ICARUS **129,** 245–253 (1997)
ARTICLE NO. IS975786

Biological Potential of Extraterrestrial Materials

2. Microbial and Plant Responses to Nutrients in the Murchison Carbonaceous Meteorite

Michael N. Mautner

Space Bioresources Laboratory, and Department of Soil Science, Lincoln University, Lincoln, New Zealand; and Department of Chemistry, University of California, Santa Cruz, California 95064
E-mail: mautnerm@lincoln.ac.nz

Anthony J. Conner

New Zealand Institute for Crop and Food Research, Private Bag 4704, Christchurch, New Zealand

Kenneth Killham

Department of Plant and Soil Science, University of Aberdeen, Aberdeen, Scotland AB24 3UE, United Kingdom

and

David W. Deamer

Department of Chemistry, University of California, Santa Cruz, California 95064

Received January 6, 1997; revised May 14, 1997

Meteoritic materials are investigated as potential early planetary nutrients. Aqueous extracts of the Murchison C2 carbonaceous meteorite are utilized as a sole carbon source by microorganisms, as demonstrated by the genetically modified *Pseudomonas fluorescence* equipped with the *lux* gene. Nutrient effects are observed also with the soil microorganisms *Nocardia asteroides* and *Arthrobacter pascens* that reach populations up to 5×10^7 CFU/ml in meteorite extracts, similar to populations in terrestrial soil extracts. Plant tissue cultures of *Asparagus officinalis* and *Solanum tuberosum* (potato) exhibit enhanced pigmentation and some enhanced growth when meteorite extracts are added to partial nutrient media, but inhibited growth when added to full nutrient solution. The meteorite extracts lead to large increases in S, Ca, Mg, and Fe plant tissue contents as shown by X-ray fluorescence, while P, K, and Cl contents show mixed effects. In both microbiological and plant tissue experiments, the nutrient and inhibitory effects appear to be best balanced for growth at about 1 : 20 (extracted solid : H_2O) ratios. The results suggest that solutions in cavities in meteorites can provide efficient concentrated biogenic and early nutrient environments, including high phosphate levels, which may be the limiting nutrient. The results also suggest that carbonaceous asteroid resources can sustain soil microbial activity and provide essential macronutrients for future space-based ecosystems.

INTRODUCTION

The emergence of life on the early Earth and possibly on Mars (McKay *et al.* 1996) poses a continuing question: What are plausible sources of essential nutrients such as C, N, and the mineral macronutrients S, P, Ca, Mg, K, Fe, and Cl, to support biogenesis and subsequent growth? The potential sources should supply constituents in sufficient concentrations for effective prebiotic synthesis, as well as concentrated nutrients in biologically available forms for primitive organisms.

A potential source for all of the required elements may be the infall of exogenous materials (Anders 1989, Chyba and Sagan 1992, Chyba and McDonald 1995). Materials in carbonaceous chondrites are moderately processed residues of the protosolar nebula (Delsemme 1995), and their composition may be similar to some types of interplanetary dust particles (IDPs), to cometary nuclei, and to C-type carbonaceous asteroids (Morrison 1977, Encrenaz *et al.* 1987, Delsemme 1995). After infall, these materials would be subject to processing under early planetary conditions (Mautner *et al.* 1995) and possibly form concentrated nutrient solutions in fissures and pores in carbonaceous meteorites (Mautner 1997) or by other mechanisms (Clark 1988, Kruger and Kissell 1989, Meurette *et al.* 1995).

0019-1035/97 $25.00

Meteorite materials contain nutrients needed for biological activity. We applied soil analysis to the Murchison C2 and Allende C3(V) carbonaceous chondrites and found bioavailable macronutrient contents similar to those in terrestrial agricultural soils (Mautner 1997). Experiments with simulated tholin materials also demonstrated the potential value of extraterrestrial materials for microbial growth (Stoker *et al.* 1994), as did observations of microbial growth on meteorite extracts (Mautner *et al.* 1995, Mautner 1997).

While the above studies have demonstrated the potential of meteorites to supply biologically important materials, the actual effects of extraterrestrial materials on biological systems have not been examined in detail. In this paper we test the ability of meteorite organics to serve as sole carbon sources for microorganisms, and we examine the growth of microorganisms on meteorite nutrients at various concentrations. We also investigate the changes in plant tissue cultures associated with exposure to meteorite materials and measure the uptake of specific meteorite nutrients by plants. The biological effects are discussed in the context of prebiotic and early nutrient roles and as resources for space-based ecosystems (O'Neill 1974, O'Leary 1977, Ming and Henninger 1989).

EXPERIMENTAL

1. Meteorite Extracts and Reference Solutions

Meteorite extracts for microbial cultures and plant studies were prepared using Murchison meteorite powder hand-ground to 40 ± 15-μm mesh size and extracted in deionized (DI) water (>18.3 Mohm/cm, 121°C, 15 min) under standard sterilizing conditions. Soil extracts were obtained from equal amounts of A horizon (0–13 cm) Lyndon area (Typic Ustochrept, loamy, mixed, mesic dark grayish brown, moderately developed) and Templeton-area (Udis Ustochrept, fine loamy mixed, mesic) New Zealand soils. Both soils were agriculturally used but not fertilized for the last 10 years. These soils were extracted by the same method applied to the Murchison meteorite.

