short-lived daughter levels and turbulence in the room air and aerosol size distribution. Despite our oversimplification, the results in Fig. 2 show that the correlation between radon in air and polonium in glass is good.

From Fig. 2 it is seen that the two sides of the door glass from house C have different polonium activities, indicating that the radon levels were different in the two rooms separated by the door. Unfortunately, this hypothesis could not be tested as countermeasures against radon have recently been taken in house C, but a room-to-room variation in house C is plausible because the radon in the house stems from the infiltration of ground air along water supply pipes and electrical cabling.

The polonium activity in the glass samples most exposed (Fig. 2) can be detected by the widely available surface barrier detector, but its sensitivity is significantly less than that of the pulse ionization chamber because of the much smaller detector area. Simple total-alpha detectors (such as ZnS detectors) may also be sensitive enough for the most exposed glass samples, but can be subject to interference from alpha-emitting nuclides other than $^{210}$Po.

Received 2 May; accepted 22 June 1988.

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# A novel free-living prochlorophyte abundant in the oceanic euphotic zone

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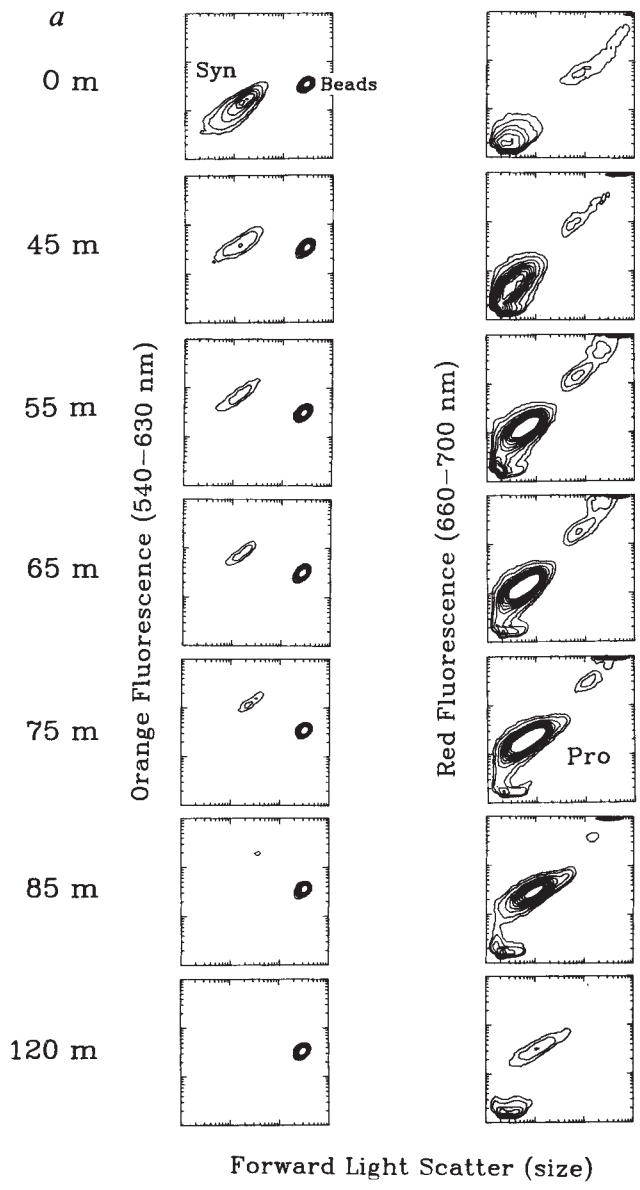
**The recent discovery of photosynthetic picoplankton has changed our understanding of marine food webs[1]. Both prokaryotic[2,3] and eukaryotic[4,5] species occur in most of the world's oceans and account for a significant proportion of global productivity[6]. Using shipboard flow cytometry, we have identified a new group of picoplankters which are extremely abundant, and barely visible using traditional microscopic techniques. These cells are smaller than the coccoid cyanobacteria and reach concentrations greater than $10^5$ cells ml$^{-1}$ in the deep euphotic zone. They fluoresce red and contain a divinyl chlorophyll *a*-like pigment, as well as chlorophyll *b*, α-carotene, and zeaxanthin. This unusual combination of pigments, and a distinctive prokaryotic ultrastructure, suggests that these picoplankters are free-living relatives of *Prochloron*[7]. They differ from previously reported prochlorophytes—the putative ancestors of the chloroplasts of higher plants—in that they contain α-carotene rather than β-carotene and contain a divinyl chlorophyll *a*-like pigment as the dominant chlorophyll.**

