

The Interplanetary Exchange of Photosynthesis

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Abstract Panspermia, the transfer of organisms from one planet to another, either through interplanetary or interstellar space, remains speculation. However, its potential can be experimentally tested. Conceptually, it is island biogeography on an interplanetary or interstellar scale. Of special interest is the possibility of the transfer of oxygenic photosynthesis between one planet and another, as it can initiate large scale biospheric productivity. Photosynthetic organisms, which must live near the surface of rocks, can be shown experimentally to be subject to destruction during atmospheric transit. Many of them grow as vegetative cells, which are shown experimentally to be susceptible to destruction by shock during impact ejection, although the effectiveness of this dispersal filter can be shown to be mitigated by the characteristics of the cells and their local environment. Collectively these, and other, experiments reveal the particular barriers to the cross-inoculation of photosynthesis. If oxygen biosignatures are eventually found in the atmospheres of extrasolar planets, understanding the potential for the interplanetary exchange of photosynthesis will aid in their interpretation.

Keywords Oxygenic photosynthesis · Biogeography · Dispersal · Endoliths

Introduction

Panspermia is the notion of the transfer of organisms from one planet to another. The idea that life could be transferred in rocks (lithopanspermia) was discussed by Lord Kelvin (Thomson 1871). Arrhenius (1908) developed in detail a proposal for the transfer of life across interplanetary space by radiation pressure.

From an ecological perspective panspermia is island biogeography applied on an extraterrestrial scale. Although panspermia has been discussed as a possible theorem for the origin of life on Earth (Hoyle and Wickramasinghe 1999), it also addresses the perhaps less controversial question of whether, once life has arisen on a planet, it can be transferred

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elsewhere, particularly within the same planetary system. For example, on Earth, organisms can be dispersed from one region of a continent to another and they can be dispersed from one continent to another (MacArthur and Wilson 1967). Panspermia addresses the question of whether planets and solar systems are biogeographical islands or whether, like continents, they can exchange biological material. In that sense it is merely an extrapolation of a well-established question in ecology.

Panspermia remains speculation at the time of writing; there is no evidence that it has occurred within our own Solar System. However, the various stages required for the transfer of organisms from one planet to another have become amenable to experimental testing, and these experiments can reveal the extent to which the selection pressures are dependent upon assumptions about the biochemistry of terrestrial microorganisms. For an organism to be transferred from one planet to another it must survive several dispersal filters (Fig. 1).

First, the ejection of organisms from a planetary surface in an asteroid or comet collision involves extreme forces of acceleration and shock with associated temperature excursions, which the target organisms must survive. Following transit through the atmosphere, the organisms must then survive the process of interplanetary or interstellar transfer, which requires tolerance of long-term desiccation, low temperatures and background cosmic and stellar radiation. Finally, organisms must survive transit through the atmosphere of the destination planetary body, and they must subsequently be able to grow in the physical and chemical conditions offered by the host planetary body (Clark 2001).

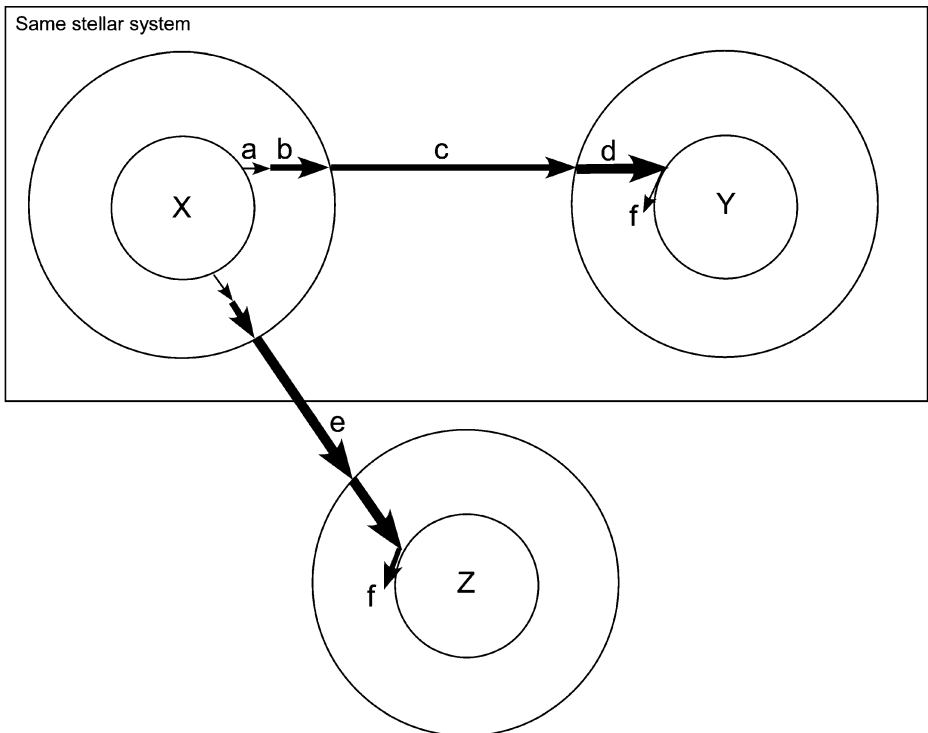


Fig. 1 Dispersal filters in planetary island biogeography for photosynthesis. *a* Launch from planetary surface, *b* atmospheric transit (exit), *c* interplanetary exchange, *d* atmospheric transit (arrival), *e* interstellar exchange, *f* ability to grow on destination planetary surface. The *thin lines* reflect weak dispersal filters, the *thick lines*, stronger dispersal filters. See Table 1

