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TERRAFORMING MARS: CONCEPTUAL SOLUTIONS TO THE PROBLEM OF PLANT GROWTH IN LOW CONCENTRATIONS OF OXYGEN

MARTYN J. FOGG
Probability Research Group, c/o 44, Hogarth Court, Fountain Drive, London SE19 1UY.
Internet: mfogg@cix.compulink.co.uk.

The widespread growth of higher plants on Mars following ecopoiesis has often been invoked as a method of generating atmospheric oxygen. However, one issue that has been overlooked in this regard is the fact that terrestrial plants do not thrive under conditions of low oxygen tension. A review of the relevant botanical literature reveals that the high oxygen demands of root respiration could limit the introduction of most plants on Mars until after terraforming has raised the atmospheric pO_2 to 20 - 100 mbar. A variety of physiological strategies are discussed which, if it is possible to implement them in a genetically engineered plant specifically designed for life on Mars, might allow this problem to be overcome.

The greatest service which can be rendered any country is to add a useful plant to its culture.

Thomas Jefferson.

The archetypal plant will be the strangest growth the world has ever seen, and nature shall envy me for it. With such a model, and with the key to it in one's hands, one will be able to contrive an infinite variety of plants. They will be strictly logical plants – in other words, even though they may not actually exist, they could exist.

Johann Wolfgang von Goethe.

Where flowers degenerate, man cannot live.

Napoleon.

1. INTRODUCTION

Since the mid-1980's, there has been a resurgence of interest in terraforming Mars – transforming that planet to suit it for terrestrial life. Many aspects relevant to such an undertaking have been subject to preliminary investigation: including potential techniques of planetary environmental engineering [1-5], possible microbial candidates for a pioneering biota [6,7] and questions of motivation, economics and ethics [8-12]. None of these studies have concluded that the terraforming of Mars would necessarily be impossible or immoral; but while all recognize the scale of the task, conclusions as to its ultimate practicality, and how far Mars' engineered environmental path might proceed in an Earthlike direction, differ widely [13,14].

This should not come as a surprise. The control space within which terraforming can be addressed as a legitimate thought experiment is presently defined by some indistinct boundaries, reflecting uncertainties in our planetological knowledge and differing assumptions on technological and industrial progress. Many of these uncertainties will only be resolved in the future, in the course of space settlement and the establishment of a population on Mars, exploring their world as part of living there [15]. Other aspects of the problem however can be better explored right now. Since the purpose of terraforming is to transplant life in a transformed alien planetary environment, the environmental parameters that constrain terrestrial life, and the life forms that survive at those boundaries, are of particular interest.

Conventionally, the terraforming process is envisaged as a continuum of environmental states starting with the inhospitable Mars of today and culminating with a planet habitable for a complete terrestrial biota, including man (see fig. 1). Technological planetary engineering would presumably initiate the transformation process until an environmental state was attained where a hardy microbiota (of 'extremophiles') could be established. This initial seeding of life is often called *ecopoiesis* [8]. Following ecopoiesis, terraforming can continue, driven by a combination of technological and biological tools.

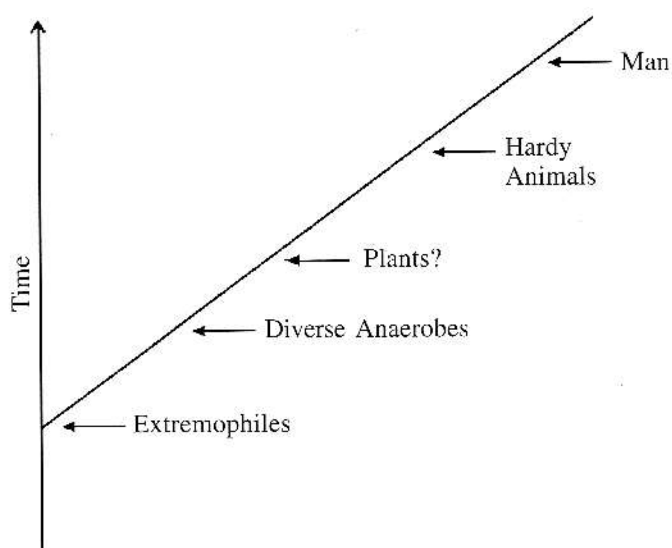

Fig. 1 The environmental trajectory for ecopoiesis and terraforming on Mars. As conditions become more habitable over time, an increasingly diverse biota can be established. An important question is the stage at which higher plants can be introduced.

Some studies lay a particular emphasis on biological transformation [2,10], especially in the generation of atmospheric oxygen and the creation of aerobic conditions that would open Mars for animal life. Creation of an oxygen rich atmosphere out of a CO_2-rich one raised at the start of planetary engineering, in a timescale less than that of a geological epoch, would require a productive biosphere and the deliberate burial of organic carbon. It has been suggested that ecosystems based on higher plants would be best for this purpose [3,11,14]. These are often more productive than ecosystems where the primary producers are bacteria or algae and biomass turnover is slower, resulting in a more massive standing crop. Hence, the biomass that grows is more convenient to harvest, transport and store. In addition, forests and prairies have superior aesthetic appeal than algal pools or microbial mats: Colonists on Mars will wish to experience these too, even if initially deprived of the sight and sounds of the fauna of their terrestrial counterparts.

