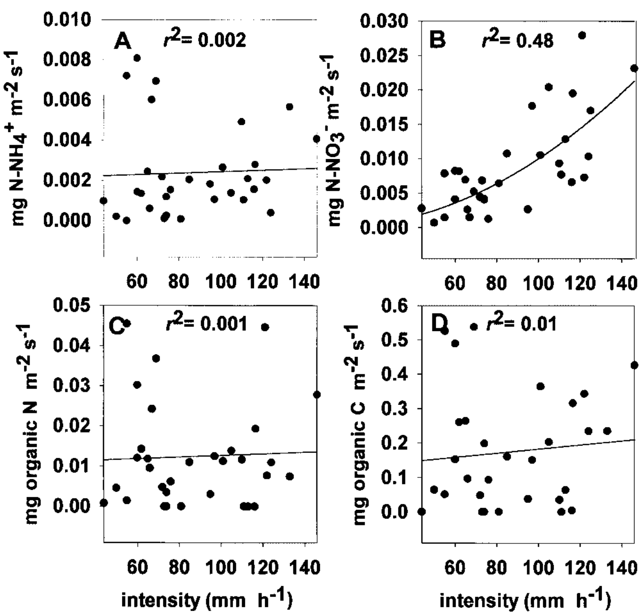

Fig. 1. Relationships between loss rates of dissolved nutrients and rainfall intensities for all annual grassland rainfall simulations. (*A*) NH_4^+, (*B*) NO_3^-, (*C*) solute organic N, (*D*) solute organic C. The R^2 values are from best fit regressions using power functions. Only the NO_3^- data showed a significant ($P < 0.05$) relationship with intensity.

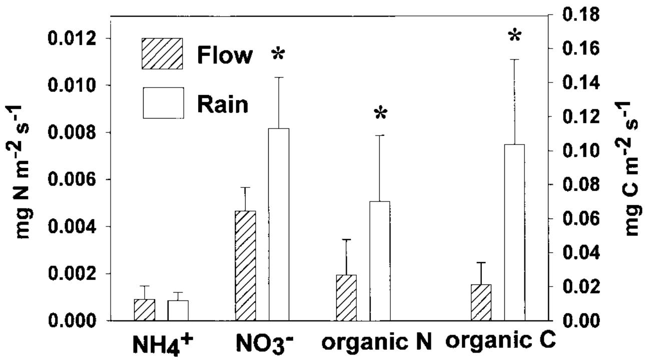

Fig. 2. Comparison of loss rates of dissolved nutrients in simulations with and without raindrop impact on a series of paired plots. Note separate axes for N and C data. * = loss rates are significantly different ($P < 0.05$) between rain and flow simulations. Error bars represent one standard error.

Unlike NH_4^+, organic C, and organic N, the diffusion of NO_3^- from the soil to the pore water may not be a rate limiting step because the anionic nature of NO_3^- makes it relatively mobile in clay-rich soils (Evangelou, 1998). The importance of rainfall intensity in NO_3^- transport suggests that rainfall simulation experiments may overestimate NO_3^- losses in runoff. The high rainfall intensities used in this and other rainfall simulation studies (60–120 mm h^{-1} [Barisas et al., 1978], 140 mm h^{-1} [Schlesinger et al., 1999], for example) may lead to overestimations of NO_3^- losses in surface runoff during natural rainstorms. However, using Eq. [1] and regional rainfall data (Figueroa Mountain Ranger Station), we can estimate that NO_3^- losses would be approximately 25 to 35% lower with natural intensities compared with the simulated rainfall intensities.

Vegetation Type and Dissolved Nutrient Losses

The average loss rates for dissolved N and C for the two trampled sage plots and the nine grassland plots are shown in Fig. 3. The trampled sage plots lost significantly more organic C ($P = 0.02$), but substantially less NO_3^-

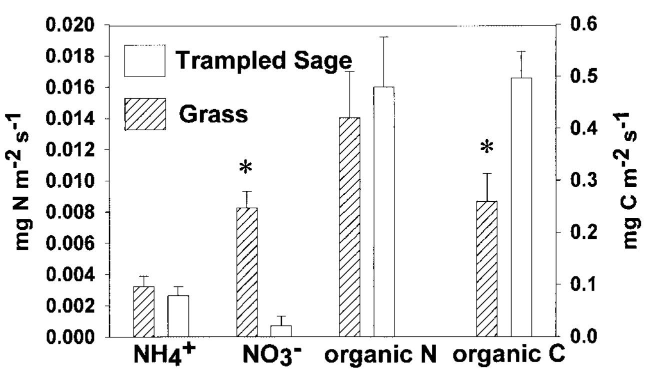

Fig. 3. Nutrient loss rates in solute from grassland and trampled sage scrub plots. Note separate axes for the N and C data. * = significant difference ($P < 0.05$) in the nutrient loss rate between sage and grass plots. Error bars represent one standard error.