In recent cruises in the North Atlantic and Pacific we discovered a flow cytometric 'signature' from extremely abundant red-fluorescing cells deep in the euphotic zone, below the *Synechococcus* maximum (Fig. 1*a*). These picoplankters typically have forward light scatter signals (which are related to cell size) less than a third of those of *Synechococcus* cells in the same sample. Most pass through a 0.8-μm Nuclepore filter and are retained by a 0.6-μm filter. They do not fluoresce in the orange region of the spectrum (540 to 630 nm), indicating the absence of phycoerythrin[8,9]. As in *Synechococcus*, both forward light scatter and fluorescence per cell increase with depth in these cells, presumably reflecting acclimation to decreasing light levels (Fig. 1*b*). The cells are very difficult to detect by epifluorescence microscopy; only in the deepest samples do microscopic counts approach those obtained by flow cytometry.

We have mapped and characterized these unusual cells on several cruises since 1985 in the southern California Bight, Panama Basin, Gulf of Mexico, Caribbean, and North Atlantic between Woods Hole, Massachusetts and Dakar, Senegal. Of the 67 stations we sampled, the cells were undetectable only in shallow, well-mixed waters on Georges Bank off Cape Cod, Massachusetts, and in the northern Sargasso Sea in May, when stratification had only recently become established. In all other instances their flow cytometric signature was clearly defined in the deep euphotic zone, although it usually disappeared into the baseline noise in samples collected from above the 5% isolume. Maximum cell concentrations at the majority of the stations ranged from $5\times10^4$ to $1.2\times10^5$ cells ml$^{-1}$. Only 10 of the stations had fewer, and these tended to be coastal locations. The depth at which the cells were easily detectable and maximally abundant was closely related to the depth of the primary nitrite maximum layer, a chemical marker for the bottom of the euphotic zone[10]. The *Synechococcus* population was always located above the nitrite maximum layer (see Fig. 1*b*), which was always 20–100 m below the top of the thermocline.

Wet mounts from a cell concentrate collected from 100 m and examined by light microscopy, revealed small coccoid to rod-shaped cells under phase contrast illumination that fluoresced red when examined by epifluorescence microscopy using the Zeiss filter set 48 77 05. Transmission electron micrographs of samples from the same cell concentrate revealed an abundance of prokaryotic cells that were smaller and more numerous than their *Synechococcus* neighbours, and had closely appressed peripheral thylakoids (Fig. 2*b*). These cells are identical in appearance to those described by Johnson and Sieburth[2] as type II *Synechococcus* which they also found to be numerically dominant at 100 m in the Sargasso Sea. These authors noted that the fluorescence properties of the cells suggested that they might not contain phycoerythrin. The tight packing of the thylakoids in these cells is similar to that seen in prochlorophytes[11], and rather distinct from *Synechococcus*. The latter have widely spaced thylakoids (40–50 nm) accommodating phycobilisomes on the outside of the membranes[12] (Fig. 2*a*). The ultrastructure of the cell shown in Fig. 2*b*, especially the arrangement of the cytoplasmic membrane system, also resembles that of nitrifying bacteria belonging to the genus *Nitrosomonas*[13]. But marine representatives of *Nitrosomonas* possess a sculptured outer cell wall layer[13] which is lacking in our cells, and their reported concentrations[14] for the open ocean are of the order of 50 cells per ml.

Dual beam flow cytometric analysis[9] of the cells, in addition to indicating the absence of phycoerythrin, revealed that the relative intensity of their red fluorescence (660–700 nm) when excited by blue light (488 nm) was about six times that when excited by green light (515 nm). This suggests the absence of phycocyanin and photosynthetically active carotenoids. Analysis of the cells' pigment composition by HPLC gave a unique combination of pigments (Tables 1 and 2): A new type of chlorophyll *a*, probably divinyl chlorophyll *a* (see footnote to Table 1), chlorophyll *b*, zeaxanthin, α-carotene and traces of another uncharacterized pigment, possibly chlorophyll *c* or a chlorophyllide. Lutein, β-carotene, and prasinoxanthin were not detected and normal chlorophyll *a* was present in traces, constituting only 1.7% of the total chlorophyll-*a* fraction. The absence of xanthophylls other than zeaxanthin, especially prasinoxanthin or lutein, is consistent with our observation that