Thus, the point at which higher plants can be established on Mars is of particular interest, especially with respect to the problem of how much oxygen must already be present in the atmosphere. It is a preliminary evaluation of this question which is the subject of this paper.

2. SOME CHALLENGES FOR PLANTS ON MARS

If higher plants are to drive environmental change on Mars, then it follows that they must be established as early as possible during the terraforming process. Most terraforming models (barring Ref [4]) postulate ecopoiesis taking place on a Mars that has been transformed to a state similar to an arid and chilly version of the Archean Earth. By releasing indigenous volatiles and applying a variety of terraforming tools, it is expected that, in about a century, planetary engineers might thus modify Martian parameters [2,3,5,14].

(1) Atmospheric Pressure: 0.2 - 2 bars, depending on physical/chemical state and capacity of indigenous reservoirs.

(2) Atmospheric Composition: Almost pure CO_2, with as much nitrogen as can feasibly be released from surface minerals and a few millibars of oxygen generated photochemically.

(3) Mean GlobalTemperature:At or above freezing, brought about by increased natural greenhouse effect, possibly supplemented by artificial trace greenhouse gases and incremented sunlight from space reflectors.

(4) Hydrosphere: Mean global depth of released water between 1 - 70 metres, depending on native reserves of ice and their method of melting and liberation.

(5) Surface Irradiation: Large atmospheric column depth reduces cosmic irradiation to safe levels but an incomplete ozone shield still permits some deadly UV light between 200 - 320 nm to reach the surface.

Such changes would greatly reduce the lethality of the Martian environment, but still leaves the planet, compared to the Earth, relatively cool, dry, anoxic, and with less visible radiation and more UV reaching the surface. Microbial ecosystems could probably be established in such circumstances [16], but what about higher plants?

On the Archean Earth, plants didn't exist (they had yet to evolve for two billion years) and therefore there were none adapted to that environment which we could use as a model in choosing a pioneer plant for Mars. To an extent however, similar adverse conditions can still be found on the Earth, although not combined into an environmental totality as they would be on Mars. A list of some such locations is given in Table 1 and it is evident that there exist widespread biomes where plants exhibit varying degrees of tolerance to low pressure, cold, drought, increased UV flux (only at wavelengths > 280 nm), lower visible illumination and high salinity (another possible complication on a terraformed Mars). Some species are known to be equipped to cope with more than one of these vicissitudes [17] and whilst one cannot point to any particular plant species that might do well on Mars, it is encouraging that the Plant Kingdom contains a wealth of adaptations to adversity that might conceivably be genetically combined within a suitable organism.

TABLE 1: *Locations of Hardy Terrestrial Plants*

Adverse Environmental Factor	Some Habitats of Tolerant Plants
Low pressure	High altitudes
Cold	High latitudes, high altitudes
Drought	Deserts, other arid regions
Increased UV flux ($\lambda >$ 280 nm only)	High altitudes
Lower illumination	Forest floors
High salinity	Sea coasts, salt marshes
High pCO_2	Acidic hot springs
Low pO_2	Wetlands

Such factors as temperature and water supply will be variable on Mars, just as they are on the Earth. However, such is the ubiquitous nature of the terrestrial atmosphere, with its high pO_2 and low pCO_2, that environments exactly analogous to the situation during Martian ecopoiesis (*low* pO_2, *high* pCO_2 and possibly low total atmospheric pressure) are virtually unknown. Plants that employ C3 type photosynthesis (the majority) have been found to prefer higher levels of CO_2 than the present atmospheric concentration of 350 ppm, to the extent that air with enhanced CO_2 levels is often used within greenhouses to boost productivity [18]. However, many plants have been found not to fare well at CO_2 concentrations much over 1000 ppm, one of the complications being a lowering of the pH and acidosis of the cellular contents. This is at a pressure equivalent of just 1 mbar, less than that in the present Martian atmosphere. There is though at least one well known alga that is tolerant to a partial pressure of at least 1 bar of CO_2. The unicellular rhodophyte, *Cyanidium caldarium*, has been cultured, and shown to thrive, under such conditions [19,20]. The explanation for this must lie in the fact that it is a resident of hot acidic springs and hence is adapted for life at a low pH. Whether such a tolerance could be conferred on more complex plants is an open question and this issue is set aside from consideration here.

The problem faced by plants of a low partial pressure of oxygen on Mars is perhaps more interesting because the plants themselves are seen as the remedy for low pO_2. It is also a problem that is easy to overlook in a superficial appraisal of plant physiology. After all, when plants grow, the rate of photosynthesis exceeds the rate of respiration resulting in a net production of oxygen. Why should plants need any oxygen from the surrounding air at all when they of producers of it? The fact is though that plants are aerobic organisms and evolved on the Earth when the atmosphere was already rich in oxygen. As will be shown below, the scarcity of oxygen on Mars following ecopoiesis will also be a major adverse factor limiting plant growth.