For plant tissue cultures, 80 mg of Murchison powder was extracted as above in 1 ml deionized water. Aliquots of 45 μl, containing also 5 mg of the extracted powder, were mixed with 45 μl of water blanks, or standard plant nutrient solutions (Murashige and Skoog 1962) or partial nutrient solutions to give the solutions listed in Table II below. The resulting culture solutions contained 3% sucrose and/or 10 m*M* concentrations of the inorganic salts specified below plus the meteorite extracts. All tools and glassware used in the meteorite and microbial preparations were cleaned in sulfuric acid/chromic acid solutions overnight.

2. Microbial Test for Carbon Utilization

To examine meteorite materials as biological energy sources, 20 mg Murchison meteorite was extracted in 2 ml deionized H_2O in three replicate experiments. After filtering through carbon-free membranes, 900-μl aliquots, or in controls, of deionized water, were mixed with 100-μl microbial cultures of late log phase *Pseudomonas fluorescens* 10586s/pUCD607 containing *Vibrio fischeri lux* A, B, C, D, and E genes on a multicopy plasmid. The microbial solutions were prepared from freeze-dried cells and resuscitated into 0.1 ml of 0.1 *M* KCl to yield populations of 3×10^9 cells/ml.

These microorganisms are sensitive probes of energy sources which they use to synthesize ATP and subsequently to produce luminescence. Light emission was measured 15 min after mixing the extract and microbial solution by luminometer measurements every 15 sec. The light output vs nutrient concentration was calibrated by the addition of 900 μl of glucose solution as a standard carbon and energy source to 100 μl microbial solution as follows (% final glucose solution and response in relative light units (rlu)): 0.009%, 2480 rlu; 0.045%, 11,230 rlu; 0.09%, 23,820 rlu.

3. Microbial Growth Methods

Microbial cultures were prepared using microorganisms that grew in unsterilized samples of Murchison meteorite powder in water. Aliquots from the liquid were spread and cultured on nutrient agar, and individual colonies that grew from these samples were then cultured in tryptic soy broth. One microorganism was a gram-positive, rod and club-shaped, coccus forming, nonmotile aerobic heterotroph. These features and fermentation analysis suggested a corynform actinomyscete, which was identified by fatty-acid analysis (Microbial ID, Newark, Delaware) with a Microbial Identification System similarity index of 0.449 as the actinomycete named, fortuitously, *Nocardia asteorides.* Another microorganism isolated from the unsterilized meteorite solution was identified with a similarity index of 0.423 as *Arthrobacter pascens* (Dohrman, K. L., personal communication). The microorganisms were grown in tryptic soy broth to populations of $>10^7$ CFU/ml, centrifuged to pellets, dispersed in 5 ml DI water, and centrifuged again to pellets; the procedure was repeated four times. This procedure achieves a dilution of residual nutrients from the soy broth by a factor of $>10^8$, to nominal concentrations of $<3 \times 10^{-7}$ g liter^{-1}, negligible compared with the organic content of 10^{-4} to 10^{-2} g liter^{-1} in the meteorite extracts. Aliquots of 10 μl from the final dispersed pellet were used to inoculate meteorite extracts (or control blanks of DI water) of 200–400 μl in 2-ml vials to yield initial populations of 2×10^4 CFU ml^{-1}.

The vials containing the samples were fitted with filters made of Pasteur pipettes and packed with 2–4 cm activated

charcoal to allow air exchange but to minimize uptake of airborne organics. The cultures were incubated in the dark at 20°C. For population counting, 10-μl aliquots were withdrawn at the time periods shown in Fig. 1, diluted by factors $1–10^4$ as necessary, spread and incubated on nutrient agar for 2 days at 20°C, and the resulting colonies were counted manually.

In each experimental series, the cultures in DI water blanks were processed in 4 replicates and each meteorite extract culture in 2 replicates. The population counts in the replicate cultures within each series was in general equal within a factor of 2, and the average values of the replicate samples were used in the final analysis. As a measure of the reproducibility of the experimental series, 4 replicate series of *Nocardia asteroides* grown in extracts of 20–50 mg Murchison powder into 1 ml DI water were performed and gave postlog populations of 2.5×10^7, 2.7×10^7, 2.0×10^7, and 3.6×10^7 CFU ml^{-1}, with an average of 2.7×10^7 and standard deviation of 0.7×10^7 CFU ml^{-1}. The DI water blanks in 4 replicate series gave postlog populations of 1.0×10^5, 7.5×10^5, 1.7×10^5, and 1.5×10^6 CFU ml^{-1} with an average of 4.5×10^5 and standard deviation of 4.7×10^5 CFU ml^{-1}. The populations in the extract are clearly significantly higher than in the DI water blanks. The growth and scatter in the water blanks can be attributed to residual nutrients carried over from the soy broth with the microbial inoculant. Comparison with the blanks shows that only a fraction of 0.017 of the population in the meteorite extract is due to the nutrient contaminant from the soy broth.

4. Plant Tissue Cultures

Plant tissue cultures were grown in the solutions described in Section 1. The tissue samples were established from *in vitro Asparagus officinalis,* cultivar Karapiro, and *Solanum tuberosum,* cultivar Iwa, cultured as described previously (Conner *et al.* 1991, Conner and Falloon 1993). The tissue cultures were grown from meristem samples that were dissected from plants grown in full nutrient medium for 10–30 days. The apical meristem shoot tips, about 1 mm long and weighing about 0.1 mg, were dissected and cultured in sealed 1.5-ml microfuge tubes for 26 days at 25°C under illumination by cool-white fluorescent lights with flux of 80 μE m^{-2} s^{-1} using 16-hr photoperiods. After the growth period, the samples were removed from the growth vials, dried of excess liquid with filter paper, and weighed within one minute for the determination of the fresh weights. Rapid weighing was essential as the small plants of several milligrams showed noticeable drying and moisture loss after 5 min.