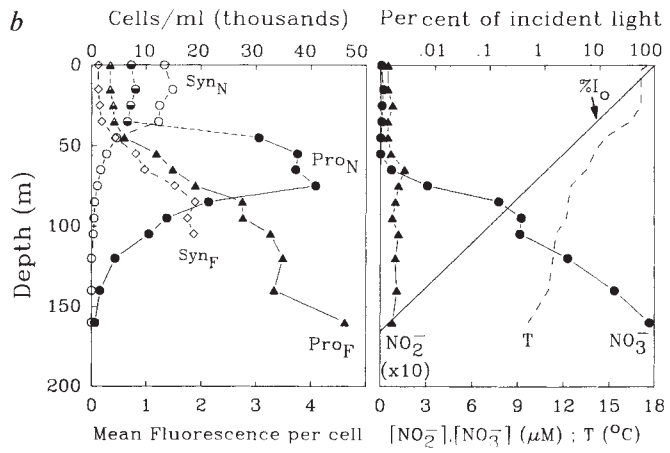




**Fig. 1** *a*, Flow cytometric signatures of *Synechococcus* and the novel prochlorophytes from a depth profile off Southern California (33°11.73′ N, 118°29.82′ W; 14 December 1987). Data from measurements of up to 50,000 individual cells per sample are presented as two-dimensional flow contour plots. Measurements were made using a Coulter Epics V flow cytometer[9]. Left, forward light scatter versus orange fluorescence (from phycoerythrin) reveals *Synechococcus* populations (Syn) in the upper waters. Fluorescent beads (0.9-μm diameter, Duke Scientific) were added as internal standards. Right, forward light scatter versus red fluorescence reveals very small cells (Pro) dominating the deeper samples. The less dense cloud of larger cells with brighter fluorescence is a mixture of eukaryotic phytoplankton cells about 2–5 μm in diameter. Signals from *Synechococcus* cells and the standard beads are not visible here because the data have been gated to show only signals from particles having no orange fluorescence. *b*, Depth profile of biological and hydrographic features at the station described in *a*. Temperature ($T$) was obtained from an expendable bathythermograph; light penetration (% $I_0$) was calculated from Secchi depth according to ($I_z = I_0 e^{-kz}$, where $I_z$ = the light intensity at depth $z$, $I_0$ = incident light intensity, and $k = 1.7$/Secchi depth); nitrate and nitrite ($NO_3^-$, $NO_2^-$) were analysed by standard techniques[24]. Samples in which we were able to see only part of a population in the flow cytometric signature are indicated by half-filled symbols and dashed lines. Mean fluorescence per cell ($Syn_F$, $Pro_F$) from flow cytometric signatures are expressed relative to uniform standard beads for each emission band[8]. Cell concentrations ($Syn_N$, $Pro_N$) were calculated as described in Olson *et al.*[8].

**Table 1** Concentrations of pigments in the prochlorophytes and their absorption maxima ($A_{max}$) compared to those reported in the literature. The samples were from 100-m depth in the Gulf Stream (38°09.5′ N, 66°50.8′ W; 19 September 1987)

| Pigment | Concentration* (fg cell$^{-1}$) | $A_{max}$† this study (nm) | $A_{max}$ reported (nm) | Reference |
|---|---|---|---|---|
| Chlorophyll *a* | trace‡ | — | 428, 660 | 22, 23 |
| Pheophytin *a* | — | 408, 667‡ | 408, 667 | 22, 23 |
| Divinyl chlorophyll *a* | 2.15‡ | — | 436, 661 | 22, 23 |
| Divinyl pheophytin *a* | — | 417, 667‡ | 417, 667 | 22, 23 |
| Chlorophyll *b* | 2.31 | 457, 646 | 455, 645 | 17 |
| Zeaxanthin | 0.69§ | (429), 450, 478 | (425), 450, 478 | 17 |
| α-Carotene | 0.29 | (423), 444, 475 | 423, 444, 473 | 28 |

* Cellular concentrations of pigments are means from five filter-fractionated (0.6–0.8 μm) samples extracted in 100% acetone and analysed by reverse phase HPLC on a Microsorb C-18, 3-μm column using a slightly modified version of the method of Mantoura and Llewellyn[27]. The samples were gravity-filtered through Nuclepore filters, and the resulting fraction was analysed by flow cytometry as well. The fractions consisted of 98% prochlorophytes according to their integrated light scatter and fluorescence signals, thus they were considered a 'pure' sample for our purposes.

