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Fertilization of the desert soil by rock-eating snails

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PLANT productivity in deserts can be nitrogen-limited. Nitrogen inputs are often low, soil nitrogen pools small, and losses from runoff, erosion, volatilization and denitrification, can be high[1–6]. We have now found an unusual, important source of soil nitrogen in the Central Negev Highlands of Israel, a limestone rock desert with patches of soil (Fig. 1). Snails feed on endolithic lichens that grow within the rock, ingesting both rock and lichens[7,8], and depositing their faeces on the soil under the rocks. Snails transfer between 22–27 mg nitrogen per m^2 per year to soil, which constitutes about 11% of total soil nitrogen inputs, at least 18% of net soil inputs, and a minimum of 27% of the nitrogen annually accumulated by endolithic lichens from dust. The substantial contribution of snails to the nitrogen cycle is probably important for higher plant production.

Three snail species in the Negev, *Euchondrus albulus* Mousson, *E. desertorum* Roch and *E. ramonensis* Granot, cut feeding trails in rocks[7,8], converting rock to soil at a rate between 69.5–110.4 g per m^2 per year—equivalent to that due to wind-borne dust deposition[7]. Snails feed on the rocks when dew is present (night and early morning), sheltering under the rocks during the day, and depositing their faeces on the soil before feeding again[7]. We measured faecal production and nitrogen content of naturally occurring densities of the dominant snail species, *E. albulus*[7], in the laboratory and field, under conditions in which the number of days of natural and/or artificial dew varied (Table 1).

The number of dew days was a significant factor determining faecal production per snail per day in two experiments (Table 1, A1). When data were expressed as faecal production per snail per dew day, there was no significant difference in faecal production between the two experiments (Table 1, B1), or between laboratory and field treatments in experiment 1 (Table 1, B2). Laboratory values were significantly greater than the two field values in experiment 2 (Table 1, B3). However, none of the field treatments in either experiment differed significantly from one another, with faecal production values varying by about 12% (Table 1, B4), a remarkably consistent faecal production rate.

Faecal nitrogen ranged between 0.40–0.52% dry weight (DW) (Table 1), and was not significantly different between laboratory and field treatments (Table 1, C1), was not related to the number of dew days (Table 1, C2), but was significantly greater, by 0.1% DW, in experiment 2, compared with experiment 1 (Table 1, C3). Faecal nitrogen was 0.06% DW lower than that of the endolithic lichen–rock layer, indicating that some portion of the ingested nitrogen was being retained for snail growth and maintenance (Table 1, D1). Nitrogen content of the rock interior was significantly lower than that of either the rock–lichen surface layer or snail faeces (Table 1, E1, E2). Fossil nitrogen in the upper surface of the sedimentary limestone contributed less than 10% of the nitrogen of the rock–endolithic lichen layer.

Snails therefore removed nitrogen from the rock–endolithic lichens, excreting a substantial portion of this nitrogen in their faeces. Field estimates of soil nitrogen input due to *E. albulus* ranged from 21.9–26.9 (average 24.3) mg nitrogen per m^2 per year (Table 1). This estimate does not include inputs from other species of rock-eating snails, one of which (*E. desertorum*) is locally abundant[7].

Estimates of the relative importance of snail-induced nitrogen cycling were made by comparing these data with the soil budget of nitrogen in the same watersheds[5,6,9] (Fig. 2). Snail faeces are estimated to represent 11% of total soil nitrogen input, and at least 18% of net soil nitrogen input. The latter estimate is

FIG. 1 The rocky Central Negev Desert Highlands, Israel, showing higher plants growing in patches of soil adjacent to limestone rock. The two substrates support different plant communities. Endolithic lichens live within the upper few mm of the limestone rocks, which cover 70% of the desert area; they are the dominant cryptogamic plants in this desert and have a low standing crop[22,23]. The soil patches, about 30% of the desert area, support a relatively large biomass of higher plants[10,11]. The endolithic lichen–rock layer contains about 0.5% nitrogen, which is taken up by the lichens from dust deposition[9]. Dew forms on rocks, providing the moisture for nitrogen uptake from dust[24]. Snails of the genus *Euchondrus* ingest the endolithic lichens and the rock within which they grow[7,8]. Snail faeces are deposited on the soil under the rocks, where the roots of higher plants grow. Nitrogen input to the soil from snail faeces is a principal component of the nitrogen cycle of this desert. (Photograph, C.G.J.).

