PLANETARY ECOSYNTHESIS AS ECOLOGICAL SUCCESSION.

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ABSTRACT

Terraforming is the process of applying global engineering techniques to transform the climate of a planet into one that is habitable for terrestrial organisms. Ecosynthesis is the process of introducing a succession of ecosystems to such a terraformed planet. The process of introducing terrestrial ecosystems to Mars can be compared to a descent down a terrestrial mountain. Each drop in elevation results in a warmer, wetter climate and more diverse biological community. Beginning with a polar desert, the sequence of ecosystems passes through tundra, boreal forest, and temperate ecosystems where moisture determines the presence of desert, grassland, or forest. Mars is like a very high terrestrial mountain. The goal of planetary engineering is to bring the climate of Mars down that mountain to the point where some areas of the planet have a climate similar to a polar desert At that point a microbial ecosystem containing bacteria, cyanobacteria, green algae and lichens can be introduced. Subsequent engineering and biological feedbacks will move the climate of Mars further down the mountain through successively more moderate climates and more diverse ecosystems. At each stage the organisms will alter the environment to prepare the way for subsequent stages. This model provides a logical framework for the sequence of ecosystems to be established on Mars. The physical requirements for the introduction of each system on Mars can be extrapolated from the known limitations on Earth. The ecosystems define the communities to search for potential colonizing species based on their physiological properties.

INTRODUCTION

Mars is a bitterly cold planet. Its average surface temperature is only –60°C compared to +15°C for the Earth. The martian atmosphere has a surface pressure of only 0.5-1 kilopascals (kPa) or 5–10 mbar, a pressure so low that liquid water is not stable. Intense ultraviolet (UV) radiation bathes the surface, and the regolith is thought to contain oxidants, which would break down any organic material. Terrestrial organisms cannot survive under these surface conditions (Clark, 1998). Spacecraft, however, have returned images of valley systems resembling dried-up river systems and wide outflow channels indicating the passage of vast quantities of water in the past. Mars Global Surveyor (MGS) returned altimeter data indicating shorelines consistent with the past existence of a northern ocean (Head et al., 1999). If water was once stable on the surface and flowed in such vast quantities, the atmosphere must have been denser and the climate warmer in the past.

These observations are the basis for the current search for evidence of past or present life on Mars (McKay, 1997). They are also the source of speculation that Mars might be returned to its former warmer climate by some sort of global engineering techniques (Sagan, 1971; Oberg, 1981; McKay et al., 1991). The new science of planetary engineering became known as "terraforming" in which an extraterrestrial body is modified to make an environment suitable for habitation by terrestrial organisms. The term "planetary ecosynthesis" emphasizes the fact that the result of planetary engineering is not a carbon copy of Earth but a habitable world with its own unique properties. Fogg gathered this early work in *Terraforming: Engineering Planetary Environments* (1995), and review articles by Fogg (1998), McKay (1999), and McKay and Marinova (2001) have established terraforming as a branch of the field of astrobiology.

As established by NASA the Astrobiology program includes the study of planetary ecosynthesis. One of the six key questions addressed by the Astrobiology Institute is: What is the potential for survival and biological evolution beyond the planet of origin? Biological evolution is a phenomenon of populations of organisms interacting and genetically changing over long periods of time. To address this question entire ecosystems (communities of organisms plus their physical and chemical environment) would have to be placed on an extraterrestrial planetary body, and Mars is the only planet in the Solar System capable of receiving terrestrial ecosystems after modification with existing technology.

The purpose of this paper is to present a model for the process of the introduction of terrestrial ecosystems to Mars. The model provides a framework for the sequence of ecosystems to be established and the physical requirements for each system. The individual ecosystems define the communities from which potential colonists may be selected based on their biological characteristics. The potential colonists then define areas for research to be performed before the actual transplantation to Mars.

A MODEL FOR ECOSYNTHESIS ON MARS

A model for the process of ecosynthesis on Mars can be found in a diagram often found in introductory biology texts. As one climbs up a mountain, each 150 m rise in

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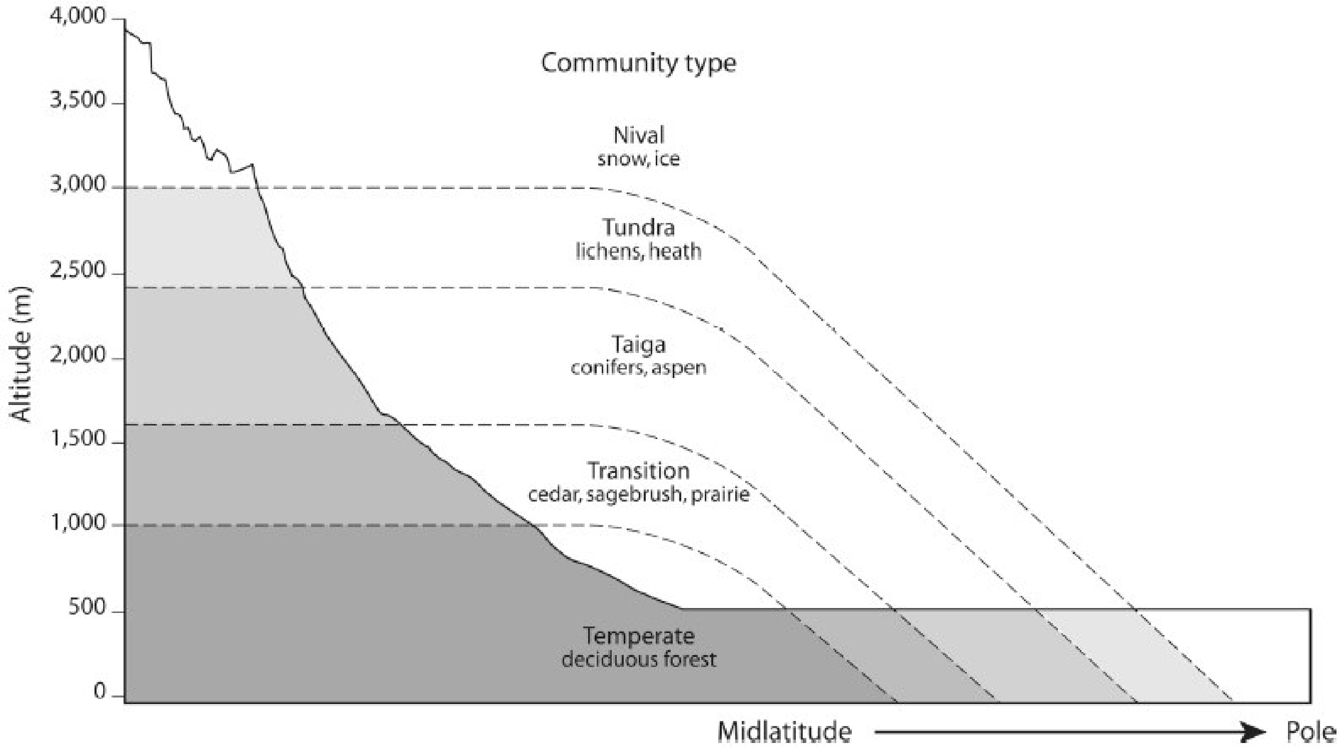

