A proposed mechanism for the formation of 'Fertile Island' in the desert ecosystem

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A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem

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Movement of nitrogen atoms throughout the environment occurs by (1) physical transport such as molecular diffusion and hydrodynamic flow, mechanisms that always disperse and (2) biological transport such as sap flow and animal movement, mechanisms that most often lead to concentration. Both types of transport are accelerated by moisture, but the physical mechanisms are more sensitive.

In the desert ecosystem, micro-, meso-, and macro-fauna are all attracted to the canopies of whatever plants exist, the place of highest moisture, lowest daytime temperature and most abundant food sources. This paper presents the hypothesis that under conditions of desert aridity the concentrating biological transport mechanisms dominate over the dispersive physical mechanisms. This causes the phenomenon known as 'fertile islands.'

Introduction

The significance of nitrogen in the desert ecosystem is of ever-increasing interest. A recent monograph of the I.B.P. (West & Skujins, 1978) deals solely with this subject. While water is the primary essential for plant growth in arid zones (Noy-Meir, 1973), there is general agreement that desert soils lack the nitrogen that would permit optimum utilization of the water that is supplied by precipitation (Charley & West, 1977; Ettershank *et al.*, 1978). Better understanding of the physical, chemical and biological mechanisms that operate in the desert nitrogen cycle is of both theoretical interest and practical importance.

The biochemical pathways by which the various nitrogen fixers are able to split and reduce elemental 'dinitrogen' to ammonia are detailed by Postgate (1982). Quantitative aspects of the nutritional requirements of plants, animals and micro-organisms have been studied extensively (Ryther & Dunstan, 1971; Mattson, 1980; Williams & Bell, 1981). The mineralization of fixed nitrogen is the subject of many papers (e.g. Bjarnason, 1971; Marumoto *et al.*, 1982; Charholm, 1985). While it is possible to construct schema of pathways for each of the chemical transformations of nitrogen, a subject about which there is only a hint in the literature (West & Skujins, 1978), it is not possible to do this for the physical mechanisms of transport by which atoms of nitrogen actually move from one place to another. This paper is the first systematic analysis of the subject.

The desert ecosystem may be divided into five zones between which nitrogen is transported by various mechanisms. These zones are (1) the atmosphere; (2) the phytosphere, which is the above-ground portion of a living plant; (3) the soil crust, which is the interface between the soil and atmosphere; (4) the rhizosphere, and (5) the exosphere, which has been defined as that portion of the soil that lies outside of the rhizosphere.

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Nitrogen moves from one zone to another by either physical or biological transport mechanisms as illustrated in Fig. 1. The pathways designated by numbers in Fig. 1 are listed and described in Table 1 by (1) origin, (2) nature of nitrogen containing material, (3) process that produces material, (4) zone to which the nitrogen is transported, and (5) the mechanism of transport.

The physical transport mechanisms consist of: (1) gaseous diffusion in the milieu of the atmosphere and the soil pore space; (2) washout of the atmosphere by rainfall of ammonia and nitrogen oxides as free gases and as adsorbates and particulates; (3) leaching which includes lateral as well as vertical movement of soil water; (4) diffusion in the soil-water milieu; (5) gravity; (6) wind.

Each of these physical transport mechanisms abides by the second law of thermodynamics and thus tends to disperse nitrogen throughout the desert ecosystem regardless of the chemical form in which the nitrogen exists.

The operative biological transport mechanisms are: (1) Phytotransport, the movement of fluids within the plant that carries nitrogen up from the rhizosphere to the phytosphere. In some cases, the direction is reversed (Mahendrappa *et al.*, 1986). (2) Zootransport by which micro-, meso-, and macro-fauna feed on the primary products of photosynthesis (leaves, flowers, sap, roots, seeds and other structural parts) or secondary products (litter in various stages of mineralization, animal prey, frass, bacteria, fungi, casts, and dead organisms) and then move from the site of consumption to a new site. At the new site, the nitrogen is temporarily immobilized by excretion or the death of the transporting animal.

Both the physical and biological transport systems are accelerated by moisture. Sensitivity to ambient moisture is, however, greater in physical mechanisms. Plants and animals, especially those of the desert, have coverings that retain moisture (Monson & Smith, 1982; Hadley, 1986). Self-mulching soils aid moisture retention: bare soil has no such protection.