Of special interest in planetary island biogeography is the interplanetary exchange of photosynthesis (Cockell et al. 2007), specifically oxygenic photosynthesis, believed to be an ancient metabolic capability (Buick 1992). Oxygenic photosynthesis is a form of energy acquisition that achieves much higher productivity than chemolithotrophic modes of metabolism. Jakosky and Shock (1998) suggest that compared to the theoretical geochemical sources of energy on Mars for a biota, the Earth's biosphere achieves biomass productivity approximately 4×10^6 times greater. Photosynthesis' principal raw materials – water and carbon dioxide – are common on terrestrial-type planetary bodies (Raymond et al. 2007). Once established, oxygenic photosynthesis produces oxygen which can be used in respiration. The release of energy from consumption of organic carbon (itself generated in large quantity by photosynthesis) in oxygen is sufficiently great to power multicellular organisms and their various modes of locomotion (Vermeij 1995). Ultimately, oxygenic photosynthesis may be required for the evolution of intelligence.

For a planet locked into chemolithotrophic modes of metabolism and associated heterotrophic activity (Jakosky and Shock 1998), the exogenous arrival of oxygenic photosynthesis, prior to its independent evolution, could profoundly affect the characteristics of its biosphere and ultimately the course of evolution, allowing for a much more rapid increase in biological productivity.

As oxygen will be one of the primary biosignatures sought in the atmospheric spectra of extrasolar planets (Lunine 2004; Ehrenreich et al. 2006), understanding the prevalence of oxygenic photosynthesis and its interplanetary promiscuity will be important in interpreting these signatures if they are ever found, particularly in stellar systems that might have multiple terrestrial-type rocky planets in the habitable zone that are thought to be capable of exchanging rocky material.

Anoxygenic photosynthesis is of less interest for the reasons explicated above, but nevertheless five groups of microorganisms have evolved to carry out this mode of metabolism compared to the one (cyanobacteria) group that innovated oxygenic photosynthesis, making it more phylogenetically widespread. The pumping of protons across cell membranes using a simple photoreceptor is an ancient evolutionary innovation and may represent one of the first types of simple cell metabolism (Skulachev 1994; Mulikidjanian and Junge 1997; Sharma et al. 2006). The dispersal filters considered here would apply to the interplanetary exchange of anoxygenic photosynthesisers and organisms using simple light-driven pumps in metabolism.

In this review I discuss experimental results on the survival of oxygenic photosynthetic organisms during the different phases of lithopanspermia, conducted by us and/with other workers. A synthesis of these data provides insights into the likelihood of the interplanetary exchange of photosynthesis.

Dispersal Filters in the Transfer of Photosynthesis—Experimental Evidence

Ejection from the Planetary Surface

The dispersal filter acting on organisms during the ejection of rocky material from a planetary surface involves acceleration, shock and high temperatures associated with the impact that causes the launch of material to escape velocity. The launch of rocks to escape velocity from a planetary surface is possible at moderate temperature and shock pressures due to spallation caused by interference of the primary and reflected shock waves (Melosh 1984). Empirical knowledge of shock pressures experienced by ejected rocks is obtained

from Martian meteorites, which show shock pressures from approximately 5 to 55 GPa (Fritz et al. 2005).

The effect of acceleration during ejection has been investigated with both *Bacillus subtilis* and *Deinococcus radiodurans* in rifle experiments (Mastrapa et al. 2001). Survival values of 40 to 100% after accelerations up to 4.5×10^6 m/s² suggested that acceleration is not a strong dispersal filter. *Bacillus subtilis* spores, isolated from Sonoran desert (USA) basalt, similarly survived accelerations up to 1.5×10^{10} m/s² (Benardini et al. 2003). *Bacillus subtilis* is a spore-forming organism and therefore might be resistant to jerk and acceleration on account of the tough spore coat (Riesenman and Nicholson 2000). These experiments are consistent with early rifle experiments reviewed by Roten et al. (1998), including experiments by N. Pustoschkin in 1895 in which greater than 88% survival of a diversity of bacteria including *Bacillus coli*, *Serratia plymuthica*, *Streptococcus pyogenes* and *Escherichia coli* were shown at acceleration of 100,000 g.

Acceleration experiments have not been undertaken on asporogenous phototrophs. However, survival of the asporogenous heterotroph *D. radiodurans* following acceleration suggests that even for vegetative organisms acceleration does not present a strong barrier.

Planetary ejection requires survival of shock pressures. Shock experiments using both light gas gun and plate-flyer apparatus carried out by numerous workers show clearly that organismal survival depends both on the nature of the cell and its local microenvironment. Spores of *Bacillus subtilis* show high resistance to shock, with survival of shock pressures greater than 50 GPa now reported from separate experiments (Horneck et al. 2001a; Burchell et al. 2001, 2004; Stöffler et al. 2007; Horneck et al. 2007). Burchell et al. (2001, 2004) showed survival of *Bacillus subtilis* up to 78 GPa.