† Absorption spectra were obtained on pigments from a much larger sample obtained by tangential flow filtration of 100 l of whole seawater from 70 m at the same station. The chlorophyll *a* pigments and their derivatives were analysed in diethyl ether; chlorophyll *b* and zeaxanthin in acetone, and α-carotene in ethanol. Numbers in parentheses indicate the presence of a shoulder rather than a peak in the spectrum.

‡ Chlorophyll *a* and the divinyl chlorophyll-*a*-like pigment are not fully resolved on the reverse-phase HPLC system used, however, their respective pheophytins are. Thus we collected the two coeluting pigments, converted them to their respective pheophytins by acidification with 1N HCL and isolated the two pheophytins. The absorption maxima of the new type of pheophytin-*a* are identical to those published by Bazzaz[22,23] for divinyl pheophytin-*a*, thus we hypothesize that the new chlorophyll *a* in our samples is divinyl chlorophyll *a*.

§ Because zeaxanthin and lutein coelute on this system, we confirmed the absence of lutein in the samples by analysing the zeaxanthin fraction on a reverse-phase isocratic tetrahydrofuran:$H_2O$ (45:55% by volume) system which separates the two pigments.

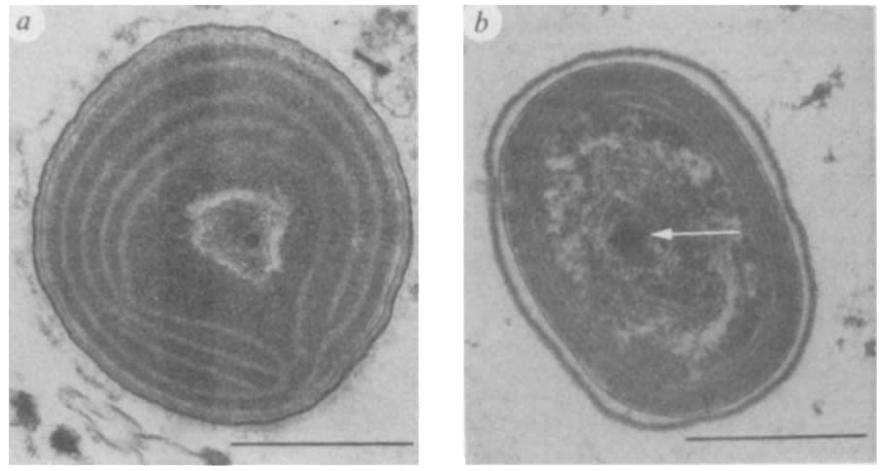



**Fig. 2** Electron micrographs of thin sections of marine *Synechococcus* (*a*) and prochlorophyte (*b*). Cells were concentrated by tangential flow filtration from 600 l of water collected at 100 m at 36°07.9′ N, 64°18.1′ W, 11 September 1987. The primary distinction between the two organisms is the arrangement of the photosynthetic thylakoids. Note the carboxysomes (arrow) in the prochlorophyte indicating that it contains one of the key autotrophic enzymes (RUBP carboxylase). Flow cytometric analysis of the cell concentrate before fixation indicated that prochlorophytes outnumbered *Synechococcus* by a factor of 100; in the thin sections examined, the ratio of prochlorophytes to *Synechococcus* was 5 ($n = 50$). We attribute the differences to losses of the prochlorophytes during fixation. Scale bar, 0.5 μm.

the cells are prokaryotic[15,16], and the presence of chlorophyll *b* confirms that they belong in the *Prochlorophyta*[11]. The presence of α-carotene is puzzling, because it is generally assumed that prokaryotes are unable to synthesize carotenoids with epsilon-rings[15,17], like α-carotene. We expect that some β-carotene was present as a metabolic intermediate, but was below our limit of detection. The chlorophyll *a*/*b* ratio measured for these cells is approximately 1, which contrasts sharply with that of *Prochloron* (4–7)[18] and *Prochlorothrix* (8–9)[19] (Table 2), but is similar to values reported for marine chlorophytes (1–3)[20].