Typical experiment sets consisted of 6–10 plants each in control media (nutrient + water) and sample media (nutrient) + meteorite extract (at concentrations of 3% sucrose and 10 m*M* each salt, when applied). Experiment sets in several of the media used were replicated 2–5 times. Scatter in resulting fresh weights may have resulted from variations in the size of the excised meristem tissue samples and from variation among the quality of source plants, especially those obtained from different cultures that may differ in stored nutrient content.

For each nutrient medium in Table II, controls and samples grown from one culture can be compared. However, samples used for experiment sets in the various nutrient media had to be obtained from different plant culture sets, and fresh weights in various media cannot be intercompared. Since the functional form of sample distributions is unknown, the p values for the differences between the controls and samples in Table II were calculated using nonparametric Mann–Whitney statistics.

For elemental analysis, the plant samples grown in various media were freeze dried to obtain 1.5–6.0 mg of dry mass for X-ray fluorescence analysis. The samples were ground, applied to a backing of cellulose, and pressed at 2000 psi for 20 sec. Measurements were performed with a Philips PW2400 spectrometer using a Rh super Sharp tube, Pe, Ge, PX1, and LiF200 crystals, with Duplex flow and sealed detectors. For measurements on the small samples, the output in X-ray counts/sec was calibrated using 2, 4, 8, 12, and 20 mg samples of NIST standard materials, containing, for example, 1.527% Ca and 0.18% S. The calibration plots were linear over the range of the sample outputs (Winter, S., personal communication).

RESULTS AND DISCUSSION

1. Meteoritic Organics as a Carbon Source

To test if the meteorite organics can serve as sole carbon sources, the genetically modified *Pseudomonas fluorescence* cultures were used as described above. Three replicates of the meteorite extract addition to the microbial cultures resulted in 4560, 7200, and 5010 rlu, or 5590 ± 1412 rlu (compared with 120 rlu with an H_2O blank). The light emission corresponds to an interpolated equivalent response to a 0.021% glucose solution that would contain 8.6×10^{-5} g/ml of organic C. In comparison, aqueous extraction of Murchison yields 0.18% of the meteorite mass as extractable C, and the samples of 20 mg extracted into 1 ml H_2O therefore yield 3.6×10^{-5} g/ml of organic C (Mautner *et al.* 1995). We note the similarity of the calibrated and measured available C. Since the light emission is proportional to the rate of ATP production, the results suggest that the extracted meteorite carbon is utilized faster than glucose by a factor of 2.4. The difference may be due to the constitution of the extracted organics, mostly short-chain carboxylic acids, and to the presence of mineral macronutrients in the meteorite extract (see below) that can enhance the metabolization rate.

TABLE I
Elemental Concentrations (μg ml^{-1}) in Microbial Culture and in Meteorite and Soil Extracts

	C	N	S	P	Ca	Mg	K	Fe	Cl
N. asteroides culture[a]	2.3	0.4	0.02	0.13	0.02	0.03	0.5	0.001	0.01
Murchison extract[b]	90	5	390	0.28	120	110	40	1.0	15
Soil extract[c]			2.1	0.12	5.1	0.83	2.5		2.6
Soil solution[d]	4		5	0.005	32	25	3.5	0.2	10
MS growth medium[e]	7800	840	48	39	120	36	740	5.6	213

[a] Elemental content in the microbial biomass in 1 ml culture of 2.7×10^7 CFU ml^{-1} of *N. asteroides*, based on microbial sizes as in text, using microbial elemental concentrations Bowen (1966) with 1:5 dry/wet biomass weight ratios.
[b] From data for hydrothermal extracts at 121°C for 15 min (Mautner 1997) recalculated for 50 mg Murchison powder extracted in 1 ml H_2O.
[c] In extracts of 25 mg Lyndon + 25 mg Templeton soils in 1 ml H_2O, extracted at 121°C for 15 min.
[d] Typical soil solution (Bowen 1966).
[e] Nutrients in standard growth medium (Murashige and Skoog 1962).

2. *Microbial Growth on Meteorite Nutrients*

The nutrient content of a typical meteorite extract used in the present experiments is shown in Table I. Previous studies showed that a microorganism tentatively identified as *Flavobacterium oryzihabitans* grew to populations $>10^7$ CFU/ml on Murchison extracts, compared with 10^5 CFU/ml in deionized water blanks (Mautner *et al.* 1995). A small nutrient effect was also observed with *Pseudomonas maltophilia.* These results showed that as sole nutrient source, the meteoritic extracts serve as a source both of energy and elemental nutrients. In this paper, we test the nutrient effects in more detail.