($P = 0.001$) than the grassland plots. Rainfall simulations were conducted immediately after trampling, so the measured organic C losses may represent an initial flush of organic C into runoff, not steady-state conditions that would develop after a season of rainstorms. Any long-term organic C removal by runoff from coastal sage scrub plots is likely to be of lower magnitude. Compared with the grassland plots, the plots under coastal sage scrub lost relatively little N as NO_3^-, possibly because nitrification rates in sage scrub soils are lower than in grassland soils (Dornelles and Schimel, 2000).

Approximately half of the total dissolved N transported in runoff from grassland hillslopes was in organic forms. This study is similar to others that have found that a substantial fraction of the N exported from watersheds is in dissolved organic forms (Hedin et al., 1995; McDowell and Asbury, 1994). On average, 75% of the dissolved inorganic N measured in runoff was in the form of NO_3^- (Fig. 2). The high cation exchange capacity of these soils (Gessler et al., 2000) presumably retards the movement of positively charged ions, such as NH_4^+, from the soil surface.

Sediment-Bound Nutrients

Loss rates of sediment during flow simulations were several orders of magnitude less than during rainfall simulations, indicating that raindrop impact is essential for soil particle detachment (Gabet and Dunne, 2002). For this reason, we only present sediment-bound nutrient loss data from the rainfall simulations.

There was little variability between rainfall simulations with respect to the percentages of C and N in the sediment collected, so values were averaged for all rainfall simulations according to vegetation type. The percentages of C and N in the trampled sage plots were 13.4 (SE = 1.25) and 0.9 (SE = 0.08), respectively. The percentages for the grassland plots were lower, 6.4 (SE = 0.07) and 0.7 (SE = 0.01) for C and N, respectively. The higher percentages of C and N in sediment from the trampled sage scrub plots are probably due to the large amounts of biotic crust and other organic detritus broken up by the trampling. As mentioned above, this probably represents an initial flush of organic matter and subsequent surface runoff events would transport sediment with lower organic matter concentrations.

The data presented above give us an estimate of the proportional losses of C and N forms from plots; by incorporating sediment loss results from the plot experiments into a numerical model we can predict rates of sediment-bound nutrient losses for an entire hillslope. The sediment loss data are only useful when incorporated into a model since the applied rainfall intensities were generally higher than natural rainfall intensities, resulting in unnaturally high sediment detachment rates. The model was only applied to annual grassland plots because overland flow does not appear to occur on undisturbed hillslopes vegetated by coastal sage scrub. The processes that determine the concentrations of dissolved load in the runoff are poorly understood, therefore, no equivalent model was used to predict rates of dissolved losses.

Table 2. Values of model parameters. Typical hillslope lengths at Sedgwick Reserve are 100 m long and, for simplicity, a planar hillslope is assumed. An entire year of rainstorms recorded by a local weather station was used as input for the Annual model run. Vegetation cover was held constant for the Annual run with the assumption that grazing intensity is the dominant control on grass cover.

Parameter	Grazing intensity	Rainfall intensity	Annual
Hillslope length, m	100	100	100
Hillslope angle, degrees	15	15	15
Infiltration capacity, mm h^{-1}	5	5	5
Vegetation cover (C_v)	0–1†	0.6	0.6
Rainfall intensity, mm h^{-1}	15	5–60†	Varied

† Indicates range of values used in series of model runs.

We did three sets of modeling experiments to: (i) investigate the effects of land-use strategies on nutrient transport, (ii) investigate the effect of climate on nutrient transport, and (iii) estimate the annual loss of sediment-bound C and N. Grazing or other land-use changes directly affect sediment and associated nutrient loss by controlling the density of vegetation cover (C_v in Eq. [1]). A series of model simulations was performed with a range of values for C_v, while holding all other parameters constant. Sediment-bound nutrient losses are also sensitive to rainfall intensity (i in Eq. [1]) so, to predict loss rates of nutrients under various rainfall intensities, a second series of model simulations was performed by varying rainfall intensity with all other parameters held constant. Finally, the model was run to simulate an entire year of rainstorms based on regional precipitation records (Figueroa Mountain Ranger Station). For all model runs, we assume that the percentages of C and N in the sediment are constant. Parameter values for the runs are listed in Table 2.

