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Correspondence and requests for materials should be addressed to P.B.S. (e-mail: sigler@csb.yale.edu). Coordinates have been deposited in the PDB under accession number 1a28.

corrections

Low nitrate: phosphate ratios in the global ocean

T. Tyrrell & C. S. Law

Nature **387**, 793–796 (1997)

See the Scientific Correspondence contribution on page 318 of this issue in which—owing to the discovery of errors in the international database on which this paper was based—the authors retract their main new conclusions. □

A caspase-activated DNase that degrades DNA during apoptosis, and its inhibitor ICAD

Masato Enari, Hideki Sakahira, Hideki Yokoyama, Katsuya Okawa, Akihiro Iwamatsu & Shigekazu Nagata

Nature **391**, 43–50 (1998)

We have noticed that the sequence of murine CAD (Fig. 5d) carries an error. The sequence of the amino acids from 47 to 76 should read SRLCLYEDGTETVDDCFGLPNDAAELLLL, instead of FPAVPVR-RWHGGDGRLLPGFPPTTLSSYCF as published. The open reading frame of the cDNA (pEF-mCAD) consists of 344 amino acids instead of 345 amino acids, and the mature murine CAD is a protein of 342 amino acids with a calculated relative molecular mass of 39,214.18. The sequence for mouse CAD in the DDBJ/GenBank/EMBL database (accession number AB009377) has been revised (24 February 1998). This mistake does not change the substance of our findings or the interpretation of our data. □

Phase-mapping of periodically domain-inverted LiNbO₃ with coherent X-rays

Z. W. Hu, P. A. Thomas, A. Snigirev, I. Snigireva, A. Souvorov, P. G. R. Smith, G. W. Ross & S. Teat

Nature **392**, 690–693 (1998)

The name of the first author on this Letter was incorrectly published as Z. H. Hu. □

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single-crystal MoS₂ have over four times the shear strength of the terraces. The weak adhesion of the HNs to the mating surface were reflected in scanning force microscopy (SFM), whereby the HN particles were brushed away by the tip in contact mode imaging. Using the non-contact mode of the SFM, which avoids shear, clear images of the HN were obtained. Transmission electron microscope (TEM) analysis of the HNs which had gone through extensive wear experiments revealed that many of them had lost their outer WS₂ shells, but that they had nevertheless preserved their overall cage shape. In contrast, the 2H material underwent extensive structural damage, amorphization and oxidation. Consequently, improved tribological behaviour of the HNs, attributed to rolling friction and absence of dangling bonds, is not lost until complete destruction of the particles occurs. The slower deterioration of the HNs is reflected by their lower wear rates, even after 12 hours of sliding (Fig. 2 legend).

The experimental results (rows 6, 7 and 8 of Table 1) clearly show that both μ and w increase with decreasing size of the 2H platelets. This observation is in agreement with the suggestion that dangling bonds mediate friction in metal dichalcogenides: as the average size of the platelets decreases, the total surface area and hence the amount of dangling bonds on the reactive (11c) surface increases. In contrast, the friction coefficient of the much smaller HN particles, which do not expose dangling bonds, is less than that of any of the different 2H particle mixtures. A decrease in particle size also tends to increase viscosity, which usually entails higher friction¹³. The HN mixture had the highest viscosity, and normalizing for this parameter would therefore give an even stronger indication of the enhanced performance of the HN material, relative to 2H-MoS₂ and 2H-WS₂.

The synthesis of HN-WS₂ uses abundant precursors and fairly straightforward conditions, and the cost of the material is therefore not expected to prohibit large-scale applications in the automotive and aerospace industry, which currently use the apparently inferior dichalcogenides. Improved control of the size distribution and shape of the nanoparticles is expected to lead to improved tribological properties. Furthermore, HN-MoS₂ might be expected to outperform HN-WS₂, by analogy with their platelet counterparts. Clearly, alternative synthetic routes for the production of HN materials could yield solid lubricants with further improved properties. □

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Low nitrate : phosphate ratios in the global ocean

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The distribution and availability of the nutrients nitrate and phosphate exert a strong control over primary production in the world ocean. Here we use a recently compiled global data set of oceanographic observations¹—a database that is at least 40 times larger than currently used data sets (for example, ref. 2)—to analyse the variation of the nitrate : phosphate concentration ratio with depth and geographical location. Although the nutrient distributions confirm the dominant influence of aerobic decomposition, in agreement with the observations of Redfield³, we also identify a hitherto unreported secondary trend at low nitrate : phosphate ratio (~2–3). These conditions of low nitrate : phosphate ratio are associated with low oxygen concentrations and are probably caused by denitrification. Examination of the geographical distribution of these low nitrate : phosphate data suggests that denitrification in the western and northern North Pacific Ocean may have been previously overlooked, and that a reassessment of the global oceanic denitrification budget may therefore be required.

