

the slope in the eastern North Pacific resulted in more effective transfer of coastal production to the deep-sea floor and thus increased SCOC. Gardner and Richardson¹³ argued that the high eddy kinetic energy at abyssal depths in the western North Atlantic increased bottom resuspension, resulting in (1) longer residence time of POC in the water column, (2) greater utilization of POC by plankton in the near-bottom water of the BBL and (3) lower mineralization rates in the sediment. This suggested intermediate step in the mineralization of organic carbon by the BBL plankton has been effectively examined only in the North Pacific, where carbon utilization (oxygen consumption) rates of the plankton community are low compared with those measured in the sediments¹⁴. If the BBL plankton are important consumers

of organic carbon in the North Atlantic, then the influence of episodic fluxes would be less apparent in the sediment community alone. In the North Pacific, however, where the sediment community is the most important consumer of carbon, the influence of episodic changes in POC flux on SCOC should be more prevalent and discrepancies between these rates more acute.

Our results stress the importance of long-time-series measurements, and the need to resolve episodic events and the activity of primary consumer groups in the BBL of the Atlantic and Pacific Oceans, if we are to elucidate variations of the carbon cycle in the deep ocean. □

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Lack of nitrogen cycling in the Atacama Desert

James R. Ehleringer*, Harold A. Mooney†, Philip W. Rundel‡, R. David Evans*, Beatrice Palma§ & Jose Delatorre||

* Stable Isotope Ratio Facility for Environmental Research, Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

† Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

‡ Laboratory for Biomedical and Environmental Science, University of California, Los Angeles, California 90024, USA

§ Instituto Biología, Universidad Católica, Valparaíso, Chile

|| Centro de Estudios Desierto, Universidad Arturo Prat, Iquique, Chile

MESQUITE (*Prosopis*) trees growing in the rainless region of the Atacama Desert produce leaves that abscise and accumulate on a concrete-like carbonate surface, often attaining litter depths of 45 cm. The virtual lack of surface moisture inhibits leaf decomposition, and prevents cycling of nitrogen, the mineral most often limiting plant growth. Leaves in the midpoint of a litter profile were aged to pre-bomb dates (older than 1950) and had both high nitrogen concentrations and a carbon to nitrogen ratio comparable to that of live leaves. The thick carbonate layer prevents root growth into the litter. *Prosopis* appear to persist by having roots that fix nitrogen in moist subsurface layers and by extracting water and other nutrients from ground water, allowing plants to persist in an ecosystem in which there is no nitrogen cycling.

The Pampa del Tamagual is a closed basin (salar) in the Atacama Desert, east of Iquique, Chile (between 19 and 21° S). This region receives essentially no rainfall¹, yet supports a forest of two *Prosopis* species². *Prosopis tamarugo* is native to the area; *Prosopis alba* was introduced from Argentina in pre-Columbian times². Trees of both species obtain their moisture from groundwater at depths of 6–8 m or more^{3–5}. This groundwater originates in the higher Andes with a replacement time of hundreds to thousands of years^{1,5}.

The salar surfaces are covered by a 20–60-cm-thick, concrete-like layer of carbonates. The lack of rainfall and low humidity levels¹ make it likely that litter decomposition should occur at

extremely slow rates. Thus, although minerals are extracted from the soil by roots and transformed into biomass, subsequent litter from dead above-ground tissues would not be incorporated back into soil for recycling by plants. Here we explore this possibility and its ramifications for *Prosopis alba* and *P. tamarugo*.

Both *Prosopis* species have an umbrella-like canopy with the outer branches reaching to the substrate surface. This structure protects the litter layer from wind dispersion. Under normal cultural practices, these outer branches are removed so that grazing animals can forage and seek shelter under the trees. But unpruned trees commonly occur as isolated individuals in remote sites.

In December 1990, we located isolated *Prosopis alba* in the centre of a large salar free from the influence of grazing animals. There was considerable accumulation of leaf litter under the trees reaching depths of 45 cm. Litter samples were collected at 5-cm depth intervals from two sample excavations. The litter layer terminated on the top of the impenetrable 30–40-cm-thick crystalline salt pan of carbonates. The litter samples were then analysed for carbon and nitrogen contents using an elemental analyser (model 2400, Perkin-Elmer) and for magnesium, potassium, and sodium contents using an arc spectrometer system⁶. We also collected both live and dead leaves attached to the tree for parallel analyses.