Figure 1. *The mountain model for ecosynthesis on Mars. The present climate of Mars can be compared to a very high mountain on Earth, one higher than any real mountain that exists in fact. The prebiotic stage of ecosynthesis employs planetary engineering techniques to bring the climate of Mars at some latitudes into the range of that in the terrestrial Dry Valleys of Antarctica. At that point the introduction of the first microbial ecosystems can begin. Continued modification of the planetary climate will permit the introduction of a sequence of ecosystems from tundra through boreal forests to temperate ecosystems.*

elevation produces a decrease in average annual temperature of about 1°C. Moisture and evaporation also change with altitude. Therefore anyone climbing up a mountain passes through a series of ecosystems from base to top. Depending on the latitude of the mountain, the base may be surrounded in tropical forest or temperate forest, a prairie or sagebrush area above that, followed by a montane or coniferous forest, an alpine tundra at higher elevations, and finally a polar desert ending in permanent snow and ice. Since the effect is similar at all latitudes, mountains in the tropics can be capped in permanent ice if the mountain is high enough. This is the model of the ecosynthesis process for Mars (Figure 1). The present climate of Mars is like that of a very high mountain on Earth. The average atmospheric surface pressure on Mars (6-7 mbar) occurs in the atmosphere of Earth at an altitude of about 37,000 m (121,000 ft), far higher than any terrestrial mountain.

The mountain model of ecosynthesis on Mars provides an order to the sequence of ecosystems that will be implanted. The initial engineering stage will employ global techniques to move the climate of Mars from its present state to one similar to a high arctic barren or polar desert. The first ecosystem will then be a microbial one dominated by the kinds of microorganisms found in the Dry Valleys of Antarctica or polar deserts in the Arctic. The second ecosystem in the sequence will be similar to arctic tundra and dominated by plants called bryophytes (mosses and liverworts) and lichens (organisms formed by symbioses between algae and fungi). The third ecosystem will be characterized by the arrival of flowering plants, initially as small numbers of herbs but with an increasing role as climate and moisture improve and ending with the first few stunted trees in favorable sites. Boreal forest will mark the fourth stage in the process, which will likely end with the establishment of temperate ecosystems on Mars. The nature of the temperate ecosystem will depend on the amount of moisture available. If moisture is low, a desert may develop, but if moisture is higher, grasslands and temperate forests may be possible. The climate of temperate ecosystems can support a martian agriculture on the surface.

Each of these ecosystems is a stage in the process of planetary ecosynthesis. Each stage may be characterized by certain physical parameters, such as oxygen levels and UV radiation, and by the dominant organisms, such as microorganisms or flowering plants. Each stage is part of a process that may extend over 1,000 years or more. The entire process of ecosynthesis can be compared to the terrestrial process of ecological succession. Consider the retreat of a glacier in a high latitude environment on Earth. As the glacier melts back within its valley, new land is exposed. The first pioneer organisms on this barren land are microorganisms, lichens, and liverworts. Their activities add organics to the rocky detritus left by

TABLE 1. The physical parameters of Mars and Earth

Parameter	**Mars**	**Earth**
Mean distance from Sun	2.28×10^8	1.49×10^8
Orbital eccentricity	0.0934	0.0167
Rotation rate	24.62 h	24.0 h
Year	668.59 sols[1]	365.25 days
Obliquity	25.19°	23.45°
Surface gravity	0.38 g	1.00 g
Mean surface temperature	-60°C	+15°C
Surface temperature range	-145°C to 20°C	-60°C to 50°C
Insolation (PAR)	860 µmol quanta m^{-2} s^{-1}	2000 µmol quanta m^{-2} s^{-1}
UV radiation	>190 nm	>300 nm
Atmospheric pressure	5 – 10 mbar	1013 mbar
Atmospheric composition	N_2 0.189 mbar (2.7%)	N_2 780 mbar (78%)
	O_2 0.009 mbar (0.13%)	O_2 210 mbar (21%)
	CO_2 6.67 mbar (95.3%)	CO_2 0.38 mbar (0.038%)
	Ar 0.112 mbar (1.6%)	Ar 10.13 mbar (1%)

[1]686.98 Earth days

Data from Carr (1981), Kieffer et al., (1992), and McKay and Marinova, (2001).

the glacier and begin to erode exposed rocks. Soon grasses and herbs colonize the area and generate a true soil. Alders add nitrogen to the soil, and finally spruce trees form a dense forest. Each stage in the succession prepares the way for the next stage by altering the environment. Similarly, on Mars each stage in ecosynthesis alters the environment such that the next stage becomes possible. The microbial stage will transform the martian regolith into a true soil and facilitate the arrival of bryophytes in the second stage. As climate improves under global engineering, the bryophyte stage will replace a pure microbial stage in favorable areas while the microbial stage will spread into areas that were not previously habitable. The microbial ecosystem will persist even on a fully terraformed Mars at high latitudes and elevations. Planetary geography always plays a strong role in the locations of ecosystems.

The rest of this paper will examine each of the stages in the ecosynthesis process. The initial planetary engineering stage will be presented in less detail because the engineering processes and their effects on martian climate have been given previously (McKay and Marinova, 2001). The physical characteristics of each stage will be considered, and the organisms present will be presented in relation to their ability to adapt and thrive under those physical conditions. Where predictable, the ways that those organisms will alter the environment of Mars to prepare for later stages will also be discussed.

THE INITIAL ENGINEERING STAGE

The physical parameters of Mars and Earth are given in Table 1. The rotation rate (and therefore the day length) and the obliquity of the two planets are very similar. Surface gravity and solar radiation are lower on Mars than on Earth, but the year length and orbital eccentricity are longer. None of these differences creates a problem for planetary ecosynthesis. Mars can be transformed into a habitable planet by altering its atmospheric composition and density. These alterations will raise the mean surface temperature, reduce the surface temperature range, and reduce the level of UV radiation at the surface.