TABLE 1 Transfer of nitrogen to soil by snails

Experiment	Treatment	Lab. or field	No. of dew days	Type of dew	Faecal production per day (mg DW faeces snail^{-1} day^{-1}) (s.e.m.)	Faecal production per dew day (mg DW faeces snail^{-1} dew day^{-1}) (s.e.m.)	Faecal nitrogen (% DW) (s.e.m.= analytical error)	Estimated soil nitrogen input (mg total nitrogen m^{-2} year^{-1})
1	1	Field	8	Natural and artificial	1.02 (0.11)	1.28 (0.14)	0.40 (0.01)	22.4
1	2	Field	4	Natural	0.50 (0.05)	1.26 (0.13)	0.40 (0.01)	21.9
1	3	Lab.	8	Artificial	1.18 (0.12)	1.48 (0.15)	0.40 (0.01)	26.0
2	1	Field	8	Natural and artificial	0.96 (0.07)	1.20 (0.09)	0.51 (0.03)	26.9
2	2	Field	1	Natural	0.11 (0.01)	1.13 (0.14)	0.52 (0.01)	26.0
2	3	Lab.	8	Artificial	1.49 (0.11)	1.86 (0.14)	0.47 (0.01)	38.3
2	4	Lab.	0	None	0.08 (0.03)	—	0.49 (0.02)	—

Faecal production (mean mg DW faeces per snail per day and mean mg DW faeces per snail per dew day, ±s.e.m.), faecal nitrogen content (mean % DW total nitrogen ±s.e.m. of 3 subsamples from pooled faeces by treatment, s.e.m. is analytical error) and estimated annual nitrogen input to soil (mg total nitrogen per m^2 per year) due to *E. albulus* feeding on endolithic lichens. Ten replicate rocks (mean area ±s.e.m. = 71.4 ± 3.2 cm^2) for each treatment in each experiment were collected in November and December, 1989, at the time of seasonal snail activity (September–June[7]), from Ramat Avdat, Central Negev Highlands. Five snails of similar weight (mean fresh weight + shell ± s.e.m. = 339.8 ± 5.1 mg snail^{-1}), collected at the same time and place as rocks, were added to each rock. The snail density per rock was that found in the field[7]. Each rock with snails was placed in a 17.5 × 28.5 × 8.5 cm, pre-washed plastic arena with a mesh cover. Two experiments (1, 2) were carried out, each with simultaneous runs over 10 days in the laboratory and the field. Experiments were carried out at ambient conditions (Laboratory: 10–20 °C range, 15 °C mean; 70% relative humidity (RH) mean, 52–98% RH range. Field: 5–27 °C range, 14 °C mean; 72% RH mean, 44–100% RH range). Naturally occurring dewfall in the field was used, recorded at the local weather station, either without (experiment 1, treatment 2–4 dew days; experiment 2, treatment 1–2 dew day) or with supplements of artificial dew (experiment 1, treatment 1; experiment 2, treatment 1—both 8 dew days). Artificial dew supplements consisted of 1.5 ml deionized water sprinkled evenly over the rock surface twice daily at 09:00 and 14:00. The same artificial dew regime was used in the laboratory (experiment 1, treatment 3–8 dew days; experiment 2, treatment 3–8 dew days) during the 10-day experiments, dew being allowed to evaporate under the ambient conditions. In experiment 2, treatment 4, ambient relative humidity only (mean 70%; 0 dew days) was used. Faeces were collected from each replicate arena at the end of the experiments, dried and weighed. Faeces from each treatment were then pooled across replicates, homogenized, and 3 subsamples (4–12 mg) withdrawn and analysed for total N by elemental analysis (Carlo-Erba CNS, ±0.01% DW) using acetonitrile as a calibration standard. Nitrogen content of the endolithic lichen–rock layer consumed by snails was estimated by removing the entire top 3 mm of 4 rocks of the same size as above, collected in the same area, using an engraving tool to simulate snail feeding, followed by elemental analysis of each replicate rock. Nitrogen content of the rock interior (sedimentary N) was determined by splitting rocks vertically in half and sampling the interior below the endolithic lichens, 1 cm down from the surface, followed by elemental analysis of each replicate rock (n = 5 rocks of the same size as above, collected in the same area). Estimates of total nitrogen input to soil were obtained by multiplying mg DW faeces per snail per dew day by the faecal nitrogen content for each treatment, and multiplying the resulting value by field snail density (21 per m^2) and average number of dew days per year (210) based on previous data[7]. Estimates of the importance of snail faecal nitrogen (Fig. 2) used data from field treatments only.