Perhaps the most unusual pigment characteristic of the cells is the divinyl chlorophyll-*a*-like molecule. This pigment elutes earlier than chlorophyll *a* and is characterized by a red-shift of the Soret peak by 8–10 nm compared to normal chlorophyll *a*. Gieskes and Kraay[21] isolated a pigment very similar to this from the less-than-one μm fraction in surface waters of the tropical Atlantic. The absorption maxima for this pigment (436 and 661 nm in diethyl ether) are identical to those reported by Bazzaz[22,23] for divinyl chlorophyll *a*.

At several stations we were able to obtain estimates of the primary production attributable to the prochlorophytes, using the carbon-14 method[24,25] coupled with post-incubation size fractionation (collecting the 0.4–0.8-μm fraction using Nuclepore filters). These data were corroborated by sorting the cells in question after incubation with $^{14}$C-labelled bicarbonate, using the cell-sorting capability of the flow cytometer[26]. The proportion of total productivity below the 1% isolume attributable to these cells ranged from 15 to 60%; absolute rates of production ranged from $7 \times 10^{-3}$ to $1.2 \times 10^{-1}$ μg C $l^{-1}$ $h^{-1}$. If we assume that the cells are 0.8-μm-diameter spheres with the same relative C content as cultured *Synechococcus*[12] (200 fg $\mu m^{-3}$), the results of our carbon fixation experiments translate into doubling times ranging from 2 to 10 days.

These prochlorophytes seem well adapted for life at the bottom of the euphotic zone; high concentrations of chlorophyll *b* as well as the red shift of the Soret peak of the divinyl chlorophyll-*a*-like pigment optimizes absorption of which blue light (460–480 nm) dominates the deep ocean. We have been unable to adequately quantify the prochlorophytes in the upper waters of the euphotic zone with the flow cytometer because of their reduced fluorescence and light scatter at these depths (Fig. 1*a*). But the divinyl chlorophyll-*a*-like molecule associated with these cells has been detected in the surface layers of the tropical and subtropical Atlantic[21], suggesting that they are sometimes abundant in the upper waters of the oceans.

Unfortunately, our attempts to isolate these cells into pure culture have failed. Johnson and Sieburth[2] reported similar difficulties with their Type II prokaryotes, although they had no difficulties isolating *Synechococcus* from the same waters. Although unequivocal identification of our red-fluorescing picoplankters awaits their isolation and nucleotide sequencing, the evidence presented here indicates that they represent a new type of chlorophyll-*b*-containing prokaryote, that is, a Prochlorophyte (*sensu* Lewin[11]). They differ from other members of this group in that they contain a different type of chlorophyll *a*, α-carotone rather than β-carotene, and the chlorophyll *a*/*b* ratio of cells found at the bottom of the euphotic zone is significantly lower than that of *Prochloron* or *Prochlorothrix* (Table 2). If our identification is correct, they represent the first free-living marine prochlorophyte, and elevate the status of this division to one of considerable importance in marine ecosystems. Regardless of taxonomic affinity, their ubiquity and abundance indicates that they are a significant component of the microbial food web and potentially important primary producers in temperate and tropical oceans.

We thank E. V. Armbrust, M. Gerath, H. Sosik, A. Lewitus and F. Valois for their assistance and the captains and crews of

**Table 2** Comparison of the pigment composition of the prochlorophyte with its prokaryotic relatives[16,17,19]

| Pigment | *Prochloron* | *Prochlorothrix* | *Synechococcus* | New prochlorophyte |
|---|---|---|---|---|
| Chlorophyll *a* | + | + | + | − |
| Divinyl chlorophyll *a*-like pigment | − | − | − | + |
| Chlorophyll *b* | + | + | − | + |
| Chlorophyll *a*/*b* ratio | 4–7 | 8–9 | | 1* |
| Phycobiliproteins | − | − | + | − |
| α-Carotene | − | − | − | + |
| β-carotene | + | + | + | − |
| Zeaxanthin | + | + | + | + |

* Note that this ratio was measured on cells found deep in the euphotic zone, and could change in cells grown in high light.

the RVs Gyre, Oceanus, Knorr and Atlantis II for their cooperation. This work was supported by grants from the US National Science Foundation and Office of Naval Research.

Received 18 May; accepted 10 June 1988.