3. TERRESTRIAL PLANTS AND ANAEROBIOSIS.

All algae and plants are eukaryotes: that is their cells contain nuclei and a variety of organelles, some of which are equipped to conduct aerobic respiration. The energetic pace and greater complexity of aerobic life forms is because aerobic respiration is much more economical in terms of carbohydrate consumption. For instance, oxidising one glucose molecule provides 38 molecules of ATP (the metabolic energy currency of all living organisms) whereas the fermentation of glucose provides just two. It turns out therefore that some oxygen is required by almost all eukaryotes for all, or a substantial part, of their life cycles. Except in some species of yeast, mitosis is inhibited in the absence of oxygen and hence growth cannot occur. No higher plant has been found that breaks this rule [17,21].

The lowest value of oxygen tension required that saturates respiration is known as the *Critical Oxygen Pressure* (usually abbreviated as *COP*) [22]. Cytochrome oxidase enzymes in the mitochondria have such a high affinity for oxygen that their activity is not limited down to a COP of ~ 0.1 mbar [23]. However, in reality respiration becomes limited at higher COPs, when measured in terms of the oxygen tension *exterior* to a given organism, since oxygen must pass through tissues by diffusion, driven by a concentration gradient. Substantially higher values of ambient pO_2 are therefore required to permit adequate oxygenation of interior tissues [21]. The oxygen concentration that divides the aerobic from the anaerobic world is known as the Pasteur Point and is often said to be around 1% O_2, equivalent to a pressure of ~ 10 mbar. Large plants would be expected to have COPs higher than this because of the barriers to diffusion caused by their bulk and the tendency to form an anaerobic core. Moreover, we would expect too that different parts of a given plant would be governed by different values of COP, because of different internal and external anatomy, varying rates of metabolic activity and access to circulating air. *It is reasonable to suppose that the organ where respiration is subject to the highest critical oxygen pressure sets the overall COP for the whole plant.*

Oxygen is supplied to a plant by diffusion from the atmosphere, though under certain circumstances may be supplemented significantly by photosynthesis. The COP of leaves therefore is unlikely to be generally limiting since these organs are the sites of oxygen production. Indeed, it has been noted that the efficiency of C3 photosynthesis actually increases progressively by reducing pO_2 from 210 mbar down to ~ 20 mbar [24]. This appears to be because a lower oxygen concentration suppresses photorespiration, a wasteful process that competes with photosynthesis. Illuminated leaves can apparently function perfectly well at an ambient pO_2 of < 0.5 mbar, no doubt because their cells are respiring locally manufactured oxygen. However, prolonged anaerobiosis in the dark is physiologically damaging and inhibits subsequent photosynthesis upon being returned to the light [24]. The measure of this "prolonged" period however is not clear, but it is likely in most species to be longer than 12 hours.

One of the organs of a plant where oxygen is in most demand is the root system, especially the apical meristem which needs energy for growth and uptake of mineral nutrients from the soil against an osmotic gradient. Since the roots are isolated from an unrestricted flow of air, are most remote from the sites of photosynthesis, and since they must compete with the soil microbiota for oxygen, it is reasonable to consider the high COP of this vital organ as limiting the whole plant.

When subject to anoxia, roots exhibit the following symptoms [25]:

(1) Phloem transport from shoot to roots is inhibited (i.e. the roots' food supply shuts down);

(2) Root growth ceases;

(3) Mineral absorption ceases;

(4) Root apices degenerate;

(5) Death.

Causes of this eventual root death are:

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(5) Reduced supply of nutrients;

(6) Leakage and loss of water to the soil;

(7) Pathogenic and toxic effects of soil microorganisms;

(8) Toxic effects of reduced soil chemistry.

Even though the Earth's atmosphere is rich in oxygen, there are many land habitats (especially those prone to flooding by stagnant water) where plant roots suffer hypoxia, or even anoxia [17,21]. The former reduces growth and prolonged exposure to the latter normally results in death. This is because oxygen is usually supplied to roots by diffusion via air spaces in the soil. When these soil pores are waterlogged, the oxygen diffusion coefficient falls by a factor of ~ 10^4 and its supply is effectively choked off. Temporary anoxia can be withstood by all plants, but not surprisingly, tolerance varies greatly. For instance, cotton roots die under anaerobic incubation in just 3 - 5 hours [26], whereas the rhizomes of certain wetland-adapted plants of the class *Monocotyledonae* (e.g. lilies, irises) can survive for over 2 months [27].

It is thus to wetland plants that we might look for clues on how to adapt plants for low pO_2 on Mars. Such plants adopt three types of strategy to cope with episodes of anoxia [21,25]:

(1) Nutrient requirements and water loss are minimized in order to reduce the adverse effects of poor root function. These are achieved with a slower growth rate of the shoot; storage of mineral nutrients in the leaves; abscission of older leaves; rapid stomatal closure; and epinasty (where the upper side of leaves grow more than the lower, making them appear to droop without losing turgor).