The main planetary engineering techniques for Mars are the manufacture and release of greenhouse gases such as perfluorocarbons from materials in the regolith and the potential use of orbiting solar mirrors to raise the amount of solar radiation at the planet's surface. If both methods are used, planetary engineering will raise the surface temperature of Mars by increasing the amount of solar radiation at the surface and the retention of that radiation through the greenhouse effect. The immediate goal of both methods is the release into the atmosphere of carbon dioxide frozen at the poles or absorbed in the regolith. The released carbon dioxide will increase the atmospheric pressure and further warm the planet by creating a runaway greenhouse effect. Estimates of the amount of this carbon dioxide vary from 2 to 200 kPa (20 to 2000 mbar), but for purposes of planetary ecosynthesis an intermediate amount of 10 to 40 kPa (100 to 400 mbar) would be adequate for the early stages. In addition to raising the surface temperature of Mars, a thicker atmosphere of carbon dioxide would also retain heat better over the day-night cycle and therefore reduce the diurnal temperature range. One objective of the engineering phase will be to raise the mean surface temperature into the range of the Dry Valleys of Antarctica (-20°C).

A denser atmosphere around a warmer planet will also permit liquid water to be stable on the surface. That Mars once had abundant liquid water running on its surface has long been established (Carr, 1981; Squyres, 1989). That it still has abundant water in its regolith has been recently shown by the Gamma Ray Spectrometer (GRS) aboard the *Mars Odyssey* spacecraft. The GRS found evidence of abundant hydrogen as water ice within one meter of the surface below 60° south latitude. The percentages of ice by mass within this one-meter depth varied from 20 to 50 percent. Abundant water ice was also detected above 60° north latitude. Water is clearly available for ecosynthesis.

Mars has relatively little oxygen in its atmosphere (0.009 mbar), but the surface is highly oxidized. Many of these oxidants will likely release molecular oxygen when a warmer wetter climate is established. The net amount of this oxygen released to the atmosphere would be slight, probably less than 2 mbar, but the fact that the surface is oxidized rather than reduced simplifies the ecosynthesis process. Oxygen produced by photosynthetic microorganisms can enter the atmosphere to raise the levels of oxygen and ozone rather than rusting reduced metals as occurred on the early Earth.

As the initial planetary engineering stage draws to a close, the atmospheric pressure on Mars will reach 10 to 40 kPa. The atmosphere is largely composed of carbon dioxide with small amounts of nitrogen, argon, water vapor, and oxygen. Average surface temperatures over some areas of the planet reach –20°C and the daily temperature range is reduced. The same greenhouse gases that have warmed the planet also provide a shield from UV radiation. Liquid water is now stable on the surface. Water will be cycling through the atmosphere and returning to the surface as some form of precipitation. It will likely collect in basins and craters and may resume flowing down ancient channels during summers. The stage is set for the introduction of the first ecosystem.

Figure 2. *A Dry Valley in Antarctica. The Antarctic Dry Valleys are the terrestrial analogue of the first ecosystem on Mars. Photo by Joby Chesnick.*

THE MICROBIAL ECOSYSTEM

It is not possible to discuss all possible microorganisms that would play some role in the first ecosystem on Mars. This discussion will therefore focus on four groups of organisms: the bacteria involved in a nitrogen cycle, cyanobacteria, green algae, and lichens, which are symbiotic associations between fungi and algae. These four groups of microorganisms occur in polar deserts such as the Dry Valleys of Antarctic (Figure 2) and will play a major role in the first ecosystem on Mars. Other groups of algae may occur, but they will be restricted to aquatic habitats and therefore less widespread initially.

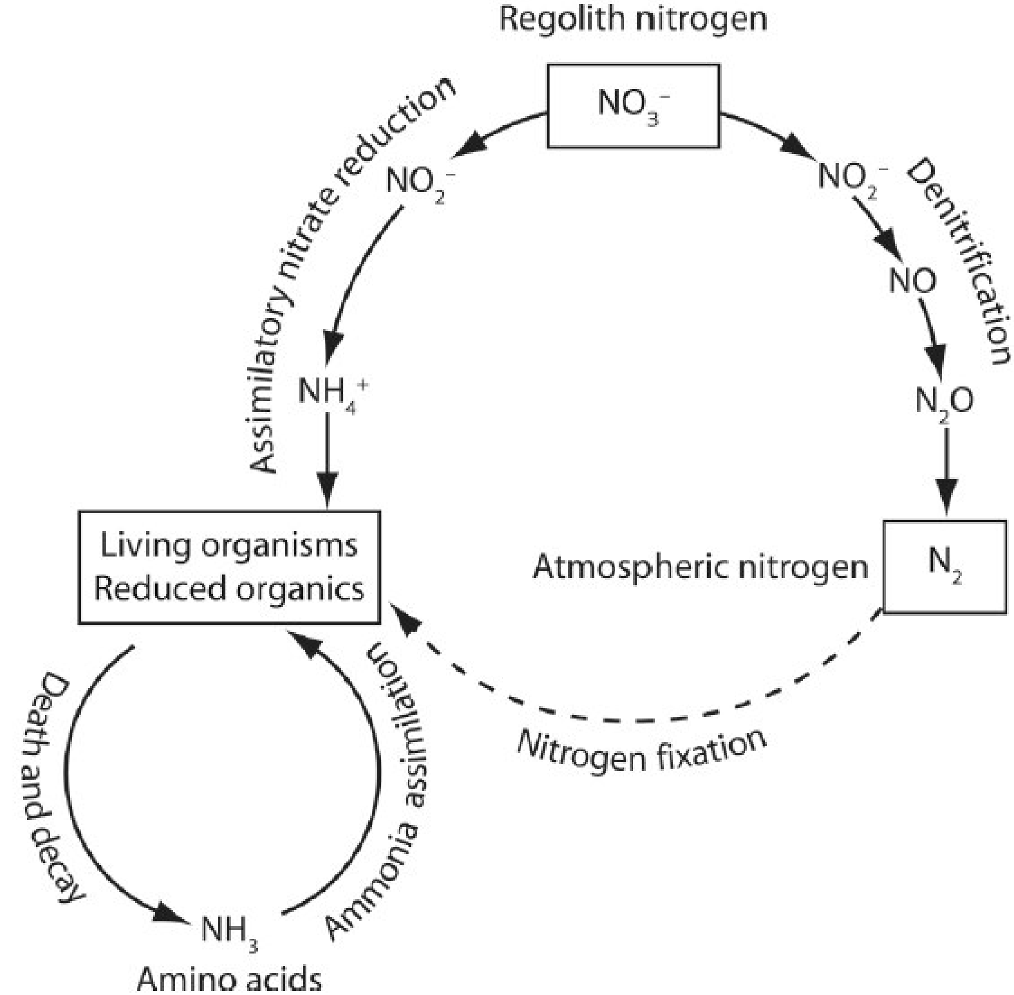

Figure 3. *The nitrogen cycle on Mars. Initially the nitrogen cycle will be dominated by denitrification of regolith nitrate and nitrite into molecular nitrogen (N_2) and the assimilation of nitrate and nitrite by microbial reductases into ammonia and amino acids. Nitrogen will cycle among microorganisms through ammonia and amino acids. As the nitrogen level of the atmosphere increases, nitrogen fixation will begin at a pN_2 of about 5 mbar.*