The World Ocean Atlas 1994 (WOA94) data set¹ is an international collection of oceanographic information covering the past 60 years. Part of this data set has previously been used to construct global contour plots of nitrate, phosphate and silicate concentrations at several depths⁴. Here the 681,381 points in the data set are used to produce a scatter plot (Fig. 1) of the concentrations of nitrate (NO₃⁻) versus phosphate (PO₄³⁻), which is then analysed. Despite the broad spatial and temporal range of the data, three features are clearly apparent. (1) A strong trend along a line of slope [NO₃⁻] ≈ (14–15)[PO₄³⁻]. (2) A positive x-axis intercept of this main trend, that is, a predominance of points near to the [NO₃⁻] = 0 axis rather than near to the [PO₄³⁻] = 0 axis. (3) A weaker trend along lines with slopes [NO₃⁻] ≈ 2[PO₄³⁻]. A least absolute deviation best-fit line⁵ to all of the data except the weaker trend (defined below in equation (2)) actually produces [NO₃⁻] = 14.1[PO₄³⁻] – 1.53 (with a mean absolute [NO₃⁻] deviation of each point from the best-fit line of 3.15 μmol NO₃⁻ kg⁻¹), although the data is biased towards surface waters (where there has been more sampling). Analysis of only the points below 1,000 m (again excluding points in the weaker trend) reveals an average deep-sea [NO₃⁻] : [PO₄³⁻] ratio of 14.6.

The main trend in the data with slope [NO₃⁻] ≈ (14–15)[PO₄³⁻] is due to phytoplankton assimilation of the nutrients in surface waters followed by aerobic decomposition of the sinking organic matter³, which recycles nitrogen and phosphorus back into dissolved form in deeper water according to the reaction⁵:

Some scatter about a straight line is to be expected due to variation in the nitrate : phosphate ratios of the plankton being decomposed⁶, localized riverine input and other factors. The positive x-intercept of the main trend in the data agrees with the observed predominance of nitrogen over phosphorus limitation at low nutrient concentrations in surface waters^{7,8}.

The most surprising aspect of the data is the weaker trend along lines with slopes [NO₃⁻] : [PO₄³⁻] ≈ 2.0. This trend can be seen

clearly in a profile of $[\text{NO}_3^-] : [\text{PO}_4^{3-}]$ against depth (Fig. 2). This feature is not remarked upon in previous nitrate:phosphate analyses^{3,9–11} because it is not apparent in the smaller data sets² which these studies have used.

To investigate this new phenomenon, a subset of the data containing the points contributing to the secondary nitrate:phosphate trend was extracted according to the following criteria:

$$[\text{PO}_4^{3-}] > 1.5 \mu\text{mol kg}^{-1} \text{ and } [\text{NO}_3^-]/[\text{PO}_4^{3-}] < 3.0 \quad (2)$$

(the shaded area in Fig. 1 inset). These criteria were chosen so as to include points at low nitrate:phosphate, but to exclude points that are only a short 'distance' away from the predominant trend in the data. For example, only a minor system perturbation or measurement error is required at lower nutrient concentrations for the nitrate:phosphate ratio to change from 15 to 2, and so our criteria only include low nitrate:phosphate ratios at higher phosphate concentrations. The low nitrate:phosphate (LNP) points resulting from this definition make up 1.8% of the total (12,469 points out of 681,381). The geographical distribution of these LNP points can be plotted (Fig. 3). Relationships with other parameters (Fig. 4) show whether the LNP points occur preferentially under certain conditions or at certain times.

The first explanation to consider for the LNP points is whether they are due solely to instrument error, for example, associated with older nutrient measurement techniques. However, there is no strong pattern in the yearly distribution of the LNP points (Fig. 4a), with a large fraction (37% = 4,599) of them being made during the past 20 years. In addition, the LNP measurements were made during cruises by many different nations, using different methodologies, in almost all oceans, and across a range of depths. LNP

points are detected by cruises visiting the same area many years apart. For instance, LNP points have been detected independently in the western North Pacific (110–180°E, 0–60°N) by Japanese, Taiwanese, USA, Chinese, USSR, Thai and Indonesian cruises in 1949, 1958 and in 21 out of the 24 years between 1963 and 1986. LNP points and normal (nitrate:phosphate ≈ 15) points were often measured at different depths within the same profile. There is strong spatial coherence (clustering) of the LNP points (Fig. 3), and they possess a spatial distribution which is different from that of the data set as a whole. There is a definite correlation with oxygen concentrations (Fig. 4b). Instrument error can be discounted as a possible cause of the LNP points.