Figure 4 shows the model estimates of C and N loss in sediment by surface runoff over a range of vegetation cover densities. As expected from Eq. [1], decreases in vegetation cover result in greater losses of sediment-bound nutrients. Likewise, sediment C and N loss from

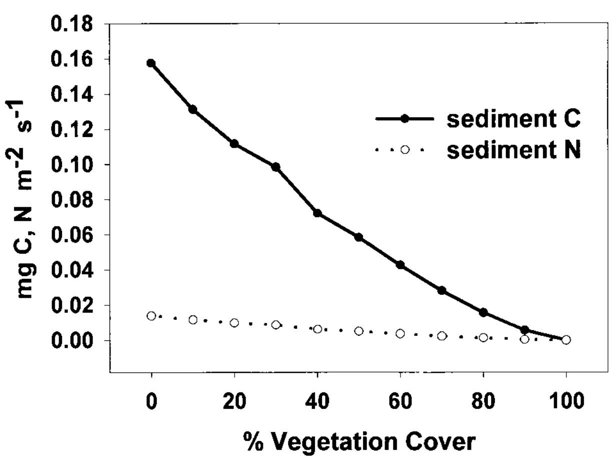

Fig. 4. Model estimates of sediment C and N loss in surface runoff from annual grassland hillslopes with changes in vegetation cover. Rainfall intensity = 15 mm h^{-1}.

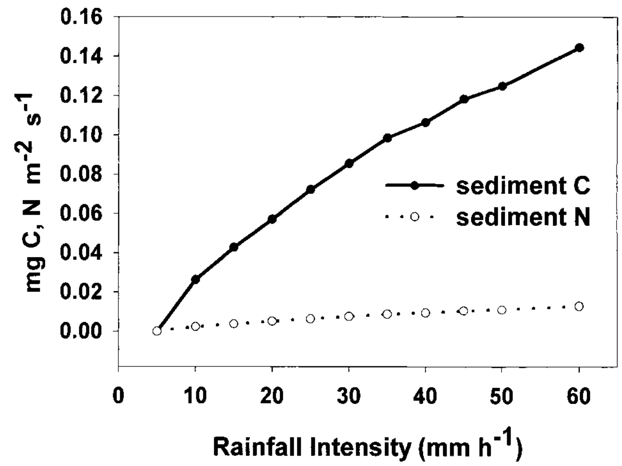

Fig. 5. Model estimates of sediment C and N loss in surface runoff from annual grassland hillslopes with changes in rainfall intensity. Vegetation cover = 0.6.

hillslopes is directly related to rainfall intensity (Fig. 5). These model results imply that regional stream water quality may be altered by the predicted increases in average rainstorm intensities in the future (Easterling, 1990; Houghton et al., 1990).

On an annual basis, the model predicts average sediment-bound nutrient losses of 0.2 g m^{-2} yr^{-1} of C and 0.02 g m^{-2} yr^{-1} of N. Over a five-year period, Castillo et al. (1997) quantified the amount of sediment lost in surface runoff from a natural, undisturbed plot in a semi-arid region of Spain. The climate and vegetation of this area are similar to those found in the Central Coast of California. If one assumes the percentages of C and N in the soil (as reported in Castillo et al., 1997) are the same as that in their collected sediments, we can calculate average rates of sediment-bound nutrient losses from their plot of 0.53 g C m^{-2} yr^{-1} and 0.036 g N m^{-2} yr^{-1}. These estimates are higher but of the same order of magnitude as our model predictions.

Seasonal Considerations

In the study region, the majority of large rainstorms occur in the winter when soils are generally moist from previous rainstorms. The majority of the data used in this study were obtained from rainfall simulations conducted during the summer, on soils that had received no antecedent rainfall for at least two months. To determine if winter rainfall simulations would yield different estimates for hillslope nutrient losses compared with summer simulations, we conducted a smaller number of rainfall simulations in the winter on grassland plots identical to those described above.