Figure 1 shows the relation between concentrations of meteorite extracts and microbial growth. The postlog phase populations increase with increasing concentration. Solutions obtained by extracting varying amounts of Murchison powder in 1 ml H_2O led to the following populations of *Nocardia asteroides* (extracted powder (mg)/ml H_2O, population (CFU/ml): water blank, 1.0×10^5 CFU ml^{-1} in the culture series shown in Fig. 1, or 4.5×10^5 CFU ml^{-1} (standard deviation 4.7×10^5 CFU ml^{-1}) in 4 replicate series; 1 mg, 2.5×10^6 CFU ml^{-1}; 5 mg, 4.7×10^6 mg ml^{-1}; 20 mg, 2.5×10^7 CFU ml^{-1}; 50 mg, 2.7×10^7 CFU ml^{-1} in the series in Fig. 1, or 2.7×10^7 CFU ml^{-1} (standard deviation 0.7×10^7 CFU ml^{-1}) in 4 replicate series; 100 mg, 5.0×10^7 CFU ml^{-1}. According to the precision observed in the 50 mg in 100 ml solutions, the dilution effects observed with the other concentrations appear to be significant. We also observed similar relations with extracts of the Allende meteorite, and for reference, with soil extracts as shown in Fig. 1 and with soy-broth nutrients. In soy broth, a 0.03 g liter^{-1} solution gave 2.3×10^7 CFU ml^{-1} and a 30 g liter^{-1} solution gave 1.7×10^9 CFU ml^{-1}. With *Arthrobacter pascens,* in an extract from 5 mg Murchison powder into 100 ml H_2O we obtained a postlog population of 2.7×10^7 CFU ml^{-1}, and in an extract from 50 mg powder into 100 ml H_2O we obtained a population of 7.1×10^6 CFU ml^{-1}. In these cultures, the decrease at the highest concentration may be due to toxic effects.

Extraction conditions have only a modest effect on the nutrient potential. For example, extracts produced from 20 mg Murchison in 1 ml H_2O at 20°C for 2 hr, 121°C for 15 min, and 300°C for 2 hr gave postlog populations of 7.0×10^6, 2.5×10^7, and 1.5×10^6 CFU ml^{-1}, respectively. The first increase for extracts produced at 121°C may be due to increased extraction efficiency, while the decreased growth in extracts produced at 300°C may be due to released toxics or to the partial decomposition of nutrients.

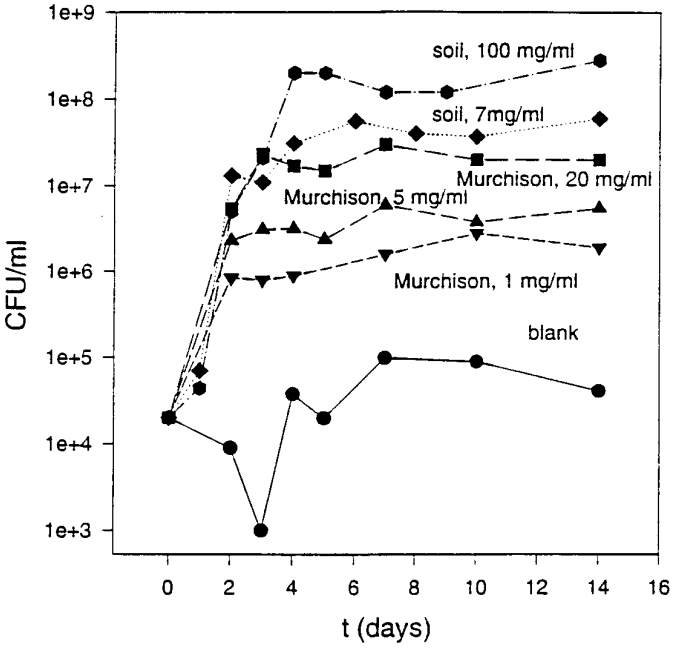

FIG. 1. Populations of *Nocardia asteroides* in extracts of Murchison meteorite powder in deionized water at powder/H_2O ratios (w/w) as shown and in soil extracts (see text).

The observed relations between extract concentration and population density support the conclusion that the extracted materials are utilized for biomass synthesis. The elemental contents of the meteorite extract and the resulting microbial populations can be compared quantitatively using the average volume of the *Nocardia asteroides* cells that we obtained from electron microscopy and average bacterial elemental contents (Bowen 1966). It should be noted that possible different specific elemental composition of *Nocardia asteroides*, and scatter in the microbial volumes, may make the quoted biomass content uncertain by an order of magnitude. Table I shows that the meteorite extract contains most macronutrients in great excess over the requirements for the observed biomass. However, for P present as orthophosphate, the amounts are comparable. The notable effect observed upon even modest dilution of the meteorite extract therefore probably suggests that P is the limiting nutrient.

We also tested the long-term viability of the cultures. Figure 1 shows steady-state populations after about 8 days, which were further tested and found to be similar at 30 days. To investigate long-term microbial survival in the meteorite extracts, populations of *Nocardia asteroides* were processed through three cycles of growth, extraction and reinoculation in Murchison extract over a total period of 192 days. The last inoculated culture in the series showed a viable population after 162 days in the meteorite extract. The morphology of this third-generation long-term culture was on the average more coccoid than the fresh cultures. In a population of 60 cells in first generation, fresh 6-day meteorite extract cultures, rod or club-shaped microorganisms had average diameters of 0.7 ± 0.1 μm and lengths of 2.5 ± 0.9 μm, compared with 0.8 ± 0.2 and 1.9 ± 0.8 μm, respectively, in the long-term populations. In the fresh populations, 47% were elongated with length/diameter ratios >4, while only 12% were coccoid with length/diameter <2. Conversely, in the long-term populations in meteorite extracts, only 15% were elongated, while 43% were coccoid. A question of interest is whether the change reflects adaptation to the meteorite nutrients or only an effect of prolonged growth in low nutrient solution.