Because the low nitrate:phosphate ratios are genuine, what could have caused them? Examination of global nitrate:silicate and silicate:phosphate plots (not shown) reveal a low trend in the former but not a low trend in the latter, so the low nitrate:phosphate ratios are caused by low nitrate, not high phosphate. As the nitrate:phosphate ratio of river water is generally greater than that of the Redfield ratio¹², and values of this ratio in phytoplankton biomass of <3 have not been reported⁶, this suggests that a nitrate removal process is responsible for the LNP points.

In particular, denitrification is usually assumed to be the explanation for low nitrate:phosphate ratios^{9,11,13}. Anaerobic decomposition by denitrifying bacteria alters the nutrient concentrations in the water according to a reaction similar to^{14,15}:

Denitrification is more likely to dominate in low-oxygen waters, although it can still be operative in more oxic waters within the

Figure 1 Scatter plot of nitrate concentration versus phosphate concentration in the global ocean, with the data points taken from ref. 1. Data were subjected to screening procedures by the National Oceanographic Data Center (NODC) before being included; historical data sets were recovered and included subject to reliability³⁰. The data comes from 68,341 different stations during cruises by 51 different countries. Only data points with no error flags are used here. Only actual measured values are used, with no interpolations being included. Observations were only included when both nitrate and phosphate were measured simultaneously, that is from the same bottle. The upper limit for phosphate in ref. 1 is $4.0 \mu\text{mol kg}^{-1}$. The shaded area in the inset shows the subset of the data designated as low nitrate:phosphate ratio (LNP ratio).

Figure 2 Scatter plot of the nitrate:phosphate ratio versus depth in the global ocean (after ref. 10), using the same data as in Fig. 1.

anoxic micro-sites in particulate matter¹⁶. The geographical distribution of LNP points (Fig. 3) provides further supporting evidence of denitrification as the source process, with LNP points predominantly observed in low-oxygen-prone coastal areas and regions of open-ocean low oxygen associated with upwelling waters.

The LNP points correspond to large nitrate deficits of between 18 and 45 $\mu\text{mol kg}^{-1}$ relative to nitrate:phosphate = 15, and the nitrogen in the missing nitrate must have been converted into some other form of nitrogen. Neither ammonium or nitrite¹⁷ are detected at such high concentrations in oxic or sub-oxic waters. However, N_2 , the end-product of denitrification, is present at concentrations of $\sim 1,200 \mu\text{mol kg}^{-1}$ due to equilibration with

the large atmospheric reservoir. Large amounts of nutrients may also exist in dissolved organic form (dissolved organic nitrogen, DON, and dissolved organic phosphorus, DOP), but there is no reason to suspect an increase in DON without a simultaneous increase in DOP, or that this should be correlated with low oxygen. Other nitrogen species in the oceans are only present at trace concentrations, and so conservation of nitrogen also suggests that a flux of NO_3^- to N_2 via denitrification is the most likely cause of the shortfalls in NO_3^- in the LNP points.

From the arguments above, removal of NO_3^- by denitrification seems by far the most plausible explanation, and the LNP points should therefore be able to be used as indicators of denitrification.

Figure 3 Geographical locations where (at any depth) measured phosphate concentration was $> 1.5 \mu\text{mol kg}^{-1}$ and the ratio of measured nitrate to measured phosphate concentrations was < 3.0 . (Data taken from Ref. 1). The distribution can be compared to a similar plot¹⁹ using an earlier and smaller NODC data set and using a different LNP criterion ($[\text{NO}_3^-] < ((15[\text{PO}_4^{3-}] - 1) - 10.0)$).