The percentages of C and N in suspended sediment and the loss rates of sediment were not statistically different between the summer and winter rainfall simulations ($P = 0.6$ and 0.8 for C and N, respectively). Therefore, our estimates of sediment-bound nutrient losses are applicable to winter rainstorm events. In contrast, there was a seasonal effect on dissolved nutrient losses. The NH_4^+, NO_3^-, dissolved organic N, and dissolved organic C loss rates were approximately 50% lower ($P <$ 0.05 in all cases) in the winter compared with the summer (data not shown). High dissolved organic C and N concentrations may be associated with the first rainfall events of the season (Fisher and Grimm, 1985), which would explain the large dissolved organic nutrient losses observed with the summer rainfall simulations. Extractable NH_4^+ and NO_3^- levels in the grassland soils are generally 75% lower in the winter than in the summer (Fierer, unpublished data, 2001), a change reflected in the seasonal differences in the dissolved losses of NH_4^+ and NO_3^- in runoff.

Therefore, by conducting the rainfall simulations during the dry season, we may have overestimated dissolved N and C losses during winter storms. However, our estimates of losses of dissolved nutrients by overland flow are applicable to the first rains of the season or summer thunderstorms. In winter conditions, sediment-bound nutrient losses would probably constitute a larger proportion of total nutrient losses. The dominance of sediment-bound nutrient losses over solute losses has been noted in other studies (Barisas et al., 1978; Lowrance and Williams, 1988).

CONCLUSION

In the Central Coast region of California, hillslope vegetation type has a strong effect on the loss rates of C and N in surface runoff. We performed rainfall simulation experiments to investigate the processes involved in runoff generation and the associated nutrient losses. Even with very high rainfall intensities, the simulations failed to generate any surface runoff on sage scrub plots. However, after light trampling, infiltration capacities were lowered enough to generate surface runoff. Results from the grassland plots were incorporated into a hillslope-scale runoff and erosion model to estimate sediment-bound nutrient losses under natural conditions. The model results show that for annual grasslands, a decrease in vegetation cover or increase in rainfall intensities (as predicted by climate change models) could increase loss rates of soil nutrients and decrease regional stream water quality. The historical loss of coastal sage scrub habitat and the subsequent conversion to annual grasslands have resulted in an increase in soil C and N loss from hillslopes in the region.

ACKNOWLEDGMENTS

The rainfall experiments were labor intensive and would not have been possible without the help of J. Wikings, C. Zelding, T. Marden, D. Ahn, and N. Dooling. We are also grateful for the assistance we received from the staff at the Sedgwick Natural Reserve, including M. Williams and R. Skillin. Supplies and salary for N. Fierer were supported by a U.C. Natural Reserves Mathias grant. Supplies and salary for E. Gabet were supported by a U.C. Regents Fellowship, U.C. Water Resources Grant UCAL-W-917, and a Mathias Grant. Computer modeling was supported in part by National Science Foundation Grant CDA96-01954 and by Silicon Graphics Inc. We thank O. Chadwick and T. Dunne for reviewing an earlier version of the manuscript and two anonymous reviewers for their helpful comments.

REFERENCES

Ahuja, L.R. 1990. Modeling soluble chemical transfer to runoff with rainfall impact as a diffusion process. Soil Sci. Soc. Am. J. 54: 312–321.

Ahuja, L.R., and O.R. Lehman. 1983. The extent and nature of rainfall–soil interaction in the release of soluble chemicals to runoff. J. Environ. Qual. 12:34–40.

Barisas, S., J. Baker, H. Johnson, and J. Laflen. 1978. Effect of tillage systems on runoff losses of nutrients, a rainfall simulation study. Trans. ASAE 21:893–897.

Belnap, J. 1995. Surface disturbances: Their role in accelerating desertification. Environ. Monit. Assess. 37:39–57.

Castillo, V.M., M. Martinez-Mena, and J. Albaladejo. 1997. Runoff and soil loss response to vegetation removal in a semiarid environment. Soil Sci. Soc. Am. J. 61:1116–1121.

Crosson, P. 1985. Impact of erosion on land productivity and water quality in the United States. p. 217–236. *In* S. El-Swaify et al. (ed.) Soil erosion and conservation. Soil Conserv. Soc. of Am., Ankeny, IA.

Davis, F.W., P.A. Stine, and D.M. Stoms. 1994. Distribution and conservation status of coastal sage scrub in southwestern California. J. Vegetation Sci. 5:743–756.

Dornelles, D.S., and J.P. Schimel. 2000. Microbial activity and nitrogen dynamics in a California annual grassland, coastal sage scrub and mixed oak woodland community. *In* Abstracts, 2000 Annual Meeting, Ecological Soc. of Am., Snowbird, UT. 6–10 Aug. 2000. Ecological Soc. of Am., Washington DC.

Dunne, T., W. Zhang, and B. Aubry. 1991. Effects of rainfall, vegetation, and microtopography on infiltration and runoff. Water Resour. Res. 27:2271–2285.