(2) Shallow adventitious roots continually develop at the stem base to replace the previous, damaged, root system. In addition, the roots develop *aerenchyma*, a system of internal pores that connect into continuous air channels. These reduce the bulk of oxygen consuming tissue; increase the internal surface area available for oxygen uptake; facilitate the supply of oxygen downwards from the shoot to the roots; dilute and remove volatile toxic fermentation products; and help oxidise and detoxify the surrounding soil.

(3) Metabolic adaptations are used to increase the time over

which cells are enabled to operate on anaerobic respiration. For instance, the activity of protective enzymes such as alcohol dehydrogenase can be increased and malate can be produced instead of ethanol as a less toxic end-product of fermentation. Furthermore, it has been speculated that some plant roots may be able to respire using nitrate anions as terminal electron acceptors in place of oxygen, much as many bacteria are known to do [28]. Anaerobic metabolism in plants however still only provides a temporary means of survival.

Thus, on Mars some oxygen will have to be present in order to satisfy the demands of root metabolism. Terrestrial plants are used to a sea level pO_2 of 210 mbar. Reduction of pO_2 from these levels, although initially beneficial for C3 plants, can be expected to increase the surface area of oxygen deficient habitats, until a point is reached where even well-aerated soils become hypoxic and a varied, vigourous and widespread inventory of higher plants is not possible. The studies that have been done on root critical oxygen pressures are therefore of particular relevance to the question of terraforming.

Experimentally determined root COPs vary, but values of $pO_2 > 100$ mbar are usually reported for *in vitro* trials on excised root tips or tissue slices [23]. *In vivo* trials on intact plants however report much lower values which are thought to be due to the fact that the experimental procedure had not breached and flooded the aerenchyma system, hence maintaining the supply of oxygen from shoot to roots. Wetland plants that are specifically adapted to cope with hypoxia and temporary bouts of anoxia are characterized by a high proportion of gas space. For unrestricted respiration in wetland species such as rice, it has been estimated that this ventilating system must be such as to maintain $pO_2 > 20$ mb in the region of the roots [29]. Non-wetland plants also seem to be able to supply some oxygen from shoot to root. In intact maize seedlings for instance it has been found that the root COP is as high as ~ 300 mbar when the shoot is maintained in nitrogen, but falls to ~ 60 mbar when kept in air [30]. These values of whole root COP seem to be a function of their densest, most metabolically active tissues such as the meristem and stele; the COP of rice root cortical cells, in close contact with the gas phase, might possibly be as low as ~ 1 mbar [29].

A summary of the range of critical oxygen pressures discussed in this Section is given in Table 2. One might tentatively conclude from it that some unicellular algae, inhabiting well stirred and aerated waters, might find enough ambient oxygen for unrestricted aerobic respiration at a pO_2 as low as 1 mbar, but ~ 10 mbar would be needed for aerobic life to become a significant ecological feature. The bulk and complexity of higher plants would constrain them to a Mars where the atmospheric pO_2 is at least ~ 20 mbar and preferably > 100 mbar [14].

This poses obvious difficulties for the concept of an early introduction of plants on Mars, as calculations of photochemical oxygen production within CO_2 atmospheres similar to those proposed as being raised by planetary engineers, suggest that pO_2 may only rise as high as 1 - 10 mbar [31]. However, since higher plants are such a desirable feature of a pioneering Martian biota, in both practical and aesthetic terms, there is a clear incentive to conceive of plants that both withstand permanent hypoxia and thrive in such conditions.

4. CONCEPTUAL SOLUTIONS FOR PLANT OXYGENATION ON MARS

Permanent hypoxia, above the soil/air interface, occurs nowhere on Earth and hypoxia or anoxia within the soil is usually a problem only when it is subject to waterlogging or freezing. It follows therefore that – setting aside all other likely environmental challenges to pioneering higher plants on Mars – they will require modification from their ancestral terrestrial stock on grounds of oxygen supply alone. *The question is, can we plausibly conceive of a design for a higher plant that is specifically adapted for life on a severely hypoxic planet?*

TABLE 2: *Summary of Critical Oxygen Pressures Relevant to Plant Growth*

Mitochondrion	~0.1 mbar
Cells: close contact with gas phase	~1 mbar
Pasteur point	~10 mbar
Whole roots with internal ventilation	~20 - 60 mbar
Whole roots with no internal ventilation	~100 - 300 mbar

One question we might first ask about *this* question is exactly what do we mean by plausible? Plants modified for Mars would presumably be rendered so by genetic engineering. There have been many fantastic claims made on behalf of the ultimate capabilities of genetic engineering, especially when sharing a common platform with nanotechnology [e.g. 32,33]. Such speculations often *start* with life (or nano-mechanical quasi life) that can survive virtually any environment, subsist on any substrate containing the right elements, and manufacture any required product [e.g. 34]. Perhaps this will be plausible, but the present reality is that whilst we can identify the genes (or programmes) for certain phenotypes and transfer them between existing organisms, we cannot yet invent genes for phenotypes not yet realized in biology. Thus, the approach adopted in this paper is to design hypothetical Martian plants by seeking analogy in forms and processes already observed on the Earth.