Statistical comparisons: **A. Faecal production per day:** (1) Main effect, dew days (all experiments and treatments). 1-way ANOVA: d.f. = 3, F = 59.23, P < 0.0001. Scheffe F a posteriori comparisons and P values: 0 vs 1 dew day, F = 0.021, P > 0.05; not significant (NS); 0 vs 4 dew days, F = 3.33, P < 0.05; 0 vs 8 dew days, F = 34.84, P < 0.05; 1 vs 4 dew days, F = 2826, P < 0.05, 1 vs 8 dew days, F = 32.71, P < 0.05; 4 vs 8 dew days, F = 12.91, P < 0.05. **B. Faecal production per dew day:** (1) Main effect, experiment (excluding experiment 2, treatment 4–0 dew days). 1-way ANOVA: d.f. = 1, F = 0.28, P = 0.60, NS. (2) Main effect, lab. vs field, experiment 1. 1-way ANOVA: d.f. = 2, F = 0.77, P = 0.47, NS. (3) Main effect, lab. vs field, experiment 2 (excluding lab. treatment 4–0 dew days). 1-way ANOVA: d.f. = 2, F = 10.30, P < 0.005. treatment 1 (field) vs treatment 3 (lab.): Scheffe F = 6.93, P < 0.05. treatment 2 (field) vs treatment 3 (lab.): Scheffe F = 8.44, P < 0.05; treatment 1 (field) vs treatment 2 (field): Scheffe F = 0.07, NS at P = 0.05. (4) Main effect, field (experiments 1 and 2). 1-way ANOVA: d.f. = 1, F = 0.13, P = 0.72, NS. **C. Faecal nitrogen:** (1) Main effect, lab. vs field (experiments 1 and 2). 1-way ANOVA: d.f. = 1, F = 0.02, P = 0.90, NS. (2) Faecal nitrogen % DW vs number of dew days (experiments 1 and 2). Regression: d.f. = 6, r^2 = 0.17, F = 1.04, P = 0.36, NS. (3) Main effect, experiment. 1-way ANOVA: d.f. = 1, F = 44.56, P = 0.0011. Mean % DW faecal nitrogen ± s.e.m.: experiment 1 = 0.40 ± 0.001; experiment 2 = 0.50 ± 0.013. **D. Rock–endolithic lichen layer nitrogen:** (1) Compared to faecal nitrogen. Mean rock–endolithic layer total nitrogen, % DW ± s.e.m. = 0.51 ± 0.01, n = 4. Mean faecal nitrogen, % DW ± s.e.m., across experiments and treatments = 0.45 ± 0.02, n = 7. 1-way ANOVA: d.f. = 1, F = 3.665, P = 0.09. **E. Rock interior nitrogen:** (1) Compared to rock–endolithic lichen layer nitrogen. Mean rock interior total nitrogen, % DW ± s.e.m. = 0.05 ± 0.01, n = 5; versus rock–endolithic lichen layer (see D1): d.f. = 7, t 2-tailed = 28.85, P < 0.0001. (2) Compared to faecal nitrogen (see D1): d.f. = 10, t 2-tailed = 17.25, P < 0.0001.