Bacteria and the nitrogen cycle

In the present atmosphere of Mars, nitrogen is present at about 2.7% (0.16 mbar), but Mars should have outgassed some 300 mbar of nitrogen. If this nitrogen gas were present initially, it was probably oxidized to nitrate by lightning and volcanic electric discharges and is now in the regolith. If nitrate is in the regolith, it is possible to propose an order in which a nitrogen cycle might be established. The initial processes will be essentially anaerobic and will utilize nitrate and nitrite in the regolith via two main pathways (Figure 3). Denitrification is carried out by a variety of bacteria that convert nitrate to nitrite, nitrite to nitric oxide, nitric oxide to nitrous oxide and finally nitrous oxide to nitrogen gas. This process could raise the partial pressure of N_2 (pN_2) in the atmosphere to 60 to 300 mbar. Experiments with denitrifying bacteria in a CO_2 atmosphere indicate that nitrate could be rapidly converted to N_2 if liquid water and organic substrates were present (Hart et al., 2000). The microorganisms performing the second pathway (assimilatory nitrate reduction) would provide the organic substrates. Many microorganisms, including algae and cyanobacteria, can perform assimilatory nitrate reduction using nitrate and nitrite reductases. Nitrate is reduced to ammonia that is incorporated into amino acids within living organisms. When these organisms die and decay, they release ammonia and amino acids into the environment where other microbes can take them up by ammonia assimilation. Ammonia thus cycles through a closed loop. These two pathways will reduce nitrate in the regolith as the pN_2 in the atmosphere rises.

The remaining process shown in Figure 3 is nitrogen fixation. Prokaryotic microorganisms such as archaeans, bacteria, and cyanobacteria can fix nitrogen, but the present atmospheric levels on Mars (0.16 mbar) are too low for fixation. Klinger et al. (1989) examined *Azotobacter* and *Azomonas* over a range of pressures of N_2. No growth occurred at a pN_2 less than 1 mbar, but both bacteria grew and fixed nitrogen at a pN_2 of 5 mbar. Limited data suggest that nitrogen fixation could begin on Mars once the pN_2 reaches at least 5 mbar. The establishment of a nitrogen cycle on Mars will profoundly change the composition of the atmosphere from one composed of mostly CO_2 at a pressure of around 90-400 mbar to one with an additional 60-300 mbar of N_2.

TABLE 2. Mechanisms of ultraviolet radiation resistance in cyanobacteria

Category	Mechanism
Avoidance	Growth in fissures, under the surfaces of porous rocks (endolithic), beneath translucent rocks, under water, and under the ice on ice-covered lakes.
Screening	Scytonemin, yellow-brown sheath pigment Phycoerythrin, red intracellular pigment Mycosporine-like amino acids (MAA), colorless
Quenching	Carotenoids, orange pigments Xanthophylls, yellow pigments Superoxide dismutase
Repair	Enzyme-based DNA repair of UV damage Polyploid genomes, up to 10 copies

Based on data in Vincent and Quesada (1994) and D. Wynn-Williams (1994)

Cyanobacteria

Cyanobacteria are widespread members of the lake, stream, soil and lithic communities in Antarctica, especially in the Dry Valleys (Vincent, 1988). They do not require oxygen and can carry out both oxygenic photosynthesis and anoxygenic photosynthesis using hydrogen sulfide as proton donor. They are highly resistant to freezing and drying. Filamentous cyanobacteria in Dry Valley streams remain freeze-dried and exposed for months until the few brief weeks in austral summer when the streams flow with water (Vincent and Howard-Williams, 1986).

Their resistance to UV radiation is varied and versatile (Table 2). They occupy a number of habitats that permit them to avoid exposure to full UV radiation. Some cyanobacteria also occur as epilithic crusts, directly on rock surfaces, at high latitudes and altitudes. Screening pigments and quenching agents heavily protect these filaments.

Phycoerythrin and mycosporine-like amino acids (MAA) are both intracellular compounds that act to screen out UV radiation in cyanobacteria. Scytonemin is an UV screening pigment found in the outer sheaths that surround cyanobacteria (Vincent and Quesada, 1994). The level of scytonemin in cyanobacteria increases with increasing light levels (Garcia-Pichel and Castenholz, 1991). Carotenoids and xanthophylls are quenching agents that dissipate excess solar energy absorbed by chlorophyll that would otherwise result in damaging free oxygen radicals and hydrogen peroxide within cells. Superoxide dismutase scavenges free oxygen radicals (O_2^-) and converts them to hydrogen peroxide. The hydrogen peroxide is then converted to water and oxygen. In Antarctica mats of cyanobacteria typically contain high concentrations of these substances as photochemical protection (Vincent and Quesada, 1994). As a final defense against UV radiation, cyanobacteria have mechanisms for repair of damage to their DNA (Levine and Thiel, 1987) and are polyploids, meaning they have multiple copies (as high as 10) of their genome. Damage to a single strand of DNA is therefore less likely to disrupt the cell. All these UV radiation adaptations to the harsh environment of Antarctica preadapt cyanobacteria to fill a wide range of habitats in the first stage of the ecosynthesis.

Green algae

Many green algae are not obligate aerobes, including members of such common genera as *Chlorella*, *Chlamydomonas*, *Scenedesmus* and *Selenastrum* (Spruit, 1962). There is one genus of green algae called *Pyrobotrys* found only in anaerobic soils (Nozaki, 1986). In the dark these algae will initially carry out fermentation and produce carbon dioxide and organic acids, as do many plants. But after some time they will evolve hydrogen gas. If anaerobic conditions persist in the light and levels of carbon dioxide and hydrogen are adequate, these algae may reduce carbon dioxide to simple carbohydrates using molecular hydrogen as electron and proton donor. Thus green algae possess a more diverse range of metabolic processes than just photosynthesis and aerobic respiration. Certain species have the ability to grow under low pH levels (Sheath et al., 1982), low temperatures, and high salinity (Vincent, 1988). The major adaptation of Antarctic green algae is the ability to survive repeated freezing and thawing (Holm-Hansen, 1963). The ability to withstand repeated freeze-thaw cycles would have considerable value during early planetary ecosynthesis on Mars.