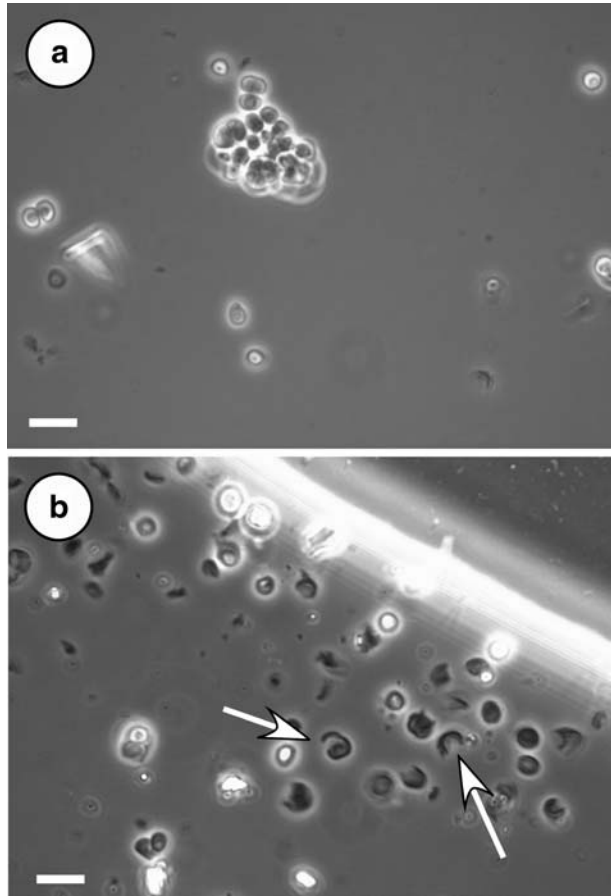
In contrast, vegetative cells are susceptible to disruption by low shock pressures. In flyer-plate experiments, we showed that the asporogenous cyanobacterium, *Chroococcidiopsis* sp., was killed at shock pressures greater than 10 GPa (Stöffler et al. 2007; Horneck et al. 2007). This organism was chosen because it naturally inhabits the interior of rocks. The ruptured cell walls observed at this and higher shock pressures (Fig. 2) suggest that the vegetative cell walls are susceptible to mechanical failure, an observation that would be consistent with the observations of the effects of shock on *Escherichia coli*, which included shock indentation of cell membranes (Willis et al. 2006).

In addition to shock, organisms will be exposed to brief temperature pulses (Stöffler et al. 2007; Horneck et al. 2007). In the case of the experiments described above, these temperature pulses were automatically factored into the experiments (1–100°C for 1.4 μs with post-shock temperatures depending on equilibration of the container with the surroundings). The maximum temperatures experienced will depend upon the nature of the propagation of the shock wave, the thickness of the biological material and the characteristics of the organisms.

The reported results suggest that for vegetative cells (which include most oxygenic photosynthetic organisms) shock pressures associated with ejection to escape velocity act as a strong dispersal filter. However, in the same experiments, conducted by a group at the University of Dusseldorf, vegetative photobionts associated with a lichen symbiosis survived shock pressures up to 30 GPa (Stöffler et al. 2007; Horneck et al. 2007). The photobiont is surrounded by the symbiotic mycobiont, which constitutes part of a thick cortex. The cortex might, in this case, offer protection for the vegetative photobiont (Stöffler et al. 2007; Horneck et al. 2007). Nevertheless, the photobiont is still relatively susceptible compared to spore-forming *Bacillus* sp.

The experiments indicate that even for desiccated vegetative cells, shock pressures at the lower end required for escape velocity from Mars (and Mars-like planets) can be survived, although in the case of *Chroococcidiopsis* sp., its threshold of survival was at the lower end

Fig. 2 Effects of shock on an asporogenous phototroph (*Chroococidiopsis* sp.). **a** Phase contrast micrograph of the organism. **b** Effects of a 10 GPa shock. *Arrows* show ruptured cells with dispersed contents. *Scale bars* are 10 μm



of shock pressures for rocks to reach escape velocity from Mars [the escape velocity of the Earth (11.2 km/s) is approximately twice that of Mars (5.02 km/s) implying higher minimum shock pressures required to reach terrestrial escape velocity]. These results suggest that impact ejection would act as a strong dispersal filter against *Chroococidiopsis* if it was in the same form as in these experiments. The presence of spore-forming states, emplacement in a thick cortex, etc., will increase the range of shock pressures under which oxygenic photosynthetic organisms (and other non-phototrophs) can survive the dispersal filter, increasing the chances of survival of planetary ejection.

The primary molecular basis of this dispersal filter is therefore exceeding the mechanical strength of cell walls/membranes. A contribution of the thermal inactivation of cellular macromolecules might also be important in some instances. The experiments conducted show that the effects are specific to the particular characteristics of cell membrane/wall and other coatings of different organisms.

Atmospheric Transit (Launch and Arrival)

Both the launch of a rock and its landing on the destination planetary body require that it pass through the dispersal filter of transit through the origin and destination planetary

Fig. 3 Effects of atmospheric transit on a cryptoendolithic habitat for phototrophs. **a** Example of a cryptoendolithic community in Beacon sandstone from the Antarctic Dry Valleys. *Arrow* shows layer of lichen growing within rock (e.g., see Friedmann 1982). *Scale bar* 1 cm. **b** Example of a cryptoendolithic community in shocked sandstone from the Hughton impact crater, Canadian High Arctic (see Cockell and Osinski 2007). *Scale bar* 1 cm. **c** Example of a cryptoendolithic community within shocked gneiss from the same impact crater (see Cockell et al. 2002). *Scale bar* 1 cm. **d** Artificial gneiss endolithic habitat made from material in **c** and inoculated with *Chroococcidiopsis* sp. *Scale bar* 1 cm. **e** Sample bolted into heat shield of Russian FOTON capsule (*white circle*), **f** capsule after re-entry showing location of sample (capsule is 2.22 m in diameter), **g** sample after re-entry showing fusion crust on surface of gneiss. *Scale bar* 0.25 cm. For a detailed discussion of **d** to **g** see Cockell et al. 2007

atmosphere. As with planetary ejection, this has proven to be experimentally tractable using sounding rockets and orbital vehicles.