It is possible in principle to conceive of a plant that subsists on aerobic respiration, but which requires no oxygen from its surroundings at all. This is because a plant, being a photoautotroph, gains the energy for carbon fixation directly from the Sun. Thus, as a plant grows, the rate of photosynthesis exceeds that of respiration, meaning that it produces more oxygen than it consumes. *Theoretically, if a plant could retain the oxygen it manufactures, and distribute it to all its organs, it would have more than enough to satisfy its respiratory needs and the ambient oxygen tension would be irrelevant.*

Of course, this view is simplistic in that it ignores the reality that photosynthesis ceases at night and such inconveniences as seasons when there is no growth. The former difficulty probably is not one as some plants are known to cope on night time anaerobic respiration; whereas the latter might only be a serious restriction at high latitudes where there is weak winter sunlight. A greater potential problem is the fact that not every stage in a plant's life cycle is photosynthetic. In particular, seeds need energy to germinate and are inhibited from doing so under anoxia (except for growth in some paddy field plants, which declines after shoot emergence if an oxygen source is not found). Fortunately however, research has shown that germination is possible in hypoxic conditions, in some cases at very low oxygen concentrations. Seeds that store their energy reserves in the form of lipids (such as turnip and cabbage) do worst, requiring an oxygen tension of 20 - 100 mbar; but those where the reserves are in the form of starch (e.g. rice and wheat) can get going at a pO_2 between 2 - 9 mbar [35]. Germination in the Martian environment, quite early on in the terraforming proc-be shown below, the scarcity of oxygen on Mars following ecopoiesis will also be a major adverse factor limiting plant growth.

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ess, seems to be plausible for certain plant types.

This returns us therefore to the fundamental problem of maintaining the respiration of a large plant by the retention and internal distribution of photosynthetically produced oxygen. Possible solutions, that might be implemented in a genetically engineered organism, are explored below in a series of thought experiments.

4.1 The 'Lung Plant'

The most straightforward way to oxygenate a Mars plant would be to supply oxygen as a gas via an internal ventilatory net. It has already been pointed out that wetland plants especially are known to possess just such a system of air tubes (aerenchyma) which facilitate the diffusion of oxygen from shoot to root. However, for most such plants the ultimate oxygen source is the atmosphere; on Mars, plants would have to have a higher resistance to air diffusion, preventing oxygen loss and hence permitting redistribution to other organs.

There are some examples of plants on Earth that suggest that such a scheme could be workable. The aquatic angiosperm *Zostera marina* (eelgrass) has been noted to rely on its photosynthetic oxygen for respiration, with the result that it experiences a daily shift between aerobiosis and hypoxia or anoxia [36]. Submerged rice seedlings exhibit exactly the same metabolic cycle [37]. The onset of darkness results in a rapid fall in loss of oxygen from the roots, a cessation of root extension and an accumulation of ethanol from glycolysis. When light is restored, oxygen loss resumes and ethanol levels fall. The explanation seems to be that the boundary layer resistance of the surrounding water prevents oxygen diffusion outwards from the leaves during the day and hinders oxygen entry at night. The result is that, when the plant is illuminated, photosynthetically produced oxygen passes internally, via aerenchyma, to the roots (at $pO_2 > COP$), permitting unrestricted aerobic respiration and re-metabolization of fermentation products.

Although aerenchyma facilitate internal diffusion, their performance as gas conduits would be greatly improved by some form of internal pressure gradient and it is now becoming apparent that some plants can actively circulate their internal gases. Small pore diameters to diffusion help to set up this pressure gradient by permitting a phenomenon called *thermal transpiration* (known in physics as *Knudsen diffusion*). When pore/tube diameters are small (~ 0.1 μm at 1 bar), such that a given molecule is likely to collide with the walls of the tube rather than with other molecules, there will be a net flow of gas from the colder to the warmer chamber. If a return flow is possible via a larger diameter pipe, circulation will continue indefinitely (see fig. 2).

Alder trees – a species that can endure long periods of flooding – are thought to exploit thermal transpiration as part of an active aeration process [38]. Brown pigments in the bark heat up in sunlight to create a temperature gradient between the inner tissues and surrounding air which are separated by a layer studded with ~ 0.1 μm diameter pores. Air then naturally flows into the tree setting up a pressure gradient that pumps gases down to the roots where it eventually escapes through larger pores into the soil.