Figure 4 Frequency plots of the LNP points against: year of measurement (a); oxygen concentration (b); depth (c); month of the year (d); and height above sea floor (e). In each case the y-ordinate is calculated as $y = (\text{LNP}_x / \text{LNP}_{\text{tot}}) / (\text{NP}_x / \text{NP}_{\text{tot}})$. Here $(\text{LNP}_x / \text{LNP}_{\text{tot}})$ is the fraction of LNP points occurring at the value or range of the parameter plotted on the x-axis, and $(\text{NP}_x / \text{NP}_{\text{tot}})$ is the fraction of all points occurring at the same value or range. As an example, the y-ordinate of the left-most point in b is calculated as $(1,186 / 10,890) \div (9,742 / 613,169)$ because 10,890 of the LNP points and 613,169 of all the nitrate:phosphate points in the data set were measured at times when oxygen was also measured, and of those, 1,186 of the LNP points and 9,742 of the whole set of points were at oxygen concentrations of 0–20 $\mu\text{mol kg}^{-1}$. To ensure that the frequency plots are fully inter-comparable, the y-ordinates were then normalized so that the average y-ordinate for each plot is 1.0. The high correlation during 1935–40 in a is not significant as only 7 LNP points were measured during that period. The correlations in e are less reliable because sea-floor depths for each station are not available in ref. 1 and so had to be obtained instead by interpolation from values in a separate data set, at $(1/12) \times (1/12)$ degree resolution.

In those areas where denitrification is identified in this way (clusters of LNP points in Fig. 3) the denitrification may be occurring in the water column^{18,19} or within the sediment^{15,20}, with subsequent exchange of substrates and products with the overlying waters. Open-ocean denitrification has been reported in the eastern tropical North Pacific²¹, the eastern tropical South Pacific¹⁴, and in the Arabian Sea²². Our criteria (equation (2)) identify the eastern tropical Pacific (north and south), but not the Arabian Sea. The Arabian Sea does not appear as a denitrification site because, although denitrification takes place, the nitrate:phosphate ratio does not fall much below 9.0 as a result²². In light of this, it is clear that the method used here will detect the majority of denitrification-affected waters, but not all of them.

It has previously been suggested, from nitrogen deficit calculations, that denitrification is taking place within the northern North Pacific²³ and the Bering Sea²⁴, but nevertheless these areas are not traditionally recognized as major sites of denitrification. The calculations reported here provide additional evidence for denitrification in these places, and additionally across large areas of the western North Pacific (Fig. 3). Nitrate concentrations are generally high⁴ and oxygen concentrations low^{25,26} in sub-surface waters in these areas, providing favourable conditions for denitrification²⁷.

Assuming similar denitrification rates per unit area, the extent of the LNP points (Fig. 3) suggests that the total nitrate loss in the west and north North Pacific region is about 20% higher than in the eastern tropical Pacific Ocean. Sedimentary denitrification contributes about half as much as water-column denitrification to the global flux²⁰, and the eastern tropical Pacific (north and south) was previously estimated to contribute ~85% of total water-column denitrification²⁷. Therefore inclusion of the western and northern North Pacific could potentially increase the total global marine denitrification flux by about 70%. This calculation is speculative, but it is clear that more detailed work should be carried out to enable more precise estimates to be made. Denitrification is the largest sink of reactive nitrogen from the oceans^{28,29}, and is therefore a critical component in the global marine nitrogen cycle. □

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Contrasting physiological and structural vegetation feedbacks in climate change simulations

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Anthropogenic increases in the atmospheric concentration of carbon dioxide and other greenhouse gases are predicted to cause a warming of the global climate by modifying radiative forcing¹. Carbon dioxide concentration increases may make a further contribution to warming by inducing a physiological response of the global vegetation—a reduced stomatal conductance, which suppresses transpiration². Moreover, a CO₂-enriched atmosphere and the corresponding change in climate may also alter the density of vegetation cover, thus modifying the physical characteristics of the land surface to provide yet another climate feedback^{3–6}. But such feedbacks from changes in vegetation structure have not yet been incorporated into general circulation model predictions of future climate change. Here we use a general circulation model iteratively coupled to an equilibrium vegetation model to quantify the effects of both physiological and structural vegetation feedbacks on a doubled-CO₂ climate. On a global scale, changes in vegetation structure are found to partially offset physiological vegetation–climate feedbacks in the long term, but overall vegetation feedbacks provide significant regional-scale effects.

The Sheffield University vegetation model simulates global vegetation under steady-state conditions of climate and atmospheric CO₂ (ref. 7). It models the physiological processes of nutrient uptake, photosynthesis, respiration and stomatal limitation of transpiration, and uses these to determine the vegetation structural character in terms of foliage density. The outputs of this model are: (1) leaf area index (LAI), the area of leaf surface per unit area of ground; and (2) daytime mean canopy conductance (g_c), the net transpirational conductance of all stomata integrated (numerically) over the canopy depth. LAI is purely a structural variable, whereas g_c contains both structural and physiological contributions. The