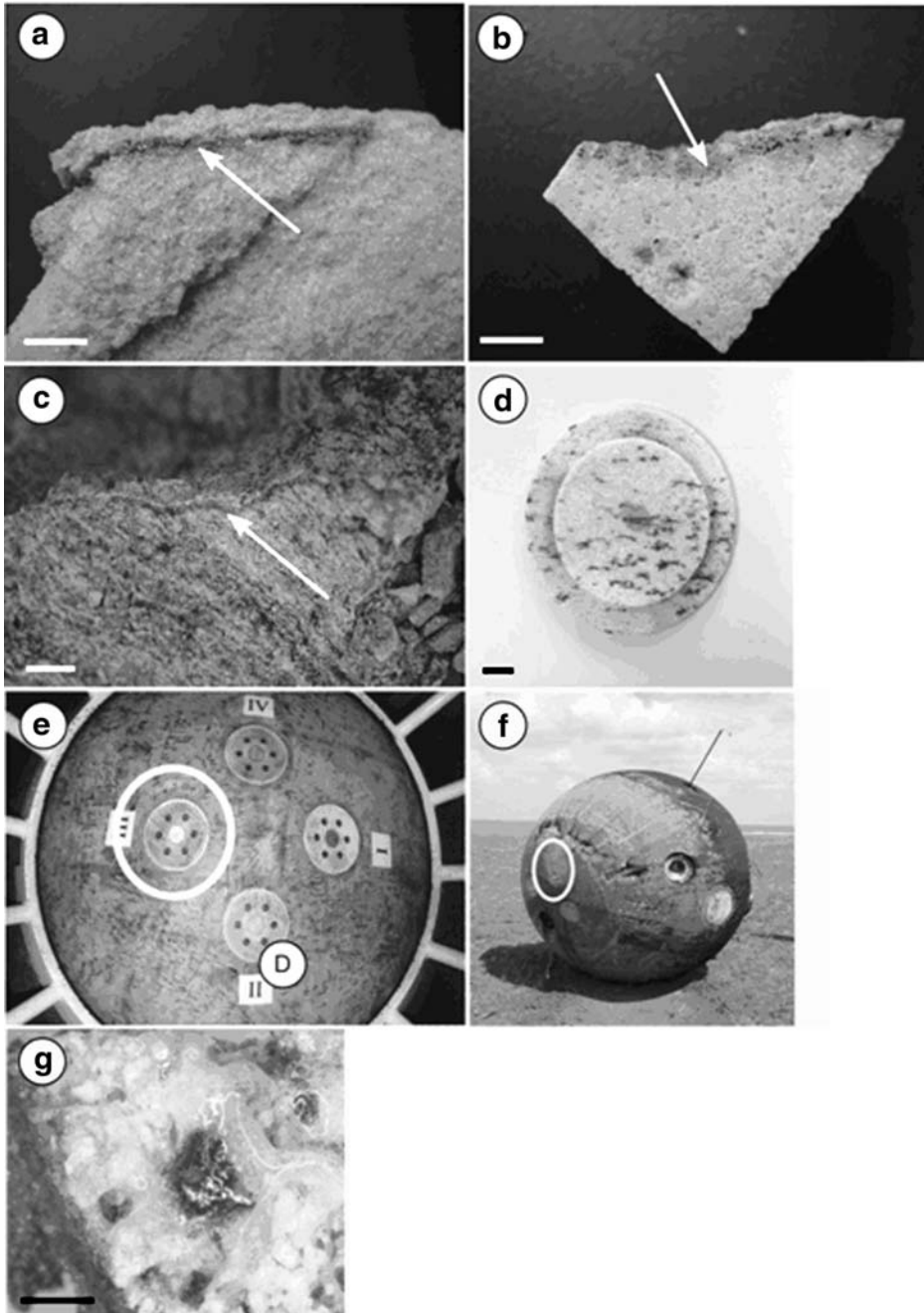
Bacillus subtilis spores inoculated onto granite domes were subjected to hypervelocity atmospheric transit (twice) by launch to ~120 km altitude on an Orion two-stage rocket (Fajardo-Cavazos et al. 2005). Spores were shown to have survived on the sides of the rock except for the forward-facing surface, which was subjected to a maximum temperature of 145°C.

Under the auspices of the ESA STONE experiment, an experimental campaign designed to investigate the survival of artificial meteorites during atmospheric entry (Brack et al. 2002), we studied the effects of atmospheric entry on photosynthetic organisms (Cockell et al. 2007). Photosynthetic organisms must inhabit a rock at a depth where light levels are sufficient for photosynthesis (e.g., Fig. 3a–c). The minimum light levels for photosynthesis are set by fundamental biophysical constraints (Raven et al. 2000).

Whereas photosynthetic organisms have been observed in the oceans at depths where levels of photosynthetically active radiation are ~10 nmol m⁻² s⁻¹ (Littler et al. 1986), theoretical calculations suggest that the minimum is more similar to ~0.1 μmol m⁻² s⁻¹ (Raven et al. 2000). Nevertheless, these numbers are similar and for any biochemical architecture there would be a lower limit for photosynthetic activity set by the biophysical constraints on photon capture and inefficiencies in the electron transfer reactions (Wolstencroft and Raven 2002; Raven and Wolstencroft 2004). Ultimately there is an insurmountable barrier to photosynthesis set by the depth at which light is completely extinguished.