conservative because losses due to volatilization, denitrification and erosion are unknown, and because net dry deposition is assumed to equal total dry deposition (whereas it is almost certainly less, because some deposition is due to local dust redistribution rather than importation of dust from other regions[9]). The net input estimate takes into account the annual net losses of nitrogen (in rain and dust, and from soil-crust nitrogen fixation) following rain-induced runoff from rocks and soil[5,6]. But snail faeces are retained in the system following runoff events, because they are deposited under rocks and are protected by plugs of soil that accumulate on the upslope side of the rock-soil interface.

We estimate that 27% of the nitrogen that is annually accumulated by endolithic lichens from dust, is transferred to the soil by snails (Fig. 2). Dry deposition of dust on rocks is the main source of nitrogen for endolithic lichens[9] because these lichens do not fix atmospheric nitrogen[5,6]; fossil sedimentary nitrogen is low, and rainfall nitrogen inputs to rock are small because rainfall is low (<90 mm per year), and infiltration of rain into rock is minimal[5,6]. The estimate of nitrogen transfer is conservative because the calculation is based on total dry deposition (rather than a lesser, but unknown net deposition), and because the calculation assumes that lichens take up all of the dust nitrogen (rather than some unknown portion of that deposited on rocks).

Snail-induced cycling of nitrogen from cryptogamic plants in the rocks to soil may influence productivity of higher plants growing in the desert soil. Snail faeces are deposited under the rocks, where the roots of higher plants grow. The rock–soil interface is a high-quality microhabitat for plant roots, because of the relatively higher soil moisture regime, compared to the uncovered soil[10,11]. Nitrogen may be limiting to higher plants in these microhabitats, because water availability is greatest here. Snail faeces are therefore being deposited in a micro-environment where they can most probably influence higher plant production.