Green algae may be as resistant as cyanobacteria to UV radiation. Green algae share the same range of habitats as cyanobacteria in Antarctica (Vincent, 1988). In the Dry Valleys of Antarctica, cryptoendolithic lichens often occur as a layer beneath the surfaces of translucent porous rocks, and the green alga *Trebouxia* is often the algal symbiont in the lichen. Beneath this lichen layer the green alga *Hemichloris*, which is endemic to Antarctica, may form another distinct layer. Flavonoids and phenolics are UV screening agents known to be present in some green algae. The level of quenching agents such as carotenoids in green algae is related to the level of exposure to direct sunlight and UV radiation (Thomas and Duval, 1995).

Lichens

Lichens are generally slow growing, but they grow faster under elevated carbon dioxide levels, at least up to about 2 mbar of carbon dioxide (Nash et al., 1983). It is possible therefore that lichens would perform better on Mars during early stages of ecosynthesis than they do on Earth because the atmosphere would be largely carbon dioxide. Antarctic lichens are extremely tolerant of desiccation and cold. Lange and Kappen (1972) found that several Antarctic lichens could survive and recover even after being cooled to –196°C, a temperature below levels that currently occur at the martian poles. Some lichens were able to assimilate carbon dioxide at temperatures as low as –12.5°C to –18°C.

Lichens are extremely resistant to UV radiation. Siegel and Daly (1968) exposed the arctic lichen *Cladonia rangiferina* to UV radiation of 3.6×10^9 $ergs \cdot cm^{-2}$ over 24 hours. This is equivalent to 4.16×10^4 $ergs \cdot cm^{-2} \cdot s^{-1}$. By comparison the UV radiation at the equator of Mars averages 7×10^3 $ergs \cdot cm^{-2} \cdot s^{-1}$. *Cladonia rangiferina* covers large areas of the arctic and presumably could also do so on Mars. Table 3 lists some of the UV radiation resistance mechanisms in lichens. Endolithic lichens lie under the surfaces of translucent porous rocks in the Antarctic Dry Valleys. The overlying rock layers shield the lichens from direct solar and UV radiation. Many lichens, however, grow as crusts on rocks where they may be colored black, brown, orange or yellow. The black and brown colors are due to melanins that screen the lichens from excess solar and UV radiation and also absorb heat to raise the temperature of the lichen above that of the surrounding air. The orange and yellow colors are due to carotenoids that are quenching agents.

TABLE 3. Mechanisms of UV resistance in lichens and mosses

Category	Mechanism
Avoidance	Endolithic lichens
Screening	Lichens: black melanins in endolithic and surface lichens Mosses: black and brown pigments and flavonoids. Phenolics in the walls of the moss *Andreaea*.
Quenching	Lichens: carotenoids Mosses: carotenoids such as violaxanthin (purple)
Repair	Mosses: polyploid genomes

Based on data in Post (1990) and D. Wynn-Williams (1994).

Although lichens are slow growing on Earth, their role in the ecological process of succession makes them important to include in the early stages of ecosynthesis on Mars. On Earth lichens are the first pioneer species to colonize bare rock. They excrete organic acids that slowly dissolve rock and free minerals to join the accumulation of organic material that slowly creates a true soil. Their growth opens the way for the establishment of other plants.

The microbial stage of ecosynthesis will begin the process of adding organic matter to the martian regolith, binding together regolith particles, and transforming the atmosphere by increasing the amount of free oxygen and converting nitrates to free nitrogen. The climate will begin as frigid-polar with average temperatures in the warmest "month" less than 0°C (Longton, 1988). On Earth a frigid-polar climate is found only in continental Antarctica. Toward the end of the first stage, the climate should warm to cold-polar where the average temperature in the warmest month falls in the range of 0° to 2°C. Maritime Antarctica and the arctic polar deserts have a terrestrial cold-polar climate. Microbial life will thrive in the regolith, on the surfaces of rocks, under the surfaces of rocks in the pores between mineral grains, and in gathering surface waters as plankton and as filaments attached to surfaces.

THE BRYOPHYTE ECOSYSTEM

Bryophytes consist of relatively simple, usually small, green plants called mosses, liverworts, and hornworts. They lack roots but form cellular extensions called rhizoids for attachment. Bryophytes are extremely important in terrestrial polar and alpine ecosystems where the severe climate prohibits most flowering plants (Figure 4).

Figure 4. *Alpine tundra. The terrestrial equivalent of the second stage in ecosynthesis on Mars. Photo by Lee Wilcox.*

In the bryophyte stage of ecosynthesis the atmosphere will be mainly carbon dioxide and nitrogen with small but increasing amounts of oxygen. Mosses show an unusual capacity to utilize carbon dioxide at high external levels, far more so than flowering plants. Silvola (1990) reported that *Sphagnum fuscum*, a widespread moss in northern peatlands, exhibited increased rates of photosynthesis up to a carbon dioxide pressure of 9 mbar, the highest level tested. *Grimmia antarctici*, a common carpet-forming moss in East Antarctica, reached its maximum rates of photosynthesis at CO_2 levels of 10-20 mbar (Tarnawski et al., 1992). Mosses photosynthesize more slowly than flowering plants at terrestrial ambient carbon dioxide levels of 0.38 mbar. At higher levels of CO_2 the photosynthetic rates of mosses approach those of flowering plants. Mosses are also capable of carrying out photosynthesis at lower light levels and lower temperatures, even under snow, than flowering plants (Oechel and Sveinbjornsson, 1978; Collins and Callaghan, 1980). Mosses do require oxygen for aerobic respiration, but how much oxygen they require is unknown. The moss *Hypnum cupressiforme* showed an increase in photosynthetic rate as oxygen was reduced to 3% (30 mbar) (Aro et al., 1984).