3. Plant Growth on Meteorite Nutrients

Samples of the plants grown from the cultures are shown in Figs. 2 and 3. In the partial growth medium in Fig. 2, mostly stem and leaf development from the meristem tissue is observed, whereas the full growth medium shows larger plants and some root development. The effect of the meteorite extract in Fig. 2 shows enhanced size, structural development, and coloration. For *Asparagus officinalis* the enhancement is larger with the more concentrated extract, while for *Solanum tuberosum,* with the more diluted extract. For *Solanum tuberosum* grown in full MS nutrient medium, the concentrated extract shows strong growth inhibition, while plants grown in the diluted extract show some enhanced morphological development. The varying effects of concentration may reflect competing nutrient and toxic effects, as observed also in the plant fresh weights as follows.

The effects of meteorite materials on the fresh weights of *Asparagus officinalis* and *Solanum tuberosum* tissue cultures are shown in Table II. For *Asparagus officinalis*, meteorite nutrients had a statistically significant effect ($p < 0.05$) on product weight when added to water, sucrose + $NH_4H_2PO_4$, or MS medium. While the p factors for other sets were larger, the observed effects were nevertheless well reproducible. For example, in sucrose + NH_4NO_3, two replicate sets with meteorite extract vs blank gave average weight ratios of 1.51 and 1.46, with corresponding p values of 0.17 and 0.05, respectively. With *Solanum tuberosum,* all the p values were >0.05, but the nutrient effects were reproducible. For example, with sucrose + NH_4PO_4, four sets gave weight ratios of 1.03, 1.20, 1.06, and 1.36, all showing increased weight with the meteorite extract vs DI water blank. Although the p values were 0.47, 0.67, 0.70, and 0.20, respectively and not statistically significant, the reproducibility, the analogy with the asparagus results, the observed morphology effects, and nutrient uptake (see below) all suggest that the nutrient effects are meaningful. The statistical scatter resulted from factors quoted above, and in part, the quantitative evaluation is made difficult because of the small absolute weights obtained.

The meteorite effects were most pronounced when the media contained sucrose plus inorganic N and/or P sources. With only sucrose or N and P salts separately, the meteorite extract also had growth enhancing, although statistically insignificant, effects. The nutrient effect of the meteorite extract was most pronounced and statistically significant in the *Asparagus officinalis* culture in the sucrose + $NH_4H_2PO_4$ media, where the main macronutrients N and P are provided by the medium. The inhibitory effect with both *Asparagus officinalis* and *Solanum tuberosum* were statistically significant.

The nutrient effects were also observed in the morphology and pigmentation of the products as shown in Fig. 2 as discussed above. The pigmentation effects probably reflect the elemental tissue contents described below.

The effects of diluting meteorite extracts on the visually observed morphological development were mixed, as discussed above. Correspondingly, the effects on the plant weights were also mixed, as shown in Table II for media containing sucrose + $NH_4H_2PO_4$. The weights of the asparagus plants increased more by adding the full than the diluted meteorite extract. However, with potato plants the diluted extract actually caused the larger increase. These observations suggest competitive nutrient and inhibitory effects, the latter decreasing more rapidly with dilution.

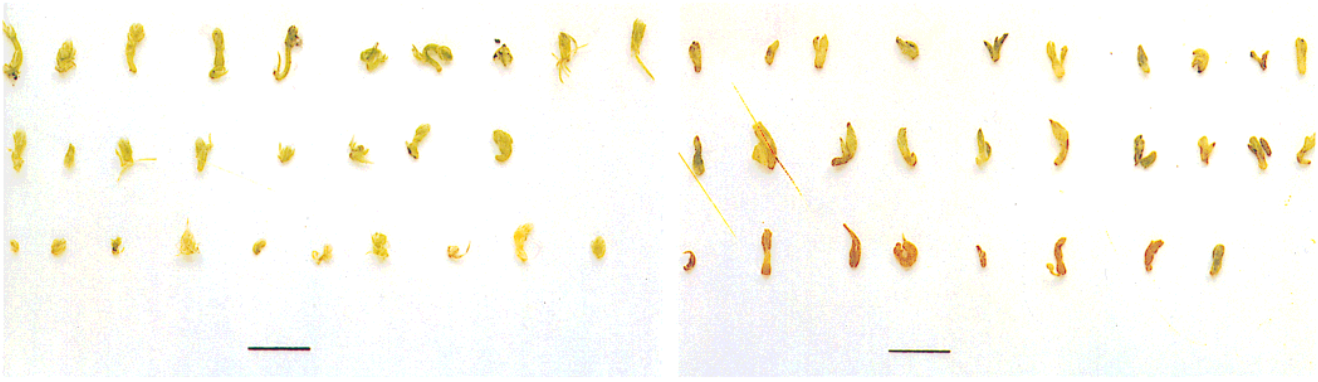

FIG. 2. Asparagus plants (left) and potato plants (right) grown in 3% sucrose + 10 mM $NH_4H_2PO_4$ without (bottom rows) or with Murchison meteorite extract (top rows), or with meteorite extract diluted by factor of 5 (middle rows). Note the increase in growth and green coloration with the meteorite extract. Note decreased growth enhancement in asparagus and increased enhancement in potato plants with dilution of the meteorite extract. Scale bars are 0.7 cm.

The inhibitory effects were observed clearly when meteorite extracts were added to cultures grown in the full MS medium, as shown in Table II and Fig. 3. In several experimental sets, root development was completely eliminated in potato plants, and inhibition of stem and leaf development was observed also in the asparagus plants. Again, possible competition of inhibitory and nutrient effects is observed in Fig. 3, where the full extract decreased the mean fresh weights from 7.2 to 3.8 mg, while the diluted extract caused an increase to 13.8 mg.