The nitrogen contents of the live leaves were relatively high, as is characteristic of nitrogen-fixing plants (Fig. 1). The leaf litter was similarly high in nitrogen and these values did not significantly change with depth ($r = 0.44$, $n = 10$, $p = 0.239$). The nitrogen content of dead leaves in the litter was not significantly different from that of live leaves (Student's $t = 1.271$, $P = 0.236$). The carbon to nitrogen ratio, an index of carbon loss through decomposition, varied between 10 and 12 (Fig. 1). Visually there were no discernable structural differences between the leaves at the top and bottom of the litter layer. Thus, there was little indication that any of the material from the nitrogen-rich leaf litter was being returned to the soil, especially given both the thick carbonate layer preventing root growth into the litter and lack of rainfall to induce decomposition activity.

How old was the litter and could it possibly represent all of the litter deposited during the lifetime of these trees? Litter samples were analysed for ¹⁴C content by the University of Arizona Radiocarbon Laboratory⁷. These results indicated that all litter samples at depths 20 cm or more below the litter surface

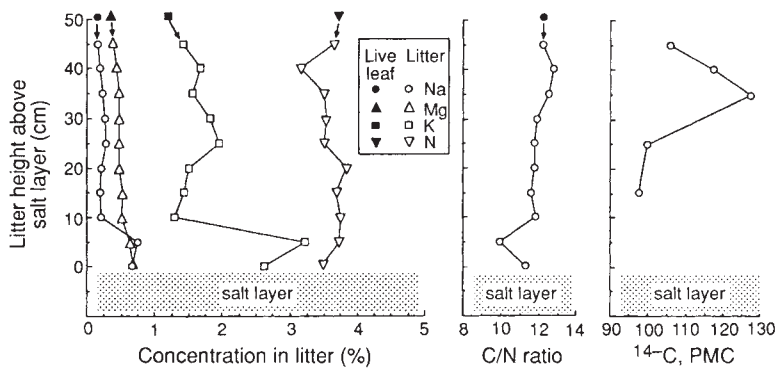


FIG. 1 Magnesium, nitrogen, potassium, sodium, carbon to nitrogen ratio and ^{14}C contents (per cent of modern carbon) of litter from different depths underneath *Prosopis alba* in the Pampa del Tamarugal of Northern Chile.

were pre-1950 (not modern carbon) (Fig. 1). The ^{14}C peak associated with above-ground nuclear testing in the 1950s and early 1960s and its decay following the Test Ban Treaty are visible in these data. Roughly 45% of the existing litter had been produced during the past 40 years and the other 55% before 1950. By linear extrapolation, the oldest litter was a minimum of 89 years old. Independently, we can estimate an age for the deepest litter, knowing productivity rates and accumulation depth. Productivity studies with mature *Prosopis* in the Pampa del Tamarugal indicate that trees produce $0.7\text{--}1.0\text{ kg m}^{-2}$ leaf litter per year⁸. The accumulated litter profile averaged $85.58 \pm 16.38\text{ kg m}^{-2}$ (mean \pm s.d.), indicating an accumulation of 86–122 years in a 45-cm litter layer, if decomposition has not occurred and we simply divide the total litter accumulation by a constant litter production rate. The latter estimate is likely to be a minimum age for the deepest litter layers, because the litter accumulation rate should increase as trees mature.

Although there is apparently no return of minerals from above-ground biomass to the soil, this is not the case for underground root tissues. *Prosopis* growing in this soil produce a dimorphic root system, with a tap root that reaches the water table at 8–12 m depth and a second dense mesh of fine roots at one or more depths between 50 and 200 cm below the salt crust³. Root hydraulic lift results in a moist layer in the upper soil regions immediately adjacent to the major roots^{3,4} and root nodules capable of nitrogen fixation were abundant in these wetted, upper soil layers.

Possible sources of plant tissue nitrogen were determined by nitrogen isotope analyses of plant and soil materials⁹. Nitrogen isotope ratios ($\delta^{15}\text{N}$) of *Prosopis* leaves were measured by combusting plant material with Cu, CuO, CaO, and silver foil under vacuum at $850\text{ }^\circ\text{C}$ ^{10,11}, isolating and purifying the diatomic nitrogen, and measuring its nitrogen isotope ratio on a mass spectrometer (delta S, Finnigan MAT).