As a consequence of this differential response to ambient moisture, the biological mechanisms of nitrogen transport become dominant as aridity intensifies. This concept is depicted in Fig. 2. The two functions that are represented by lines are wide bands

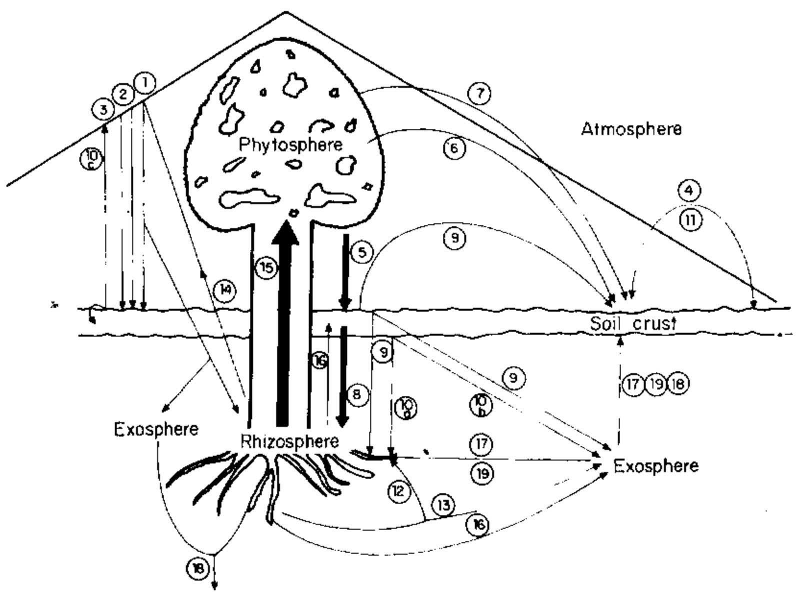

Figure 1. Transport mechanisms in nitrogen cycle.

Table 1. *Summary of nitrogen transport mechanisms in desert ecosystems*

Nitrogen originating in the atmosphere

Pathway	Material	Production process	Transported to	Mechanism
1	N_2	(Natural state)	(a) Soil crust (b) Rhizosphere (c) Exosphere	Gaseous diffusion
2	NO_x	(a) Natural electrical discharge (b) Anthropogenic activity (high temperature combustion)	(a) Soil crust (b) Exposure	Rainfall
3	NH_3	Volatilization from alkaline soils	Soil crust	Rainfall Gaseous diffusion
4	Particulate $NH_3 + NO_x$	Wind erosion	Remote soil crust	Wind transport of dust

Nitrogen originating in the phytosphere

Pathway	Material	Production process	Transported to	Mechanism
5	Litter including (a)seeds (b) frass	Phenology Insect browsing	Soil crust	Gravity
6	Plant material as excreta	Herbivory	Remote soil crust	Zoo-transport
7	Litter	Many processes	Remote soil crust	Wind

Nitrogen originating in the soil crust

Pathway	Material	Production process	Transported to	Mechanism
8	Organic-N and NH_3 (of varying composition due to cycling *in situ*)	(a) Litter fall (b) Animal excreta (c) Grazing of surface thallophytes	Rhizosphere	Leaching Diffusion
9	As in 8 plus seeds	As in 8	(a) Rhizosphere (b) Remote surface (c) Exosphere	Zoo-transport
10	NH_3	N-fixation by cryptogamic crust	(a) Rhizosphere (b) Exosphere (c) Atmosphere	Leaching Diffusion Volatilization
11	$NH_3 + NO_x$ on dust	Surface accumulation	Atmosphere	Wind erosion

Table 1. *Continued*

Nitrogen originating in the rhizosphere

Pathway	Material	Production process	Transported to	Mechanism
12	NH_3	N-fixation by rhizobacteria animal excreta	(a) Plant (b) Exosphere	Absorption Diffusion
13	NO_x	Nitrification	Exosphere including water table	Diffusion Leaching
14	N_2	Denitrification	Atmosphere	Gaseous diffusion
15	Plant sap	Absorption and bio processes	Phytosphere	Phyto-transport
16	Root litter-N	Decomposition	(a) Crust (b) Exosphere	Zoo-transport