To identify the nutrients responsible for these effects, freeze-dried samples were subjected to elemental analysis by X-ray fluorescence. One set selected for these studies was grown in medium containing sucrose, where addition of the meteorite extract led to enhanced green pigmentation and to increased fresh weight by a factor of 1.2. Figure 4 shows that the effects correlated with large increases in S, Ca, Mg, and Fe contents, which are in very high concentrations in the meteorite extract (Table I). With the full MS medium, the addition of the meteorite extract caused large increase in the S, Mg, and Fe contents, and the observed growth inhibition may be related to toxicity at high levels of these elements. The meteorite extract also caused a decrease in the tissue contents of K, Cl, and especially P, possibly by binding these nutrients as insoluble complexes, which would also contribute to decreased weights. The meteorite extract can also contain toxic polycyclic aromatics and phenols (Cronin and Chang 1993).

TABLE II
Meteorite Nutrient Effects on Plant Growth

	Asparagus officinalis				*Solanum tuberosum*			
	Blank[a]	Murchison[a]	n[b]	p[c]	Blank[a]	Murchison[a]	n[b]	p[c]
Water	1.3(0.4)	1.9(0.3)	20	0.01	1.8(0.6)	1.8(0.5)	25	0.55
$NH_4H_2PO_4$	1.5(0.3)	2.1(0.8)	6	0.27	3.0(1.2)	3.9(1.2)	6	0.13
Salts	2.5(0.6)	2.3(1.1)	5	0.46	5.3(2.0)	4.2(1.5)	6	0.30
Sucrose	3.0(1.2)	3.0(1.0)	14	0.86	10.7(4.0)	12.6(3.0)	11	0.32
Sucrose + NH_4NO_3	1.4(1.0)	2.1(0.6)	15	0.17	1.9(0.8)	1.9(0.9)	5	0.87
Sucrose + $NH_4H_2PO_4$	2.2(0.8)	3.7(1.3)	18	0.001	2.1(0.9)	2.3(0.8)	29	0.42
		2.4(1.0)[d]				3.1(1.0)[d]		
MS medium	9.3(4.3)	3.0(1.1)	12	0.003	7.2(1.9)	3.8(3.2)	13	0.08

[a] Mean fresh weight (and standard deviation), mg. Results for one representative set when several sets were run.
[b] Total number of samples in all sets for a given nutrient.
[c] Probability for the comparison of samples and controls derived from nonparametric Mann–Whitney analysis on a combined total of all samples from several sets.
[d] Effect of Murchison meteorite extract prepared as in text and diluted 5:1.

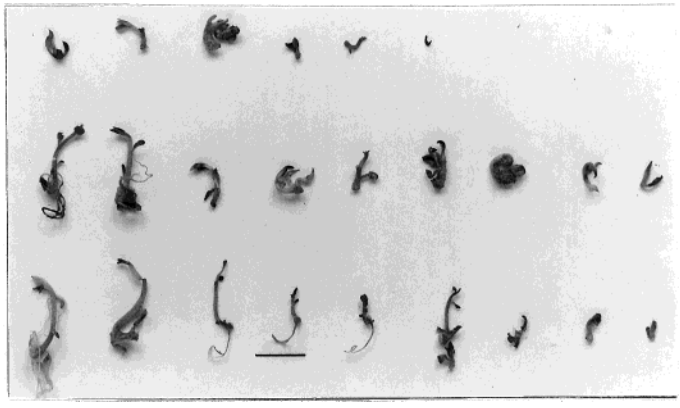

FIG. 3. Potato plants grown in standard growth medium (Murashige and Skoog 1962), without (bottom row) or with Murchison meteorite extract (top row), or with meteorite extract diluted by factor of 5 (middle row). Scale bar 1 cm.

The competition between the nutrient and toxic effects seems to be best balanced in favor of growth by using extracts obtained using solid/H_2O ratios of about 20 : 1 in the present experiments. Table I shows that at this ratio the meteorite extract is concentrated in most macronutrients, except P, by about an order of magnitude more than a typical soil solution, but less concentrated than an optimized plant growth medium. It is similar, except for P, within a factor of 10 to the optimized MS medium and to normal plant tissue content. With respect to P, we observed that exposure to humid air or liquid water can increase the extractable amounts by an order of magnitude. (Mautner 1997). Because meteorite powder was included along with the extract in the plant tissue culture experiments, its exposure to water in the culture may have contributed extra phosphate to the plants.

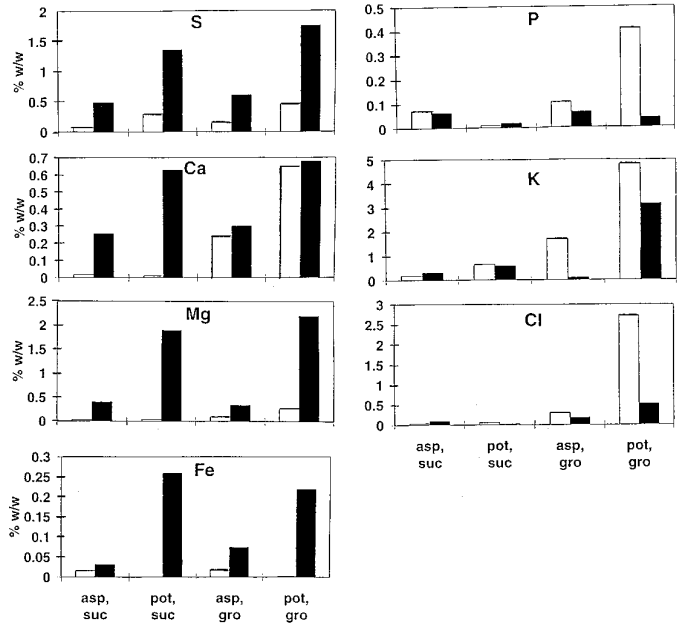

FIG. 4. Elemental contents in freeze-dried biomass of *Asparagus officinalis* (asp) and *Solanum tuberosum* (pot) grown in 3% sucrose (suc) or in standard growth medium (Murashige and Skoog 1962) (denoted (gro)), without (blank areas) and with (filled areas) meteorite extracts.