Better than this for the purposes herein is the "through-flow" system discovered in some rhizomatous wetland plants such as the yellow water lily (*Nuphar luteum*) [39]. The pores responsible here for the solar-pumped pressure gradient (up to 2 mbar above ambient pressure) appear to be those surrounding the internal air cavities of young leaves between the palisade and spongy parenchyma tissues. So long as the plant is illuminated, the outside air should be colder and gas will continue to be

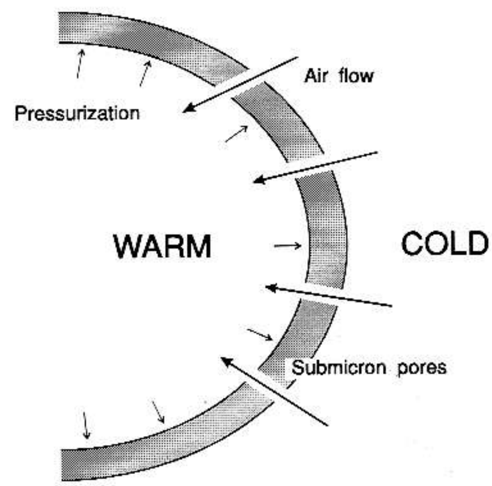

Fig. 2 Thermal transpiration. If two chambers at different temperatures are connected by submicron sized pores, then there will be a net diffusion of gas from the cold to the warmer chamber. This phenomenon is exploited by some plants to pressurize and circulate gas through their interiors.

pumped down into the rhizome. Since the pressurization originates in the leaves, then one might expect photosynthetic oxygen to be entrained in the flow. Maximum rates of 60 ml of air per minute have been observed in water lilies, this being theoretically capable of aerating huge rhizomes up to a metre in length. In addition to supplying gas below ground, the pressurized flow aids the removal of volatile products of fermentation, such as CO_2, acetaldehyde and ethanol vapour. These are flushed upwards, though the stem and exit the plant via older leaves which are more porous and have a lower diffusive resistance. The alcoholic smell this process sometimes generates has lead to *Nuphar luteum* being nicknamed the "brandy bottle".

Wetland plants will not be appropriate at most locales on Mars in the early stages of terraforming and, unfortunately, measurements of the composition of lacunar air in *Nuphar luteum* have shown it to be almost the same as the outside atmosphere [39]. However it might be possible to engineer a more generic Mars plant by recreating its features of a through-flow ventilation (atmosphere → young leaves → rhizome → old leaves → atmosphere) and combining it with the sort of photosynthetic self-oxygenation seen in eelgrass. An influential environmental parameter in this regard would be the high atmospheric CO_2 content, probably at a partial pressure hundreds of times greater than on the Earth. Carbon dioxide would thus tend to enter leaves much more readily which could allow a dramatic reduction in trans-stomatal transpiration. This would be because open stomata represent a compromise between maximising carbon dioxide absorption and minimizing water loss [40]. With such an excess of CO_2 present – well above the needs of photosynthesis – the diffusive resistance of the leaves of Mars plants could be much greater. Stomata could be fewer, smaller, or closed more often and surface to volume ratios of leaves could be less, as in succulent plants. Whilst some upwards movement of water would still be needed in order to move nutrients and for temperature control, much less water need be lost from the plant in order simply to supply its chloroplasts with CO_2. The *water use efficiency* (moles CO_2 absorbed / moles water lost) of Mars plants could be very high, even relative to terrestrial desert plants. This would be an advantage, not just in coping with the parched Martian environment, but also in promoting the function of the self-pressurizing, oxygen-retaining, internal ventilation system discussed above.

Thus, by a process of analogy with naturally occurring plants, it is possible to conceive of a Martian plant, that is plausible in terms of some aspects of plant physiology, which would be adapted to a hypoxic environment (and incidentally surroundings that are also arid and rich in CO_2). Perhaps genetic engineers might succeed in breeding a plant combining features of a wetland monocot and a cactus. The epidermis of our "lung plant" would be covered with a thick cuticle and marked by small, infrequent stomata. During the day these would be partially, or fully closed, permitting the entry of CO_2 just at the rate required by photosynthesis. Oxygen diffusion outwards is hindered and instead thermal transpiration inflates the plant and pumps gas via the ventilatory net throughout its figure. The excess oxygen produced, either escapes through the roots into the soil, or via more permeable leaves. After dark, the plant respires for an hour or so on residual oxygen in the aerenchyma and then switches to anaerobic respiration. The unwanted products of anaerobiosis are flushed out of the plant the next day when the solar-pumped ventilation resumes.

We might therefore envisage Mars plants created by terraformers "breathing" in concert with the daily cycle of their new planetary home.

4.2 The 'Blood Plant'

Food is transported from its site of manufacture in the leaves to non-photosynthetic parts of a plant as dissolved sugars via the phloem system. This raises the question as to whether oxygen could be transported in the phloem as well. To adequately export the capacity of aerobic respiration, six molecules of O_2 would have to be translocated for every molecule of glucose. This does not seem inherently impossible: vertebrate blood is a fluid that does just this, carrying both fuel and oxidiser. As with blood however, simply dissolving oxygen within the phloem sap of Mars plants would be inadequate; a carrier molecule, such as haemoglobin, capable of binding oxygen and greatly increasing its concentration would be needed.

It so happens that plants can make such a molecule, known as *leghaemoglobin*, and the genes for its synthesis are thought to be widespread [41]. In most plants, it is probably of minor physiological significance, merely acting as a signal molecule indicating oxygen deficit. However, in plants that have root nodules containing symbiotic nitrogen fixing bacteria, leghaemoglobin plays and important and delicate role [42]. Nitrogen fixation is inhibited by oxygen and yet is dependent on an adequate supply of ATP from aerobic respiration. This problem is resolved in root nodules by their having an anaerobic core due to diffusive resistance, with the internal supply of oxygen (and hence the production of ATP) being facilitated and regulated by leghaemoglobin. Essentially, leghaemoglobin allows diffusion of oxygen in an environment of very low mean O_2 pressure. Since leghaemoglobin is a similar molecule to the haemoglobin in vertebrate blood, root nodules often appear pink in colour.