Mosses are not thought to have a high degree of resistance to UV radiation, but this may be due to lack of experimental data. Mosses occur in the same habitats as lichens and cyanobacteria, including on the surfaces of rocks exposed to full solar radiation at polar latitudes and alpine locations. Like lichens, mosses in polar and alpine environments may be dark brown or black in color. These pigments screen out harmful UV radiation and excess visible light while warming the body of the moss (Table 3). Phenolics such as flavonoids occur in the walls of a number of mosses, and these phenolics act to screen out UV radiation and possibly also reduce desiccation (Graham et al., 2003). Markham et al. (1990) reported UV protective flavonoids in the Antarctic moss *Bryum argenteum*. The lower the level of ozone over the field sites the higher the level of protective flavonoids. Mosses also possess quenching agents such as carotenoids. The Antarctic moss *Ceratodon purpureus* produces the carotenoid violaxanthin as a photoprotective pigment (Post, 1990). Mosses are generally polyploid.

Mosses will likely play an important role in planetary ecosynthesis by sequestering large amounts of carbon dioxide in the form of decay resistant organic compounds in martian peatlands. At the same time these peatlands will add large quantities of oxygen to the atmosphere of Mars. Martyn Fogg (1995) estimated that a cover of peatlands on Mars could produce 20 mbar of atmospheric oxygen in about 700 years. Since mosses photosynthesize faster in a CO_2 atmosphere than on Earth, martian peatlands might be able to produce this amount of oxygen in less time, depending on the degree of surface cover and moisture availability. For bryophytes to sequester large amounts of carbon in peatlands, planetary engineering must raise the climate of significant areas on Mars to the level of mild-polar environments on Earth (Longton, 1988). Mild-polar habitats have average monthly temperatures in the warmest month of 7° to 12°C. On Earth they occur in Alaska and northern mainland Canada. These conditions permit *Sphagnum* moss to form the extensive peatlands that sequester so much carbon on Earth.

With the full development of the bryophyte ecosystem, the surface of Mars will appear vastly different from that shown in the cameras of *Spirit* and *Opportunity*. Rocks will be dotted with lichens and mosses. In areas where water collects, *Sphagnum* moss may form extensive peatlands. Mars will assume a distinctly green aspect interrupted by bright spots of yellow, orange, and red lichens. At some point in this stage the partial pressure of oxygen will surpass 20 mbar, a value that is significant for the next stage in planetary ecosynthesis.

THE FLOWERING HERBS ECOSYSTEM

The crucial factor in determining the transition to the third stage in martian ecosynthesis, which is characterized by the arrival of flowering plants, is the level of atmospheric oxygen. In most terrestrial environments only two types of flowering plant structures risk low oxygen levels: seeds and underground organs such as roots, rhizomes and tubers (Crawford, 1992). Rhizomes and tubers are underground stems. Many seeds show reduced germination if oxygen falls below 10 kPa or 100 mbar. On Earth oxygen always limits to some extent the depth to which roots can penetrate. Armstrong and Gaynard (1976) found that 20 to 25 mbar was the critical oxygen pressure to maintain root respiration in rice (*Oryza sativa*) and the aquatic sedge *Eriophorum augustifolium*. Fogg (1995) used this data when he proposed that the minimum pO_2 for plants would lie around 20 mbar or 2% O_2 in the martian atmosphere. Higher values, however, have been reported for other plant species. Corn (*Zea mays*) had a critical oxygen pressure of 6kPa (6% or 60 mbar) (Saglio et al., 1984). A third way in which low oxygen can constrain flowering plants is through restricting animal pollinators. Many plants require animal pollinators to produce seeds. Hard data are lacking but a pO_2 of 20 mbar is unlikely to support pollinators such as flying insects and certainly not bats and birds. Cockell et al. (1999) examined a number of insects from different orders and found that all species seemed to function normally down to a pressure of 200 mbar (about 40 mbar of oxygen) for up to 24 h. Low oxygen levels will likely prohibit certain plants from colonizing Mars until oxygen levels rise enough to permit their animal pollinators to thrive also. The first flowering plants on Mars will have anoxia-tolerant seeds and underground organs and mechanisms for reproduction that do not require animals.

Seeds, rhizomes, and whole plants under low oxygen

Seeds may store food reserves as lipids, proteins or starch. The germination rate of seeds that store lipids or proteins begins to decline if external oxygen levels fall below 10kPa or 100 mbar. Starch seeds, however, can maintain 50% germination rates when the pO_2 drops below 1kPa or 10 mbar and can germinate at about 20% even at 0.1kPa (1 mbar). Rice is an aquatic monocot, and its seeds can still germinate when pO_2 falls below 0.01kPa (0.1 mbar) and even extend their shoots above water (Al-Ani et al., 1985). Starch fermentation powers germination.

Although roots cannot survive more than a few days of anoxia, the underground rhizomes of a number of aquatic plants can survive under total anoxia for two to three months (Crawford 1992). Survival depends on a large reserve of carbohydrates that the rhizome ferments into ethanol to generate energy in the form of adenosine triphosphate (ATP). The ATP from fermentation maintains the rhizome in winter and also powers the extension of a new shoot in spring (Braendle and Crawford, 1987). Once the shoot has elongated and the leaves expanded, aquatic plants develop another mechanism to thrive in an oxygen-poor environment–a special tissue called arenchyma. Aerenchyma consists of interconnected gas-filled channels through stems and roots that provide a pathway for the movement of oxygen, carbon dioxide, and ethanol. Aquatic plants are also tolerant of high levels of carbon dioxide. A number of aquatic plants should be good candidates for colonizing Mars early in the third stage.

One other group of flowering plants possesses considerable tolerance of anoxia. A number of vascular plants from Spitsbergen in the High Arctic have an exceptionally high level of anoxia tolerance (Crawford et al., 1994). This anoxia tolerance extends to the entire plant including the leaves. The anoxia tolerance of these high arctic species appears to be an adaptation to ice-encasement, which may last as long as 8 to 10 months. The extraordinary anoxia tolerance of these plants makes them prime candidates for colonization on Mars.

Reproduction without animals at low oxygen

Flowering plants have a number of reproductive mechanisms that do not require animal pollinators. These mechanisms include vegetative reproduction, apomixis, autogamy, and anemophily. In vegetative reproduction certain somatic (body) cells divide to produce structures called runners, rhizomes, or bulbils. Runners are aboveground stems that spread out from the parent plant and establish new roots and leaves. Strawberry plants are a familiar example of a plant that spreads by runners. Rhizomes are underground stems that spread out from the parent plant. The crab grass in your lawn and the *Iris* in your garden both spread by rhizomes. The final type of vegetative reproduction is less familiar. Bulbils are small, bud-like plants born on the parent plant. The common houseplant *Kalanchoae* produces bulbils along the margins of its leaves, from which the bulbils drop off and root in the ground.