In a diversity of rock types normally conducive to the growth of photosynthetic organisms the minimum depth required for photosynthesis corresponds to a depth of approximately 5 mm or less (see, for example, Matthes et al. 2001; Cockell et al. 2002; Hughes and Lawley 2003). Generally rocks suitable for endolithic growth are sedimentary as they possess sufficient porosity and translucence to allow for the growth of photosynthetic organisms (e.g. Friedmann 1980, Fig. 3a), although impact-shocked crystalline rocks can also host cryptoendolithic organisms (Cockell et al. 2002, Fig. 3c) and granites can host chasmoendolithic communities within cracks (De Los Rios et al. 2005).

Qualitatively, the depth at which photosynthetic organisms can grow within a rock is much shallower than the depth likely to be ablated and heated to above the upper temperature survival limit for cells during atmospheric transit. Ceplecha et al. (1998) estimate that 70% of a meteorite is ablated during atmospheric transit. Gladman (1997) suggests that 10–20% of the radius of a hand-sized meteorite is destroyed. In computer calculations Mileikowsky et al. (2000) showed that a rock requires a diameter of >0.2 m to avoid being heated to above 100°C throughout. Although the escape velocity from Mars is lower than for the Earth, the frictional heating will still be sufficient to heat the surface regions of rock to well above the upper temperature limit for the survival of phototrophs.



Photosynthetic organisms can potentially inhabit rocks at depths of centimetres within cracks, where the cracks allow light to be channelled through the rock matrix. However, these cracks are likely to themselves channel hot gases to the enclosed biota during atmospheric transit, or they will act as sites for fragmentation of the meteorite.

To test the hypothesis that the limitation imposed by the requirement to live near the surface of the rock would provide a strong dispersal filter against photosynthetic microorganisms during atmospheric transit, we used a re-entry vehicle entering the atmosphere at 7.5 km/s (determined from the re-entry profile) to examine the survival of *Chroococcidiopsis* sp. inoculated into a gneissic impactite (Fig. 3d–g). The organisms were inoculated into the rock to the depth at which phototrophs are found growing in the material in the natural habitat (Fig. 3d). The rock was fixed into the heat shield of the re-entry capsule (Fig. 3e) and launched to orbit using a Soyuz rocket. After orbiting the Earth for 16 days the habitat and its inhabitants were de-orbited and the sample was retrieved in Kazakhstan (Fig. 3f). Neither the organisms nor their biomolecules survived (e.g., Fig. 3g). Although the scope of the experimental design was necessarily limited by its cost and logistical complexity (there was a limitation of a single sample, for instance), it provided a simple, but empirical demonstration of the effectiveness of atmospheric transit as a dispersal filter (see later section) in the transfer of photosynthetic organisms (Cockell et al. 2007).

The molecular basis of this dispersal filter is therefore the thermal inactivation of the cells and their constituent biomolecules. An important feature of this dispersal filter is that it is universal and makes no assumptions about the nature of the biochemistry involved in the organisms, since, by definition, phototrophs must live near the surface of a rock where light is available. If an atmosphere is thick enough to sustain planetary conditions suitable for life, the depth of ablation and heating during transit through that atmosphere will likely be greater than the depth at which photosynthesis can be sustained.

The experiment also showed that epilithic photosynthetic organisms (those growing on the surface of rocks) would be destroyed by atmospheric transit. Organisms such as surface cyanobacterial, algal biofilms, lichens or epilithic heterotrophs (including those associated with phototrophs) have little chance to survive this filter.

This simple experiment is significant because it shows that the survival of the other phases of lithopanspermia would be rendered irrelevant if the organisms are killed during atmospheric transit. Thus, although photosynthetic organisms, including cyanobacteria (Mancinelli et al. 1998) and lichens (Sancho et al. 2007) have been shown to survive the extreme conditions of interplanetary space, their survival of the interplanetary transit phase would be rendered valueless by their destruction during atmospheric transit, an illustration of the importance of considering all phases of panspermia in unison, rather than as separate challenges to the biota.

The potential ineffectiveness of this atmospheric transit filter if organisms are at sufficient depths within some rocks is evidenced by the recovery of Martian meteorites with minerals inside them indicating that they experienced temperatures no greater than 40°C since their launch (Weiss et al. 2000). Although the sounding rocket experiments performed by Fajardo-Cavazos et al. (2005) did not reach velocities associated with meteoritic atmospheric entry, the survival of *Bacillus* sp. spores during atmospheric transit in these experiments, together with the mineralogical evidence presented by Weiss et al. (2000), suggests that conditions in the interior of rocks may allow for the survival of atmospheric transit by heterotrophs and chemotrophs. In our experiment the rock thickness (1 cm) was not sufficient to test this possibility as it was heated sufficiently to kill non-photosynthetic organisms (*Bacillus subtilis* spores) that had been placed on the underside of the rocks by other investigators. Thicker rock sections were not possible on account of the requirement not to break the integrity of the heat shield.

The filter described will not only act against organisms transferred between one planet and another, but it will also reduce the chances for the re-inoculation of photosynthesis on a planet subjected to heavy bombardment (Wells et al. 2003; Gladman et al. 2005), since

rocks must first exit and then enter the atmosphere to re-inoculate the planet. As light-driven proton pumps may represent the earliest types of metabolism (Skulachev 1994; Mulkidjanian and Junge 1997; Sharma et al. 2006), the inability to survive atmospheric exit and entry would have meant that early photoreceptor-driven cells would have less chance to survive a period of bombardment, again selecting in favour of chemotrophs and heterotrophs.