In this nodular context, the analogy between leghaemoglobin and animal haemoglobin is only appropriate on the cellular scale. Nevertheless, one is tempted to speculate over the following question: *What if leaves could be induced to manufacture large quantities of leghaemoglobin?* One can perhaps plausibly imagine leghaemoglobin binding to oxygen where the concentration is high, being carried alongside sugars in the phloem sap, and releasing their oxygen elsewhere where the local concentration is lower. The phloem sap therefore would be behaving like blood, enabling Mars plants to efficiently retain and redistribute their oxygen. If deoxygenated leghaemoglobin can somehow be moved from the phloem to the xylem and transported back to the leaves, then the efficiency of the system would be much improved. However, since the plant vascular system is not a simple circulatory one as in animals, achieving this may be problematic.

The xylem of plants might combat the hypoxia problem in another way, by transporting dissolved ethanol to the leaves. Anaerobic respiration is only energetically wasteful if ethanol, the end product of glycolysis, is lost. If it is instead transported to tissues with better aeration and metabolized there then the energy loss is minimised [43]. Again, this is a feature already observed in terrestrial plants and ethanol can frequently be detected rising through the trunks of forest trees.

Thus, as an alternative to the internal ventilation of Mars plants, one can propose leghaemoglobin in the phloem as a solution to the problem of oxygen redistribution and xylem transport as a way to remove and remetabolize ethanol. One amusing feature of such Martian "blood plants" would be that their vascular bundles, and maybe even their interstitial tissues would be coloured pink, somewhat resembling the "red weed" in H.G. Wells's "War of the Worlds". A terraformed Mars might not be so green after all.

4.3 The 'Window Plant'

A substitute to transporting photosynthetic oxygen to underground organs would be to guide the light there and hence generate oxygen *in situ*. Again, some species are known to do this. Succulent plants of the genera *Lithops* and *Frithia* have fleshy leaves that are so translucent that they act as optical fibres [44]. Only the blunt tips of the leaves protrude above the ground (see fig. 3) where they collect light and conduct it to photosynthetic cells in the cool and relatively moist microclimate at the base of the plant.

Succulent plants are adapted to harsh, dry, climates and their low surface to volume ratio promotes water retention, but reduces the capacity to absorb carbon dioxide. This latter aspect is a disadvantage on Earth, but would be the opposite on Mars. So perhaps we might imagine succulents being the basis of engineered Martian "window plants": translucent plants of simple, rounded, shape and capable of photosynthesis and oxygen production throughout most of their bulk.

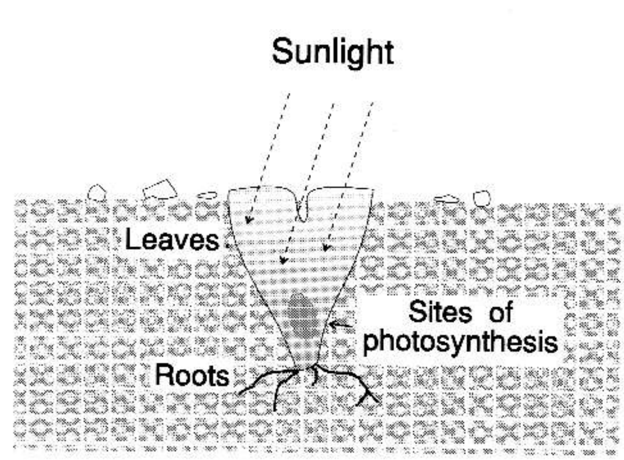

Fig. 3 *Frithia*, the Stone Plant. A desert succulent that lives buried, save for the tips of its fleshy leaves. These leaves are translucent and conduct light to deep-seated photosynthetic tissues.

4.4 Conclusions

Until recently, the likely dearth of oxygen has been an underappreciated difficulty implicit in suggestions that Mars might be rapidly terraformed to a state habitable for both microorganisms and plants. Whilst microbial pioneers are likely to available from present terrestrial stock, this seems improbable in the case of higher plants. However, the creative scoping of the problem here illuminates it with a fresh ray of hope.

The three thought experiments presented suggest that there may be ways to modify plants and adapt them to withstand a condition of permanent ambient hypoxia. The plants "invented" by no means exhaust possible physiological approaches to tackling the problem. Some of the proposed strategies might be combined to their advantage, such as an internal ventilatory net and oxygen conducting phloem in the same organism; "window plants" however would have to be kept free of internal air spaces and pigmented fluids in order to preserve their translucency.