Apomixis is asexual seed formation, but there are a number of different types of apomixis (Asker and Jerling, 1992). The type most suitable for colonizing Mars is called autonomous apomixis. Autonomous apomictic plants reproduce independently of pollination. The familiar lawn and garden dandelion (*Taraxacum officinale*) is an example of a common autonomous apomictic flowering plant. The flowering plant family Asteraceae, which contains daisies, sunflowers, and

TABLE 4. Flowering plants growing in the cool-polar regions of Earth that reproduce without animal pollinators.

Genera and species	Common name	Reproductive mechanism(s)
Cassiope tetragona	Arctic bell heather	Autogamous
Dryas integrifolia	Mountain avens	Autogamous
Epilobium latifolium	Dwarf fireweed	Autogamous
Erysimum pallasi		Apomictic
Lesquerella arctica		Autogamous
Papaver radicatum	Arctic poppy	Autogamous
Pedicularis arctica *P. hirsute* *P. lapponica* *P. sudetica*	Arctic lousewort Hairy lousewort Lapland lousewort Sudetan lousewort	Autogamous Autogamous Autogamous/vegetative Autogamous
Potentilla nivea	Snow rose	Autogamous/apomictic
Saxifraga tricuspidata *S. flagellaris* *S. cernua*	Three-pointed saxifrage Whip saxifrage Nodding saxifrage	Autogamous Apomictic/vegetative Apomictic/vegetative
Silene acaulis	Cushion pink	Autogamous
Taraxacum arctogenum	Arctic dandelion	Apomictic

Some may use insects if available. Based on data from Kevan (1972) and Williams and Batzli (1982).

dandelions, has many autonomous apomictic species and therefore many potential martian colonists (Graham, 2003).

Autogamy means literally self-marriage. An autogamous plant acquires pollen for fertilization of its egg cells from itself. Autogamy is a form of sexual reproduction, and it is widespread among flowering plant families.

Anemophily (wind loving) or wind pollination is normal sexual cross-pollination where the agent transporting the pollen is wind rather than animals. Wind pollination dominates the gymnosperms and prevails in the flowering plant families Poaceae (grasses), Cyperaceae (sedges), and Juncaceae (reeds)(Faegri and van der Pijl, 1979). These three families dominate terrestrial wetlands. Wind-pollinated plants form a fourth group of potential martian colonists.

These alternative mechanisms of reproduction occur in many different groups of flowering plants and in many environments, but the flowering plants of polar and alpine environments utilize them to an extreme degree. In these harsh environments populations of animal pollinators are often severely restricted by low temperatures, and population size may vary widely from year to year. If animal pollinators are scarce and unreliable, then reproduction is best insured by having some mechanism that is not dependent on them. The maritime Antarctic is a cold-polar environment where the mean temperature in the warmest month is only 0-2°C (Longton, 1988). There are only two native species of flowering plants: the grass *Deschampsia antarctica* and the carnation *Colobanthus quitensis*. *Colobanthus* is autogamous and *Deschampsia* is apomictic.

Cool-polar environments, such as occur in Greenland and the Canadian Islands in the High Arctic, and isolated islands such as South Georgia and Macquarie around Antarctica, are the first polar environments with significant flowering plant communities. In a cool-polar environment the average temperature of the warmest month is 3° to 7°C. Table 4 lists a number of cool-polar plants that are known to be capable of reproducing without animal pollinators. *Dryas integrifolia* has roots that harbor nitrogen-fixing bacteria. The whip saxifrage (*Saxifraga flagellaris*) has yellow apomictic flowers, which form seeds for long-distance dispersal, and long whip-like runners to spread locally. During the stage of flowering herbs the level of atmospheric oxygen should continue to rise and exceed 60 mbar. Beyond this point the level of oxygen should no longer be a significant constraint on the subsequent ecosystems on Mars. The remaining constraints will be the same as those that operate on Earth, namely temperature and moisture. The next stage begins when the climate of parts of the martian surface reaches that of a boreal ecosystem.

THE BOREAL FOREST ECOSYSTEM

During the later part of the third stage of ecosynthesis, sheltered sites insulated by martian winter snows could harbor dwarf trees of birch (*Betula*) and willow (*Salix*) up to one meter tall and stands of open, stunted trees consisting of birches, larches (*Larix*) and spruces (*Abies*) could be common in sheltered valleys where water flows. But the development of true forests on Mars will first occur when the climate of some regions reaches that of the terrestrial taiga or boreal coniferous forest (Figure 5). The climate of the boreal forest can be defined by the average temperature of the warmest month of the year, which is 13 to 18°C in July (Elliott-Fisk, 2000). Alternatively, the boreal climate can be defined by the length of its growing season, which on Earth is 30 to 120 days with a daily mean temperature above 10°C (Walter, 1973). The lower figure represents the northern boundary of the boreal forest and the higher figure the southern boundary. On Mars these numbers should be revised upward to 54 and 218 sols to account for the longer seasons. On Earth annual precipitation in a boreal forest varies from 30 to 50 cm (Elliott-Fisk, 2000). The revised values for Mars would be 55 to 90 cm per martian year. These temperature and precipitation values define the requirements for establishing a boreal coniferous forest on Mars.

On Mars as on Earth a boreal coniferous forest is a spruce–fir forest. White spruce (*Picea glauca*), black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) are the most widespread North American dominants. Black spruce and tamarack (*Larix laricina*), a deciduous conifer, are common in bogs. Jack pine (*Pinus banksiana*) and two deciduous flowering plants, paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) dominate disturbed areas (Vankat, 1979). The deciduous flowering trees are wind pollinated. The seeds of all three disturbance-site species are adapted for wind dispersal, a feature that will aid their spread across the surface of Mars. Willows, dwarf birch (*Betula glandulosa*), green alder (*Alnus crisps*), and members of the heath family (Ericaceae) make up most of the shrubs in the boreal coniferous forest. The understory layer is dominated either by mosses in wet areas or lichens in drier environments. Bogs dominated by *Sphagnum* moss are the most common form of wetland within the boreal coniferous forest zone.

Figure 5. *Boreal forest. The terrestrial analogue of the fourth stage in martian ecosynthesis. Photo by the author.*

The North American boreal coniferous forest is the most diverse boreal forest on Earth, but its diversity is still the lowest of any forest in North America. For additional conifer species to use in ecosynthesis, the best sources are montane coniferous forests. Montane coniferous forests occur in the Appalachian Mountains, the Rocky Mountains, and the Sierra Nevada and Cascade Mountains of North America. Another potential source of martian forests might be the high altitude montane forests of the tropics. With a timberline at or above 4000 m in Mexico (Beaman, 1962; Lauer, 1978), these montane forests are adapted to grow and reproduce at lower atmospheric pressures, higher levels of radiation, and lower levels of moisture than sea-level forest species.