Interplanetary Transfer Phase

During the interplanetary transit phase photosynthetic organisms near the surface of the rocks are potentially subject to high ultraviolet (UV) radiation. Interplanetary UV radiation has been considered to be a significant detrimental factor for organisms being transferred between planets (Horneck et al. 2001b; Nicholson et al. 2005; Cockell et al. 2005). The flux of UV radiation penetrating to an organism will depend upon the distance from the star that the rock is located, its orientation, the thickness and UV absorption and scattering properties of the material covering the organisms. Without the protective effects of atmospheric absorption, particularly CO₂, which screens UV radiation below 195 nm, the surface of rocks in interplanetary space will be exposed to the full UV wavelength range emitted by the star.

A diversity of published work shows that layers of different mineral types can significantly reduce UV radiation (Mancinelli and Klovstad 2000; Schuerger et al. 2003; Rettberg et al. 2002; 2004). Mancinelli and Klovstad (2000) showed that even dust layers of 12 µm could provide some shielding to *Bacillus subtilis* spores, with 10% survival measured after exposure to 12.3 kJ m⁻². In a study focused on panspermia Horneck et al. (2001b) showed that *Bacillus subtilis* spores mixed within clay, sandstones or Martian meteorite (Zagami) were protected against UV radiation, although thin layers were ineffective, possibly due to UV penetration through cracks or the formation of toxic photochemical products. The work of Schuerger et al. (2003) supports the fact that these layers must be sufficiently thick to completely block all wavelengths of UV radiation.

The data on the thickness of material required to provide UV protection, when compared with information on the extent of the ablation of rocks entering the atmosphere (for example, Ceplecha et al. 1998) and the experiment reported by Cockell et al. (2007) suggests that the depth of ablation of a rock during two atmospheric transits is likely to be much greater than the depth required for UV protection, i.e., if an organism is deep enough to survive ablation and heating caused by atmospheric transit (at the very least several millimetres), it is, by default, deep enough to be completely protected from UV radiation during the period in interplanetary space.

As UV radiation is mutagenic, and its intensity in interplanetary space is potentially high, then it is not surprising that it has attracted attention as a potential dispersal filter in panspermia. However, it illustrates the problem in considering each phase of panspermia in isolation. The relevance of different dispersal filters must be considered in the context of all phases. As the depth required to survive atmospheric transit during the ejection and planetary entry phases is much greater than the depth at which UV radiation experienced during the interplanetary transit phase is likely to be extinguished, except for the most transparent materials, such as clear quartz, then it follows that UV radiation, for most rock types, is not an important factor for panspermia.

Another detrimental factor is cosmic radiation, which is more penetrating than UV radiation. Mileikowsky et al. (2000), using experimental data on the survival on *Bacillus subtilis* spores to heavy ion doses, suggest that behind 1 m of shielding spores could survive for about 1 million years, with this survival period dropping to 300,000 years

behind 10 cm of shielding due to secondary radiation effects. Clark similarly finds that within 1 million years a meteorite would be sterilized to 1 m depth. Clark calculates that the top 3 cm of a rock, i.e., the zone within which oxygenic photosynthetic organisms would live, would be sterilized within 100,000 years (Clark 2001). Although computer models suggest that rocks can potentially be transferred between Earth and Mars, for instance, in 10 years, more typical times are likely to be 10^5 – 10^7 years (Gladman et al. 1996; Gladman 1997). Thus, even if one assumed that near surface-dwelling photosynthetic organisms somehow survived the dispersal filter of atmospheric transit during planetary ejection and arrival at the destination planet, in most cases they would be effectively killed by cosmic radiation during interplanetary transit, which, unlike UV radiation, will effectively penetrate to depths of a few millimetres or centimetres where such organisms would normally grow. They would be additionally susceptible to killing by secondary radiation effects near the surface of the rock. The primary molecular basis of this dispersal filter will be radiation damage to nucleic acids and other cell macromolecules.

Despite these strong filters, evidence suggests that phototrophs can survive other dispersal filters associated with conditions in space. Mancinelli et al. (1998) flew the halophilic cyanobacterium *Synechococcus* sp. isolated from a salt deposit in Baja California in Earth orbit for 15 days on the BIOPAN facility. Temperatures during the flight ranged from -18 to 15°C and the total solar UV radiation dose was 10^4 KJ. The organisms exhibited nitrogen fixation and carbon uptake upon their return. Similarly, lichens flown in BIOPAN exhibited unaltered physiological activity after 16 days in Earth orbit (Sancho et al. 2007), consistent with ground-based experimental results (de Vera et al. 2004).

These experiments were of short duration, much shorter than the duration required for interplanetary exchange and they did not expose organisms to long duration interplanetary cosmic radiation, but they nevertheless suggest that these dispersal filters are weak. Given that some photosynthetic organisms, such as *Chroococcidiopsis* sp., exhibit highly desiccation, radiation-resistant forms (Grilli Caiola et al. 1993; Billi et al. 2000) it is likely that some phototrophs have a chance to survive for periods of time at least as long as *Bacillus subtilis* spores, which were shown to survive in orbital experiments for 6 years (Horneck et al. 1984; Horneck et al. 1994).

Survival on the Destination Planet

The survival of an organism on the destination planet depends upon the organisms' physical and chemical range of growth and whether they match the combined physical and chemical conditions to be found in the destination environment. For example, the survival of a phototroph launched from a freshwater system and landing in a marine environment or vice-versa, will depend upon the halotolerance of the organism. The growth temperature range of the organisms will determine the required match between the origin and destination planetary temperatures. Many cyanobacteria in the arctic are optimally adapted to temperatures higher than environmental temperatures (Tang et al. 1997), the mismatch being explained by the fact that competition is low and there is not a selection pressure for the maximum growth rate to match the environmental temperatures. For cosmopolitan phototrophs with wide physiological ranges, the probability of arrival in a compatible environment on a destination planet will obviously be greater than for phototrophs with narrow physiological ranges. The molecular basis of this dispersal filter is therefore physical and chemical conditions inappropriate to cell physiological and metabolic functions.