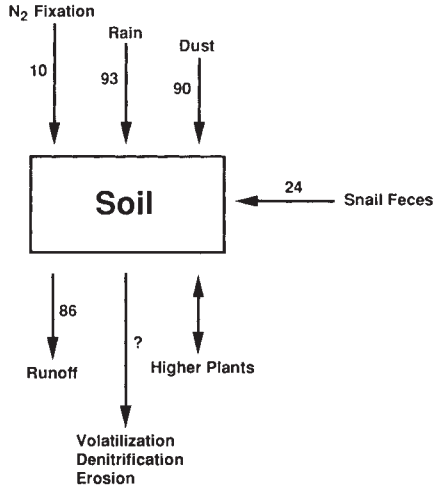

FIG. 2 Inputs and outputs of nitrogen for patches of soil in the Negev Desert Highlands watersheds. Values are average mg total nitrogen per m^2 per year. Data on nitrogen budgets are from studies carried out in 1984–1987[5,6,9]. Rain water (68 and 118 mg nitrogen per m^2 per year, 1984–1985 and 1985–1986, respectively, average 93) for nitrogen determination was collected 1 m above the desert surface throughout 1984–1986. The bulk collector was cleaned of dust every 2 days and washed when clouds indicated a potential rain event. Nitrate was determined with NAS reagent, ammonium with indophenol blue, and nitrites with a modified Gries method[25]. Runoff from rocks and soil is a net annual loss of nitrogen. After each watershed runoff event (20 and 153 mg nitrogen per m^2 per year, 1984–1985 and 1985–1986, respectively, average 86), water samples were taken from a network of pools behind a set of stage recorders, filtered and analysed for NO_3 and NH_4 [5,6]. Unfiltered samples were analysed for dissolved and particulate organic nitrogen by the Kjeldahl method. Dust samples (total dry deposition) were collected on a bulk collector, monthly through 1987, weighed and analysed for NO_3, NH_4 and total nitrogen, as above[9] (monthly range 2.9–10.7, average 7.5 mg total N per m^2; annual estimate 90 mg N per m^2). Maximum potential for nitrogen fixation was determined by acetylene reduction[26] for samples of soil crust and rocks along transects in 1986. No detectable nitrogen fixation occurred on rocks[5,6], and endolithic lichens do not generally fix nitrogen, on the basis of studies in other desert and antarctic environments[27]. The actual amounts of fixation due to soil crust algae–bacteria is probably less than the small amount shown, because the acetylene reduction method tends to overestimate fixation[28,29]. Nitrogen losses due to volatilization, denitrification and erosion are unknown. Estimates of the importance of snail faecal nitrogen inputs to soil were calculated as follows. Percentage total soil nitrogen input (11%) = [snail input (average, 24)/{snail input (24) + rain (93) + soil crust nitrogen fixation (10) + total dry deposition (90)}] × 100. Percentage net soil nitrogen input (18%) = [snail input (24)/{snail input (24) + rain (93) + soil crust nitrogen fixation (10) + total dry deposition (90) − runoff (86)}] × 100. Percentage snail transfer of rock nitrogen (27%) = [snail input (24)/total dry deposition (90)] × 100.

Our study demonstrates the importance of invertebrate consumers in nitrogen cycling, and suggests that ecosystem productivity in this arid environment would be less in the absence of the herbivores. There is considerable debate over the importance of consumers in nutrient cycling[12–18]. This study, together with studies in other deserts on the role of insects such as ants, termites and cicadas[19–21], show that invertebrates can have a critical role. □

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Hormonal control of Mg^{2+} transport in the heart

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MAGNESIUM is abundant in the mammalian body and the second most abundant cation in cells[1,2]. Because the concentration of intracellular free Mg^{2+} is relatively high (0.2–1 mM)[1,3], Mg^{2+} is unlikely to act as a second messenger, like Ca^{2+}, by rapidly changing its cytosolic concentration. But changes in Mg^{2+} do have profound effects on cellular metabolism, structure and bioenergetics[3–7]. Key enzymes or metabolic pathways[1,6–8], mitochondrial ion transport[6,9–11], Ca^{2+} channel activities in the plasma membrane and intracellular oganelles[3,12,13], ATP-requiring reactions, and structural properties of cells[4,6,14] and nucleic acids[1,3,7] are modified by changes in Mg^{2+} concentration. Yet, although some information is available from giant cells[3,15] and bacteria[3,16,17], little is known about the regulation of intracellular Mg^{2+} in mammalian cells. Here we report a new transport mechanism for Mg^{2+} across the sarcolemma of cardiac cells in both intact hearts and dissociated myocytes. We show that noradrenaline, through β-adrenergic stimulation and increase of cyclic AMP, stimulates a large efflux of Mg^{2+} from cardiac cells. This transport is of major dimensions and can move up to 20% of total cellular Mg^{2+} within a few minutes.

Figure 1 shows the Mg^{2+} efflux from a perfused rat heart. Every 20 s perfusate was collected and assayed for Mg^{2+} by atomic absorbance spectrophotometry. Ten minutes before measurements began, the perfusion medium was shifted to one containing zero Mg^{2+}. In controls (Fig. 1*a*), the Mg^{2+} content in the perfusate was 7.5 μM progressively decreasing to 2 μM over 30 min perfusion. By contrast, the addition of noradrenaline (NA) to the perfusate results in a large efflux of Mg^{2+} from the heart (Fig. 1*b*). In different hearts this efflux was stimulated by NA in the perfusion medium in a dose-dependent fashion and was observable over a dose range 0.04–10 μM. Qualitatively similar results (not shown) were obtained using adrenaline and isoprenaline.

Figure 2*a* shows Mg^{2+} efflux from perfused hearts after successive short stimulations with 0.2 μM NA. Each stimulation