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# Mineral nutrition and spatial concentrations of African ungulates

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**Africa's abundant large herbivores are very heterogeneously distributed, both geographically and regionally[1]. Within a region, some localities contain dense animal concentrations although areas nearby may be virtually unoccupied. Mixed-species herds are a conspicuous feature of areas where animals concentrate[2-4]. The prevailing explanations of local distributional concentrations are (1) that different herbivore species facilitate each other's foraging, and (2) that animals are protected from predation by both intraspecific and interspecific association[5-9]. If facilitation of grazing were an overriding factor, mixed species herds should move extensively with localized rain showers to obtain the greatest forage yield[10]. If predation were the major factor influencing animal densities and distributions, rapid, unpredictable spatial movements would further reduce predation. But because resident, non-migratory species tend to occupy home ranges that are stable over time[11], neither of these hypotheses is totally compelling. Because tropical forages are of lower quality than temperate ones and are often chronically deficient in mineral elements[12], I tested the hypothesis that areas where animals concentrate are localities supporting forages of higher mineral content. I report here that the mineral content of foods is an important determinant of the spatial distributions of animals within the Serengeti National Park, Tanzania. Based on ecological critieria, magnesium, sodium and phosphorus appear particularly important.**

Areas supporting high densities of animals were identified using data and observations collected since 1974 in the course of studies of the grazing ecosystem in the park[13-15] and from the records of the Serengeti Ecological Monitoring Programme, mainly concentrated from 1969 to 1978 (ref. 16). No locations were sampled on the Serengeti Plains because they are not occupied by herbivores all year around. During the 1986 wet season, samples of the youngest leaf blades on actively growing grasses were collected from grasslands on and adjacent to areas of high and low animal density, dried, returned to Syracuse University, and analysed by inductively coupled plasma spectrometry using standard sample preparation and analytical protocols[17-19]. Soil samples from the upper 10 cm immediately below sampled grasses were collected simultaneously and treated with similar protocols. Data for the 19 elements determined in forage samples were analysed for location by discriminant analysis followed by a Kruskal-Wallis rank analysis to determine which elements differed significantly between the different localities. Soil samples were compared by the Kruskal-Wallis test for elements discriminating between forage samples.

Discriminant analysis indicated that the mineral contents of forages differentiated areas of high and low animal density with a high degree of accuracy. Only two of 33 control and two of 36 from areas of high animal density were misclassified ($\chi^2 = 69.9$, $P < 0.000001$; canonical correlation = 0.843). Ten of the 19 elements differed significantly between control forages and those supporting a high animal density (Table 1). The largest proportional difference was in Na concentrations, which averaged over three times higher in the latter forages. Concentrations of Al and Fe were over 80% higher in these forages; P concentrations were 50% greater, Mn and Pb 40% greater, and Ca, Mg and V 10-23% greater. Ni was much lower in forages supporting high animal densities. Elements important to plants but of minor, if any, importance to animals, such as B, did not differ between localities.

Underlying edaphic and geological properties can contribute to differences in plant mineral concentrations[20-21]. But none of the soil variables aided in interpreting plant variation (Table 2). Thus, ecological factors other than the underlying differences in general physical environments govern the mineralogical differences between forages from grasslands supporting high and low animal densities.

Nutrient availability to both plants from environmental pools and to herbivores from plant tissues is determined by many complex factors involving both the biotic and the abiotic components of ecosystems[22-26]. Mineral concentrations in plants are a complex function of environmental variables as well as such plant properties as species, ecotype, growth stage, tissue and growth rate[27], many of which will vary between the grazed grasslands of areas of high animal density and the ungrazed areas sampled here as controls[10,13-15]. But the restriction of samples to the youngest leaves of actively growing grasses would have stabilized many potential variables[22-27]. Animal nutritional status will also depend upon a wide variety of factors, including the plant variables above, as they affect intake and digestibility, as well as other complex environmental and animal properties[24-26]. But forage mineral analysis is a reliable index of the general ability of forages to meet animal mineral needs[12], and the data reveal several potentially important nutritional differences between forages on areas of high animal density and control locations. Using beef cattle feeding standards[28] as an approximate index of nutritional requirements of ruminants, of those elements distinguishing forages from the two types of localities, on control locations Mg and Na were below general standards, whereas P was below the requirements for lactating cows and growing animals. There can be little doubt that Na is an important component of the nutrition of wild animals[29-32] and the data indicate that grazers on the Serengeti can meet their dietary Na needs solely from forages with high nutrient concentration, an unusual occurrence in animal nutrition[12,24-26]. Based on