Another factor is the light regimen available for photosynthesis. In our own Solar System the photosynthetically active radiation (PAR) level at the outer orbital position of Pluto is ~ 30 μmol

$\text{m}^{-2} \text{s}^{-1}$, approximately 300 times above the theoretical minimum required for photosynthesis. Although atmospheric attenuation reduces this light level, the point is that throughout our own Solar System, light levels are generally sufficient for photosynthesis where the Sun's solar radiation directly impinges. In a similar system elsewhere, the availability of light would therefore not be dependent upon the output from the star, but the location where the rock landed, the penetration of PAR through the atmosphere, and orbital parameters which determine the exposure to PAR (Raven and Cockell 2006).

Interstellar Transfer

Interstellar space is likely to act as an effective dispersal filter to organisms, including photosynthetic organisms. Melosh (2003) used a Monte Carlo approach to investigate the likelihood of the transfer of meteorites between terrestrial-like planets in different stellar systems. The probability of a terrestrial rock ejected from our Solar System colliding with a terrestrial-type extrasolar planet is 10^{-4} in a total period of 4.5 Gyr, making transfer a low probability event. Similarly, Adams and Spiegel (2005) considered the transfer of rocks between stellar systems in star clusters where star densities are much higher than our local galactic neighbourhood. They arrive at similarly low probabilities. Pre-stellar systems might sputter incoming material and increase the chances for the dispersal of organisms (assuming they survive the substantial time periods of interstellar transit) (Wallis and Wickramasinghe 2004). Material exiting from a solar system can disintegrate, through collisions with dust, to particle sizes sufficient to allow for ejection from the solar system by radiation pressure, offering another mechanism for interstellar distribution (Napier 2004). Nevertheless, the models reported to date suggest the interstellar transfer of oxygenic photosynthesis, let alone any organisms, to be a very low probability event. In addition, the integrated exposure to cosmic radiation over such long durations of time will likely be sterilizing, at least extrapolating evidence on the viability of terrestrial microorganisms preserved in ice (Bidle et al. 2007).

An additional consideration specific to photosynthesizers is the match of the photosynthetic pigments of organisms to the light emitted by the destination star. Photosynthetic organisms from a planet orbiting a G star with similar pigmentation to terrestrial organisms, for instance, would achieve low productivity on a planet orbiting a cool M star, where the spectral fit was poor on account of the shift of the radiation output towards longer wavelengths (Wolstencroft and Raven 2002). Wostencroft and Raven speculate on a three-photon system for phototrophs (as opposed to the terrestrial two photon system) on M star planets, which would allow sufficient energy acquisition from long wavelength photons in the spectra of such stars for photosynthesis. As M stars are common in the Universe, they are a likely destination for any phototroph ejected from another planetary system.

Survival of the Filters

Few ecological dispersal filters are completely effective. Each of the filters described above could be survived on account of specific physical factors or evolutionary innovations. The experiments so far conducted yield some insights into what these circumstances might be. In the case of ejection from the planetary surface, the experiments with *Chroococcidiopsis* sp. show that even these vegetative cells could survive shock pressures at the lower end of that documented in Martian meteorites (~5 GPa). The upper threshold of pressure resistance might be increased by tough shock resistant states, experimentally tested examples being the spore coat of *Bacillus* spp. and the cortex microenvironment of phototrophs in lichens, increasing the range of pressures under which photosynthetic organisms could achieve

escape velocity. Thus, although planetary ejection is shown experimentally to be a potentially strong dispersal filter, these same experiments show that shock pressures close to those required to achieve escape velocity, at least for Mars-like planets, can be survived even for vegetative phototrophs without special protection.

The dispersal filter of atmospheric transit is the most effective dispersal filter for photosynthesis. Any process that allows the cells to be embedded deep within a rock and preserved there during planetary exchange would allow them to survive the filter. Physical processes might include, for example, an impact into ocean where photosynthetic organisms become incorporated within the rock below the zone of heating and ablation as it is displaced through the photic zone, although the physical reality of such a process is difficult to assess.

Specific evolutionary innovations that might allow a phototroph to survive the filter include motility. An organism that had become located within the deep pore space of a rock, and preserved there during ejection and exchange, might then be released after landing. On Earth, a diversity of cyanobacteria, for example, some *Synechococcus* species, display motility (e.g., Bhaya et al. 2000). Mixotrophs, which can both photosynthesize and use organic carbon as an energy source (Hitchman and Jones 2000), might grow deep in a rock using organic carbon and then be transferred to a new planet and released, initiating photosynthesis (Cockell et al. 2007), although the presence of mixotrophs naturally inhabiting the deep interior of rocks has not been reported.

Thus, the planetary exchange of photosynthesis might not be impossible, but quite specific physical situations and/or evolutionary innovations are required to create conditions where a photosynthetic organism happens to be buried deep within a rock during ejection to survive atmospheric transit.

The discussion in this paper has focused on microorganisms. Tepfer and Leach (2006) discuss the idea of the transfer of plant seeds. The authors suggest that small seeds ($\leq 200 \mu\text{m}$) might have the capability of floating through a planetary atmosphere, analogously to interstellar dust (Coulson 2006), thus avoiding atmospheric frictional heating. Such a process would overcome the filter of atmospheric transit described by Cockell et al. (2007). The seeds would have to be ejected at escape velocity either individually or embedded within a rock to escape frictional heating during planetary ejection.