The current leaf $\delta^{15}\text{N}$ values averaged 0.3% and 0.4% for *P. alba* and *P. tamarugo*, respectively. These values are virtually identical to that previously reported for *P. glandulosa* in North America and are typical of plants exclusively obtaining their nitrogen through nitrogen-fixation⁹. A second analysis was conducted using *Pluchea absinthioides* (Asteraceae) and *Distichlis thalassica* (Poaceae), both non-nitrogen-fixing plants occurring occasionally in *Prosopis* stands. *Pluchea* leaf $\delta^{15}\text{N}$ values averaged 7.2%, whereas those of *Distichlis* averaged 6.7%. Both values serve as a reference for the $\delta^{15}\text{N}$ value of mineral N in the ecosystem, derived either from soils or from groundwater sources. Soils beneath the *Prosopis* canopies at the same depths as nodules had $\delta^{15}\text{N}$ values that averaged 10.2%, consistent with an expected isotopic fractionation during mineralization of $\sim 3\%$ and almost exactly 3% more positive than observed for the non-nitrogen-fixing species¹².

Using an autoanalyser, nitrate and ammonium concentrations were then measured on water samples from a well. Total nitrogen content of ground waters were low, averaging only 0.71 mg l^{-1} . All nitrogen in the well-water was as nitrate; ammonium was

not detectable, confirming earlier observations of low nitrate contents and an absence of ammonium in both surface salt layers and groundwaters in a nearby salar¹³.

We measured the total plant-available nitrogen with depth in the soil profile under *Prosopis* canopies and the carbon to nitrogen ratios of live and dead fine roots in the upper rooting horizon. Available soil nitrogen was low, averaging $0.49\text{ }\mu\text{g g}^{-1}$ through the top 1.5 m of the soil profile. In the root-mat regions, available soil nitrogen was significantly higher ($0.88\text{ }\mu\text{g g}^{-1}$), but still sufficiently low to rank the soils as low in nitrogen. Carbon to nitrogen ratios of live and dead fine roots were 23.5 and 18.9 in the upper moist soil layers, respectively, indicating that some root nitrogen is being recycled in the soil. But the leaf and soil nitrogen isotope ratio data indicate that available soil nitrogen is not a significant component of the total *Prosopis* nitrogen budget.

Because total nitrogen contents of the groundwaters are low and the nitrogen isotope data indicated that essentially all of the nitrogen in *Prosopis* was derived from nitrogen-fixation activity, it would seem that there is effectively no nitrogen cycling in this ecosystem. This unusual nutrient pattern involves nitrogen production by nodules located in the moist soil layers 0.5–1.5 m below the surface, nitrogen translocation to the shoots where it is incorporated into leaves, essentially complete loss of this nitrogen during leaf abscission (with little if any recovery by the plant), and deposition of the nitrogen onto the salar surface where it remains undecomposed and not recycled. Given the high energetic costs associated with N_2 fixation as well as the low nitrogen contents of groundwater, it is surprising that so little of the *Prosopis* leaf nitrogen is retranslocated back into the plant before leaf abscission.

In terms of nitrogen, these plants behave as open systems, continually producing large amounts of nitrogen through nitrogen fixation activities and then annually depositing all of that nitrogen onto a surface litter layer that is never recycled through decomposition. Redistribution of this surface pool of litter may occur as highly irregular surface erosion events, but nevertheless it never enters the normal biological nitrogen cycle, making this Atacama Desert ecosystem unique in its nutrient cycling characteristics. □

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Predictable eye-head coordination during driving

Michael F. Land

Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

LARGE changes in the direction of gaze are made with a combination of fast saccadic eye movements and rather slower head movements. Since the first study on freely moving subjects¹, most authors have agreed that the head movement component of gaze is very variable, with a high 'volitional' component². But in some circumstances head and eye movements can be quite predictable, for example when a subject is asked to shift gaze as quickly as possible³. Under these conditions, laboratory studies have shown that the eye and head motor-systems both receive gaze-change commands, although they execute them in rather different ways³⁻⁶. Here I reconsider the way gaze direction is changed during free movement, but in the performance of a task where the subject is too busy to exert conscious control over head or eye movements. Using a new portable and inexpensive method for recording head and eye movements, I examine the oculomotor behaviour of car drivers, particularly during the large gaze changes made at road junctions. The results show that the pattern of eye and head movements is highly predictable, given only the sequence of gaze targets.

If there are 'natural' patterns of oculomotor coordination that emerge in every day situations these should be detectable from the predictable way that head and eye movements co-vary. Let us assume that from time to time the brain specifies new gaze targets for the oculomotor system to fixate, and that their directions represent the commands to the system. An appropriate and severe test of the system's predictability would then be that the amplitudes and time courses of both the head and eye movements involved in every change of gaze should be dictated uniquely by the sizes of the gaze changes themselves. This study presents evidence in favour of this, and offers a simple model which generates realistic eye and head movements from gaze commands.