Easterling, W. 1990. Climate trends and prospects. p. 32–55. *In* R. Sampson and D. Hair (ed.) Natural resources for the 21st century. Island Press, Washington, DC.

Edwards, W., and L. Owens. 1991. Large storm effects on total soil erosion. J. Soil Water Conserv. 46:75–78.

Eldridge, D.J. 1998. Trampling of microphytic crusts on calcareous soils, and its impact on erosion under rain-impacted flow. Catena 33:221–239.

Eldridge, D.J., M.E. Tozier, and S. Slangen. 1997. Soil hydrology is independent of microphytic crust cover: Further evidence from a wooded semiarid Australian rangeland. Arid Soil Res. Rehabilitation 11:113–126.

Evangelou, V. 1998. Environmental soil and water chemistry. John Wiley & Sons, New York.

Fisher, S., and N. Grimm. 1985. Hydrologic and material budgets for a small Sonoran desert watershed during three consecutive cloudburst events. J. Arid Environ. 9:105–118.

Gabet, E., and T. Dunne. 2002. Sediment detachment by rain power. Water Resour. Res. (in press).

Gessler, P.E., O.A. Chadwick, F. Chamran, L. Althouse, and K. Holmes. 2000. Modeling soil-landscape and ecosystem properties using terrain attributes. Soil Sci. Soc. Am. J. 64:2046–2056.

Gifford, G., and F. Busby. 1973. Loss of particulate organic materials from semiarid watersheds as a result of extreme hydrologic events. Water Resour. Res. 9:1443–1449.

Hamilton, J.G. 1997. Changing perceptions of pre-European grasslands in California. Madrono 44:311–333.

Hedin, L.O., J.J. Armesto, and A.H. Johnson. 1995. Patterns of nutrient loss from unpolluted, old-growth temperate forests: Evaluation of biogeochemical theory. Ecology 76:493–509.

Houghton, J., G. Jenkins, and J. Ephraums. 1990. Climate change. The IPCC Scientific Assessment. World Meteorological Organ. Cambridge Univ. Press, Cambridge.

Johansen, J. 1993. Cryptogamic crusts of semiarid and arid lands of North America. J. Phycology 29:140–147.

Lowrance, R., and R. Williams. 1988. Carbon movement in runoff and erosion under simulated rainfall conditions. Soil Sci. Soc. Am. J. 52:1445–1448.

McDowell, W.H., and C.E. Asbury. 1994. Export of carbon, nitrogen and major ions from three tropical montane watersheds. Limnol. Oceanogr. 39:111–125.

Mooney, H. 1977. Southern coastal scrub. p. 471–487. *In* M. Barbour and J. Major (ed.) Terrestrial vegetation of California. Univ. of California, Davis.

Owens, L., W. Edwards, and R. Keuren. 1991. Baseflow and stormflow transport of nutrients from mixed agricultural watersheds. J. Environ. Qual. 20:407–414.

Pimentel, D., and N. Kounang. 1998. Ecology of soil erosion in ecosystems. Ecosystems 1:416–426.

Schlesinger, W., A. Abrahams, A. Parsons, and J. Wainwright. 1999. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: I. rainfall simulation experiments. Biogeochemistry 45:21–34.

Shipman, G.E. 1972. Soil survey of Santa Barbara County. USDA Soil Conserv. Serv., Washington, DC.

SPSS. 2000. Systat for Windows. Release 10. SPSS, Evanston, IL.

Viney, N. 2000. A conceptual model of nutrient mobilisation and transport applicable at large catchment scales. J. Hydrol. (Amsterdam) 240:23–44.

Walton, R.S., R.E. Volker, K.L. Bristow, and K.R.J. Smettem. 2000. Solute transport by surface runoff from low-angle slopes: Theory and application. Hydrol. Processes 14:1139–1158.

Wells, W.G. 1982. Hydrology of Mediterranean-type ecosystems: A summary and synthesis. p. 426–430. *In* C. Conrad and W. Oechel (ed.) Proc. of the Symp. on Dynamics and Management of Mediterranean-Type Ecosystems. Pacific Southwest Forest and Range Exp. Stn., Berkeley, CA.

West, N. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Adv. Ecol. Res. 20:180–208.

Westman, W. 1981. Diversity relations and succession in Californian coastal sage scrub. Ecology 62:170–184.

Williams, J.D., J.P. Dobrowolski, and N.E. West. 1999. Microbiotic crust influence on unsaturated hydraulic conductivity. Arid Soil Res. Rehabilitation 13:145–154.