Designing a Martian flora is an extremely speculative exercise as we do not yet have a complete knowledge of plant physiology; we cannot predict the capabilities of genetic engineering to effect suitable and viable alterations; and have very little experimental data on the survival of plants in relevant conditions. Such survival experiments on a wide range of existing plants are an obvious necessity before the need to undertake the more difficult task of engineering new species. One experiment performed in a simulated Martian atmosphere, as it was thought to be in 1962 (almost pure N_2, with 1.39% Ar, 0.24% CO_2 and 0.09% O_2), demonstrated slow growth of *Secale cereale* (winter rye) seedlings and, after 21 days, emergence of the shoots but no primary leaves [45]. A more recent set of 7 day experiments [46] tested the germination of wheat (*Triticum aestivum*) in a more realistic simulated Martian atmosphere (SMA ≡ 2.71% N_2, 0.13% O_2, 0.07% CO, 1.61% Ar, 276 ppm H_2O, the balance being CO_2) at pressures of 10, 101 and 1013 mbar. In all three cases, no seeds were found to germinate. In SMA at 10 mbar, with added increments of oxygen, germination only occurred when supplemented with a pO_2 of 33 mbar. Detailed evaluation of wheat germination in 10 mbar SMA plus 50 mbar O_2 showed growth, but at a slower rate than the control grown in an atmosphere of laboratory pressure and composition. This lesser performance was shown to be a combined effect of low pO_2 and high pCO_2, both of which serve to reduce the rate of respiration.

More such experiments, especially those that maintain several generations of plants under proposed Martian conditions, are needed alongside deliberate research to identify terrestrial flora that come closest to being suitable for ecopoiesis. However, until such a program of study receives funded backing, it must suffice to scour the botanical literature for the most relevant analogies. This at least allows us to list a number of existing features of plant physiology that would promote survival in a hypoxic environment (see Table 3). It remains to be seen how easy it will be to integrate such features within a viable Martian plant.

TABLE 3: *Plant Features Promotion Survival in Low Oxygen Partial Pressure*

- Small size (less tendency to form anaerobic core). ¶
- Small surface/volume ratio (facilitates self-oxygenation). ¶
- Shallow Roots (pO_2 decreases with soil depth).
- Slow growth (less need for ATP)
- High internal porosity (lowers COP: cells closer to gas phase)§
- Internal ventilation (facilitates self-oxygenation and removal of volatile toxins)
- Diffusively resistant epidermis (facilitates self-oxygenation)
- Nitrate respiration (more ATP than fermentation)¤
- Oxygen translocation in phloem (facilitates self-oxygenation)¤
- Ethanol translocation to leaves (rectifies energy deficit of fermentation)
- Translucent tissues (allows deeper photosynthesis) §
- Starch seeds (germinate at low pO_2)
- Pollination by wind, water or self (no animals present)

Notes: Some features conflict (e.g. ¶), are mutually exclusive (e.g. §), or hypothetical(¤)

5. SUMMARY

The salient points raised in this paper are summarized below.

(1) The growth of higher plants on Mars, as early as possible in the terraforming process, is desirable for ecological, economic and aesthetic reasons, as well as in managing the oxygenation of the atmosphere.

(2) A pioneering Martian plant will need to be adapted to multiple adverse environmental factors, such as cold, drought, increased UV flux, low pressure, high pCO_2 and low pO_2. The latter three would pervade every niche on the planet.

(3) If higher plant photosynthesis is to be used to oxygenate Mars, then pioneer species must be tolerant of conditions of severe hypoxia, or anoxia, pertaining over their entire life cycles. No known plants fit this description and so Martian plants will have to be modified from terrestrial stock on grounds of oxygen supply.

(4) The root systems of plants are most intolerant of ambient oxygen deficit due to their high metabolic rates, continual growth, competition with soil microbiota, and distance from the atmosphere and organs of photosynthesis. Successfully growing the great majority of terrestrial plants on Mars will probably require an ambient pO_2 of ~ 20 - 100 mbar to satisfy the demands of root respiration.

(5) Since growing plants produce more oxygen via photosynthesis than they consume in respiration, it is possible to conceive of a plant that, by retaining and redistributing self-made oxygen, is unaffected by low ambient pO_2.

(6) It is possible to plausibly consider several physiological strategies that might permit plants to grow on a hypoxic or anoxic Mars. The realism of implementing these in an engineered organism however cannot be assessed at present, but appears promising due to the range of adaptations to temporary oxygen deficit observed in terrestrial plants.

(7) Such strategies include self-oxygenation, internal ventilation, oxygen translocation, night-time anaerobic respiration, ethanol re-metabolization, deep tissue photosynthesis, and the production of seeds capable of germinating under low pO_2.

(8) The current botanical literature can only be partially applicable to the questions of plants designed for life on Mars. In order to be answered, these questions must be tackled directly with relevant research and experimentation.

In the strict sense of the word, *terraforming* implies the modification of an alien planetary environment to suit it for terrestrial life. Yet when life itself is to be used as the planetary engineering tool, the issue arises of modifying life to suit that environment. This is akin to a concept known as *pantropy*, where the emphasis rests on biological, rather than environmental plasticity. In order to make Mars an aerobic world, we need anaerobic plants and a merging of terraforming and pantropy into a unified process.

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