The device used to record eye movements consisted of video camera mounted on a cycling helmet. This took a 'head's eye'

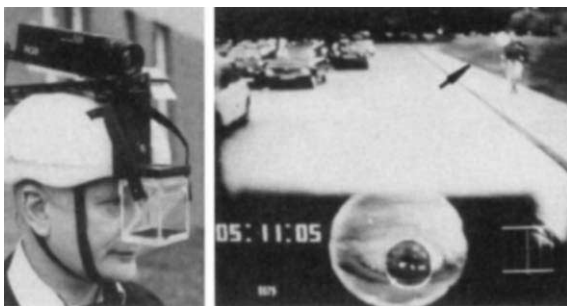


FIG. 1 Left, The scene-and-eye camera. A light-excluding shield has been removed for clarity. Right, VDU image showing a road scene with the inverted image of the eye at the bottom. The iris is ringed by a cursor which generates the gaze spot visible next to the pedestrian (indicated by arrow).

view of the world ahead. Attached to the camera was an arrangement of two mirrors and a lens which projected an enlarged image of the right eye onto the bottom of the camera's field of view (Fig. 1). The mirror in front of the eye was only 30% silvered, so that the driver's view was almost unimpeded. Recordings were made using available light, with a portable video cassette recorder and small battery pack. After the drive, the videotape had a clock signal added, and was viewed in combination with an image generated by an Acorn Archimedes computer. This contained a cursor program which modelled the outline of the iris on an eye rotating around its centre; the cursor could be moved with a tracker-ball so that it coincided exactly with the image of the iris on each video frame⁷. The angular coordinates used to generate the cursor were then taken as those of the direction of the axis of the eye itself, and they were in turn used to generate a spot on the image of the scene ahead, corresponding to the direction of view of the fovea (Fig. 1). The combined video and computer images were dumped frame-by-frame to a single-frame recorder (Panasonic AG-6720), and the coordinates of eye position stored simultaneously in the computer. Calibration consisted of fixating a series of points at known angular locations, and adjusting the cursor generator until the direction-of-view spot matched the appropriate point on the image to within 1°. Measurements were repeatable to 1°, and the absolute accuracy over a 40° field was about 2°. Head movements were measured directly from the video, by tracking distant objects across the calibrated monitor screen. The accuracy is similar to that of the eye movements. The temporal resolution is 50 Hz. Two subjects were each videotaped through three intersections like that shown in Fig. 2, providing a total of 112 saccadic gaze changes.

An example of the fixation points made while negotiating a road junction, with the corresponding horizontal eye and head

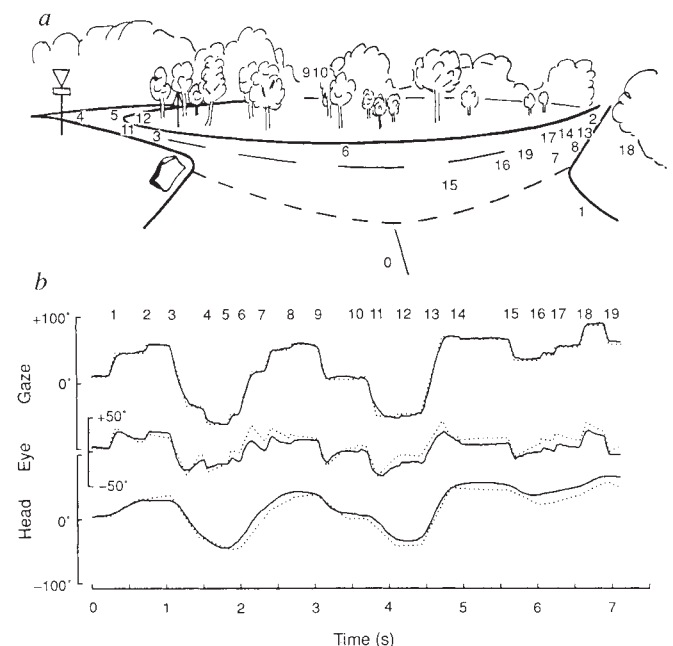


FIG. 2 a, Sequence of gaze fixation directions of subject M.L. during an approach to, and right turn at, an intersection. The sketch represents a 180° view and was made from photographs taken at a position corresponding to second 2 in b. The fixation points are taken from the video record. b, Horizontal eye, head and gaze movements during the sequence shown in a. Numbers above designate individual saccades. Right is represented vertically in all records. Head and gaze movements are relative to external coordinates, not the car, which was fully stationary only between saccades 10 and 14. The solid curves are the records themselves, and the dotted curves the outcome of the model described in the text and Fig. 3.