CONCLUSIONS

The soil nutrient measurements on meteorite materials in the preceding (Mautner 1977) and present paper show that meteorite solutions can provide essential nutrients for biological growth. Micoorganisms can use the meteorite extracts as an energy source, and from the observed growth, also as biosynthetic sources. Plants also show uptake of essential macronutrients from the meteorite solutions and exhibit mixed growth-enhancing and inhibitory effects by these solutions.

These observations may have some interesting implications for biogenic processes and early metabolism and on future space-resource utilization.

For biogenic processes, synthetic reactions and nutrition of early organisms with inefficient feeding mechanisms require concentrated solutions. These solutions could have been achieved by several mechanisms. For example, cometary materials could have accumulated in lakes at impact sites (Clark 1988), but vaporization of the cometary nuclei would make suitable impacts rare. Concentrated solutions could be also obtained in porous interstellar dust particles (Kruger and Kissell 1989, Meurette *et al.*1995), but diffusion from the porous structures or the collapse of the porous structures in water (Mautner *et al.* 1997) may make these sites inefficient.

The meteorite nutrient results suggest another alternative. The soil extraction measurements (Mautner 1997) suggest that microcavities in meteorite fissures, similar to a recent martian sample (McKay *et al.* 1996), would have provided an environment with concentrated solutions of organics, inorganic salts, and especially phosphate, when exposed to aqueous planetary conditions. These materials had biogenic properties, as we demonstrated for the Murchison meteorite (Mautner *et al*. 1995, Mautner 1997). Up to 50% of the meteorite organics, including biogenic components, could be extracted and preserved under hydrothermal conditions simulating the early Earth environment. Amphiphilic components of the hydrothermal extract, such as nonanoic acid, formed bilayer vesicles (Deamer 1985), and polycyclic aromatic compounds found in carbonaceous meteorites have been proposed as potential chromophores for primitive photosynthetic processes (Deamer 1992). As well, meteorites contain amino acids

and other biogenic materials (Cronin and Chang 1994, Chyba and McDonald 1995).

All of these components would be present in cavities and fissures of carbonaceous meteorites exposed to aqueous planetary environments. In the present results we observed nutrient effects best balanced against toxic effects in extracts obtained with a solids/H_2O ratio of 1 : 20. The mineral surfaces can provide catalytic sites, and planetary cold/heat, hydration/dehydration cycles would facilitate intracavity synthesis. Subsequently, the same solutions can provide nutrients to the first microorganisms, until they adapt to the external planetary environment. Although meteorites represented only a small fraction of the early infall, they did provide large absolute quantities of material ($>10^{12}$ kg C in the first Gyr of impacts (Chyba and Sagan 1992)) to allow such processes.

Solutions in meteorite interiors in planetary environments, or possibly in the parent bodies during the hydrothermal processing period (Chyba and McDonald 1995), could have therefore provided a favorable microenvironment for prebiotic and early biological processes. Since early cells would have lacked efficient membrane transport mechanisms, the intracellular elemental composition would have been similar to that of the meteorite solution, and the present biological elemental contents may reflect the early environment. In particular, phosphate would have been available in the meteorite solutions at much higher concentrations than in other natural solutions, such as soil solution or lake or marine waters (Bowen 1966) and would have been closer to the P content of biological tissue. In fact, according to the results in Table I, P would be the limiting element for biological populations in the meteorite solutions.

In relation to the early nutrient roles, effects on primitive anaerobic thermophile microorganisms would be most pertinent. We observed that an anaerobic thermophile eubacterium deeply rooted by 16srRNA phylogeny and probably closely related to early microorganisms, *Thermotoga maritima* (at 80°C), and the thermophiles *Thermus aquaticus* and *Thermus thermophilus* (at 70°C) can grow on the meteorite extract as a sole carbon source (Morgan, H. W., personal communication). These experiments are difficult because of the application of thermophile and anaerobic methods to small meteorite-based samples. Nevertheless, we intend to follow up these preliminary observations.

The uptake of nutrients from meteorite extracts supports proposals to use carbonaceous asteroids for space-based agriculture (O'Neill 1974, O'Leary 1977, Ming and Henninger 1989). This application depends on soil microbial ecology. The responses of species of *Flavobacterium, Pseudomonas, Nocardia,* and *Artherobacter* to meteorite-based nutrients suggest that a diverse soil microbial ecosystem can be sustained. Alternative to soil-based ecology, the present small-scale hydroponic cultures demonstrate that meteorite extracts can provide nutrients for hydroponic solutions, after toxic factors are eliminated.

Similar to the growth on meteorite materials, the results suggest that microorganisms may grow on similar nutrients in carbonaceous bodies, if transported by natural mechanisms or directed panspermia to asteroids, comets, and newly accreting planetary systems (Arrhenius 1908, Crick and Orgel 1973, Mautner 1995, Mautner 1997b).