TEMPERATE ECOSYSTEMS

Temperate ecosystems represent the culmination of planetary ecosynthesis on Mars. On Earth the growing season ranges from 120 days to 250 days with mean daily temperatures above 10°C. The amount of annual precipitation determines whether a temperate ecosystem is a forest, grassland, desert grassland, or desert. The eastern temperate deciduous forest of North America varies in annual precipitation from a maximum of 150 cm along the Gulf Coast to a minimum of 75 cm around the Great Lakes (Vankat, 1979). Annual precipitation in temperate grasslands varies from less than 75 cm to 25 cm, where desert grasslands may occur. Deserts generally receive less than 20 cm in precipitation per year. On Mars these temperate zone figures would be a growing season of 220 to 455 sols. A martian deciduous forest would receive from 135 to 275 cm in annual precipitation, grassland from 45 to 135 cm, and desert less than 45 cm in precipitation per year. Temperate ecosystems would permit a widespread open surface agriculture on Mars, just as they do on Earth.

Because the type of temperate ecosystem depends so strongly on the amount of annual moisture and on Mars moisture levels are likely to be lower initially in a stage, the first temperate systems to consider are arid ones, deserts and desert grasslands. A good terrestrial analogue of a martian temperate desert would be the Great Basin Desert. The soil is low in organic matter and high in salinity. A sagebrush (*Artemisia tridentata*) community dominates lower salinity soils, and a shadscale (*Atriplex tridentata*) community occurs on higher salinity soils. Sagebrush is apomictic, and shadscale is autogamous. Grasses such as grama grass (*Bouteloua* spp.) and wire grass (*Aristidia* spp.) dominate desert grasslands. The grasses are all wind-pollinated. Both arid systems should be capable of colonizing Mars.

TABLE 5. Genera of wind-pollinated flowering trees north of Mexico.

Genus	Common name	Genus	Common name
Ulmus	Elm	*Lithocarpus*	Tanoak
Fagus	Beech	*Celtis*	Hackberry
Quercus	Oak	*Morus*	Mulberry
Corylus	Hazel	*Maclura*	Osage orange
Alnus	Alder	*Planera*	Planertree
Betula	Birch	*Trema*	Trema
Juglans	Walnut	*Platanus*	Sycamore
Carya	Hickory	*Liquidambar*	Sweetgum
Fraxinus	Ash	*Populus*	Poplar
Castanea	Chesnut	*Ostrya*	Hophornbeam
Castanopsis	Chinkapin	*Carpinus*	Hornbeam

When the genera of conifers are added to the above list, the groups represent 240 species or 30% of 787 native trees in the region. Data from Regal (1982).

Grasslands are especially important to establish on Mars because they generate some of the most fertile soils for agriculture on Earth. Grasses are wind-pollinated but they also reproduce by vegetative growth, spreading by underground stems (rhizomes) or above ground stems (runners) to form mats. Grasslands also include many species from the sunflower (Asteraceae) and pea families (Fabaceae) that contain numerous apomictic and autogamous species.

Temperate deciduous forests can also generate good to excellent soils for agriculture as well as timber for wood and paper products. Many of the genera of trees that dominate the temperate deciduous forest are wind-pollinated (Table 5). The genera listed include some 240 species or about 30% of the 787 native species of trees in the region (Regal, 1982). A temperate deciduous forest contains five vertical strata: two tree layers, a shrub stratum, herb layer and surface layer. The surface layer includes lichens, mosses and liverworts. The herb layer in cool, wet forests may have a number of ferns and species of *Lycopodium* (ground pine). None of these plants requires animal pollinators. The flowering plants of the herb layer contain many species that are autogamous or apomictic. The rose family (Rosaceae) contains a number of genera and species of shrubs that are apomictic, including *Crataegus* (hawthorn), *Cotoneaster*, *Rubus* (blackberries) and *Sorbus*. Some species of *Sorbus* are subcanopy trees. It should be possible to assemble a temperate deciduous forest on Mars using species that do not require animal pollinators.

The establishment of temperate ecosystems on Mars permits the eventual development of agriculture on the open surface, even if animal pollinators are still restricted by low levels of oxygen. All our major cereal crops such as wheat, oats, barley, corn, rice, and rye are wind-pollinated cereal grasses. Many other crops, such as tomatoes, some potatoes, beans, lettuce, and strawberries are autogamous. Agriculture on the open surface would permit a large, self-sufficient martian civilization.

DISCUSSION

The data used to develop this manuscript came from basic research on biological phenomena that were not directly related to astrobiology. The parameters of temperature and moisture that define different types of ecosystems and the zonation of ecosystems along an altitudinal gradient are a long established part of the ecological literature. The discovery of an ozone hole over Antarctica prompted research on the effects of UV radiation on various organisms, particularly microorganisms. This research was very important in assessing organisms for planetary ecosynthesis. The effects of elevated levels of carbon dioxide on growth of photosynthetic microbes and plants had been largely unexamined until rising levels of CO_2 were detected in the terrestrial atmosphere. Most studies, however, focused on levels of CO_2 less than 5 mbar. It is still not known how well plants can adapt to higher levels of carbon dioxide, as occurred on the early Earth or will occur during planetary ecosynthesis. Relatively little is known about the minimum oxygen requirements of many terrestrial plants, especially bryophytes, yet this information is crucial to the transitions to both the second and third stages in the ecosynthesis process. The discovery of anoxia tolerant plants on the island of Spitsbergen was especially important to the arrival of flowering plants on Mars (Crawford et al., 1994). Even less is known about the oxygen requirements of terrestrial insects that might act as pollinators in transplanted ecosystems. If some insects can function as pollinators at low ambient oxygen levels, then the dynamic process of planetary ecosynthesis would be altered considerably. New discoveries will continue to be made, but until there is actual funding for ecosynthesis research, these discoveries will be made for other reasons than their significance to astrobiology.

This manuscript has attempted to describe the process of establishing functional ecosystems containing communities of terrestrial organisms on the surface of Mars. The process is likely to take from 500 to 1000 years to approach the final stage. Given the vast scope of the process, it has been necessary to describe it in somewhat broad terms. Although the data upon which this description is based are incomplete, the broad picture should be correct. Planetary ecosynthesis on Mars will be a long and great adventure. It will yield a vast amount of new knowledge and become one of the great acts of positive creative energy by the human species.

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