Nitrogen originating in the exosphere

Pathway	Material	Production process	Transported to	Mechanism
17	NH_3	Free living bacteria fixation animal excreta	(a) Crust (b) Rhizosphere	Gaseous diffusion
18	NO_x	Nitrification & diffusion inputs	(a) Crustal microflora (b) Water table	Diffusion Leaching
19	Organic-N	Ingestion and *in-situ* decomposition of wind borne litter—Seeds collected by gramivores	Rhizosphere and dispersion in crust and exosphere	Zoo-transport

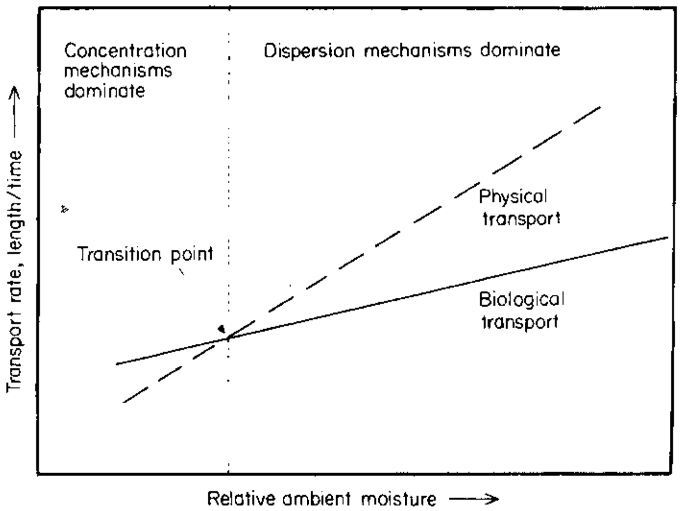

Figure 2. Moisture/rate of transport relationship.

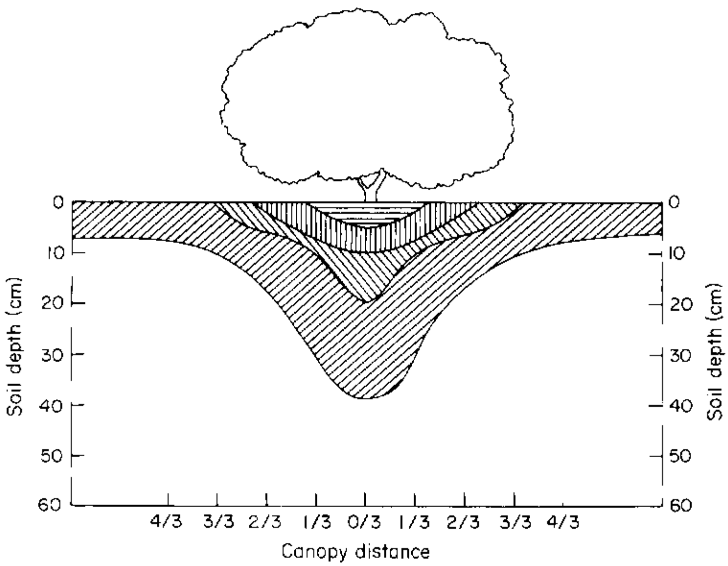

Figure 3. 'Fertile island' from Klemmedson & Barth (1975) (with permission). Total N%: ▤ >0·06; ▥, 0·05–0·06; ▧, 0·04–0·05; ▨ 0·03–0·04; □, 0·02–0·03.

comprised of many different mechanisms. Moreover, the actual curves could be exponential, logarithmic, parabolic or any other conceivable shape. There remains, nonetheless, a level of ambient moisture below which biological mechanisms tend to dominate over the physical mechanisms.

The biotransport mechanisms function largely to concentrate nitrogen. The 'fertile island' (Romney *et al.*, 1978) is the consequence of zootransport mechanisms that: (1) gather nitrogen from the area surrounding the island and (2) retain in the island the nitrogen that is already present. The structure of fertile islands has been established by Klemmedson & Barth (1975). There is much evidence that the fertile island is not only the point of concentration of nitrogen as shown in Fig. 3, but also the site of highest moisture concentration, greatest shade, and lowest daytime temperature as well as the major source of food for most herbivores and the animals that prey on them.

The phenomenon of fertile islands in the desert has been assigned the term 'insularity'. It is our thesis that insularity is the consequence of the dominance of concentrating zootransport over dispersive physical transport mechanisms.

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