ACKNOWLEDGMENTS

We thank Drs. R. R. Sherlock and R. L. Leonard for helpful discussions, Mss. L. J. Hassall and M. L. McCloy and Mr. R. J. Creswell for help with soil analysis, Mr. M. Ingerfeld for electron microscopy, Mr. C. Frampton for statistical analysis, and the Smithsonian Institution for samples of the Murchison and Allende meteorites. This work was funded in part by NASA Grant NHEW-4235.

REFERENCES

Arrhenius, S. 1908. *Vernaldas Ultveckling.* Stockholm.

Anders, E. 1989. Pre-biotic matter from comets and asteroids. *Nature* **342,** 255–258.

Bowen, H. J. M. 1966. *Trace Elements in Biochemistry.* Academic Press, New York.

Chyba, C. F., and G. D. McDonald 1995. The origin of life in the Solar System: Current Issues. *Annu. Rev. Earth Planet. Sci.* **23,** 215–249.

Chyba, C. F., and C. Sagan 1992. Endogenous production, exogenous delivery and impact-shock synthesis of organic molecules: An inventory for the origins of life. *Nature* **335,** 125–132.

Clark, B. C. 1988. Primeval procreative comet pond. *Orig. Life Evol. Biosphere* **18,** 209–238.

Conner, A. J., M. K. Williams, R. C. Gardner, S. C. Derolus, M. L. Shaw, and J. E. Lancaster 1991. *Agrobacterium*—Mediated transformation of New Zealand potato cultivars. *New Zealand J. Crop Hort. Sci.* **19,** 1–8.

Conner, A. J., and P. G. Falloon 1993. Osmotic versus nutritional effects when rooting in vitro asparagus minicrowns on high sucrose media. *Plant Sci.* **89,** 101–106.

Crick, F. H., and L. F. Orgel 1973. Directed panspermia. *Icarus* **19,** 341–346.

Cronin, J. R., and S. Chang 1993. Organic matter in meteorites: Molecular and isotopic analyses of the Murchison meteorite. In *The Chemistry of Life's Origins* (J. M. Greenberg *et al.,* Eds.) pp. 209–258.

Deamer, D. W. 1985. Boundary structures formed by organic components of the Murchison carbonaceous chondrite. *Nature* **317,** 792–794.

Deamer, D. W. 1992. Polycyclic aromatic hydrocarbons: Primitive pigment systems in the prebiotic environment. *Adv. Space Res.* **12,** 183–189.

Delsemme, A. H. 1995. A cometary origin of the biosphere: A progress report. *Adv. Space Res.* **15,** 49–57.

Encrenaz, T., J. P. Bibring, and M. Blanc 1987. *The Solar System.* Springer-Verlag, Heidelberg.

Kruger, F. R., and J. K. Kissel 1989. Biogenesis by cometary grains—Thermodynamic aspects of self-organization. *Orig. Life Evol. Biosphere* **19,** 87–93.

McKay, D. S., K. L. Gibson, H. Thomas-Kerpta, C. S. Vali, S. J. Romanek, X. D. F. Clemett, C. R. Chillier, C. R. Maechling, and R. N. Zare 1996.

Search for past life on Mars: Possible relic biogenic activity in the martian meteorite ALH84001. *Science* **273,** 924–930.

Mautner, M. N., R. L. Leonard, and D. W. Deamer 1995. Meteorite organics in planetary environments: Hydrothermal release, surface activity and microbial utilization. *Planet. Space Sci.* **43,** 139–147.

Mautner, M. N. 1995. Directed panspermia. 2. Technical advances toward seeding other solar systems and the foundations of panbiotic ethics. *J. British Interplanet. Soc.* **48,** 435–440.

Mautner, M. N. 1997a. Biological potential of extraterrestrial materials. 1. Nutrients in carbonaceous meteorites, and effects on biological growth. *Planet. Space Sci.* **45,** 653–664.

Mautner, M. N. 1997b. Directed Panspermia. 3. Strategies and motivation for seeding star-forming clouds. *J. British Interplanet. Soc.* **50,** 93–102.

Mautner, M. N., M. S. El-Shall, S. T. Li, and D. Kane. Extraterrestrial materials in planetary environments. 2. Solvent and heat effects on simulated porous interstellar particles. *Planet. Space Sci.*, submitted.

Meurette, M., A. Brack, G. Kurat, M. Perreau, and C. Engrand 1995. Were micrometeorites a source of prebiotic molecules on the early Earth? *Adv. Space Res.* **15,** 113–126.

Ming, D. W., and D. L. Henninger, (Eds.) 1989. *Lunar Base Agriculture: Soils for Plant Growth.* Amer. Soc. for Agriculture, Madison.

Morrison, D. 1977. Sizes and albedos of the larger asteroids. In *Comets, Asteroids and Meteorites* (A. H. Delsemme, Ed.) pp. 177–184. Univ. of Toledo Press.

Murashige, T., and F. Skoog 1962. A revised medium for rapid growth and bioessays with tobacco tissue cultures. *Physiol. Plant* **15,** 473–497.

O'Leary, B. T. 1977. Mining the Apollo and Amor asteroids. *Science* **197,** 363–364.

O'Neill, G. K. 1974. The colonization of space. *Physics Today* **27,** 32–38.

Oro, J., T. Mills, and A. Lazcano 1995. Comets and life in the universe. *Adv. Space Res.* **15,** 81–90.

Stoker, C. R., P. J. Boston, R. L. Manicelli, W. Segal, B. N. Khare, and C. Sagan. Microbial metabolism of tholin. *Icarus* **85,** 241–248.