However, the dispersal filters associated with this mode of panspermia are potentially more formidable than those with microscopic oxygenic phototrophs, particularly the requirement for conditions conducive to seed germination and growth on the host planet. Plant seeds require sufficient oxygen for germination as respiration is required for the formation of shoots to initiate photosynthesis. Within the first few days of germination most plant seeds are net oxygen consumers and thus landing on an anoxic planet would prevent seed germination. Wheat seeds were unable to germinate in simulated Martian atmospheres (Schwartzkopf and Mancinelli 1991). Thus, for seeds to survive and grow, they likely require the presence of oxygenic photosynthesis in the first place. Nevertheless, the exchange of oxygenic photosynthesis in the form of sub-millimetre sized resting states of multicellular and unicellular organisms which drift into planetary atmospheres, preventing atmospheric friction, expands the envelope of possible mechanisms for transfer that avoid this strong dispersal filter.

Exchange of Oxygenic Photosynthesis and Biosignatures on Extrasolar Planets

Understanding whether oxygenic photosynthesis can be transferred between planets may aid interpretations of the atmospheric compositions of extrasolar planets. For example, the discovery of two planets in a planetary system, one of which has a biosignature of oxygen

Table 1 Dispersal filters to the interplanetary exchange of photosynthesis

Letter in Fig. 1	Phase of panspermia	Dispersal filter and comments	Likely molecular basis of dispersal filter	Citations
a	Launch from planetary surface	<i>Acceleration (weak dispersal filter), shock and high temperatures (potentially strong dispersal filters)</i> . Phototrophs not tested for acceleration, but vegetative cells can survive acceleration required (<i>D. radiodurans</i>). Phototrophs shown to survive the lower shock levels for ejection from Mars	Mechanical strength of cell membrane/wall exceeded. Thermal destruction of cell macromolecules	Mastrapa et al. 2001; Burchell et al. 2001; Horneck et al. 2001b; Stöfler et al. 2007; Horneck et al. 2007. Also see review and discussion of early experiments by Roten et al. 1998
b	Atmospheric transit (exit)	<i>Heating of surface layers (strong dispersal filter)</i> . Kills phototrophs near surface. Filter is universal	Thermal destruction of cell macromolecules	Fajardo-Cavaros et al. 2005; Cockell et al. 2007
c	Interplanetary exchange	<i>Cosmic radiation (and secondary radiation) (strong dispersal filter)</i> . Kills near-surface dwelling organisms. <i>Desiccation and low temperatures</i> . Phototrophs e.g. <i>Chroococcidiopsis</i> can survive these prolonged extremes	Primarily radiation damage to nucleic acids and other cell targets. Also macromolecular disruption by extreme desiccation	Mancinelli et al. 1998; Mileikowsky et al. 2000; Clark 2001; Sancho et al. 2007
d	Atmospheric transit (arrival)	<i>Heating of surface layers</i> . Kills phototrophs near surface (see b)	Thermal destruction of cell macromolecules	Fajardo-Cavaros et al. 2005; Cockell et al. 2007
e	Interstellar exchange	<i>Long term exposure to radiation in metabolically inactive state and low probability of reaching habitable planet</i> . Not specific to phototrophs. Strong dispersal filter	Primarily radiation damage to nucleic acids and other cell targets. Also macromolecular disruption by extreme desiccation	Melosh 2003; Napier 2004; Wallis and Wickramasinghe 2004; Sancho et al. 2007
f	Ability to grow on destination planetary surface	<i>Interplanetary (potentially strong dispersal filter)</i> —mismatch between environment of origin and destination planet. <i>Interstellar (strong dispersal filter)</i> —mismatch between spectrum of star in origin planetary system and star in destination system	Lack of basic physiological requirements for cell growth (solar energy at compatible wavelengths, nutrients, other essential elements)	Wolsteneroff and Raven 2002

Table 2 Attributes that make species potentially good interplanetary colonizers (structure of table headings after MacArthur and Wilson 1967)

	Dispersal			Colonization		Potential examples of model organisms on earth
	Preferred habitats superior as point of dispersal	High dispersal power of propagules as point of arrival	Preferred habitats superior	Characteristics that confer large K	Characteristics that confer large r/A	
Microorganisms	Tendency to occupy interior of rocks below zone that is ablated during atmospheric exit and host planet atmospheric entry	Ability to survive impact ejection and extremes of interplanetary space (primarily desiccation, low temperatures, ionizing radiation)	Habitats protected from extremes of host planet and with required nutrients and liquid water	Cosmopolitan species able to occupy diverse physical and chemical environmental extremes	Low doubling times in diverse conditions, tendency to grow in colonies	Spore-forming <i>Bacillus</i> spp.
Microbial phototrophs	Same as above	Same as above and ability to temporarily occupy the deep interior of rock below ablation zone where light is not available during dispersal (enabled by e.g., motility, spore formation)	Same as above and habitats where light is available at above minimum required for photosynthesis either permanently or transiently	Motility and/or survival of airborne dispersal to increase chances of access to diverse environments on host planet	Same as above	Motile <i>Synechococcus</i> spp., desiccation resistant cyanobacterial akinetes, mixotrophs
Multicellular organisms	Same as above	Same as above and ability of multicellular functions to survive desiccation	Habitats protected from extremes of host planet and with required nutrients and liquid water	Same as above	Same as above	Tardigrades

K refers to population size permitted by the environment and r/A refers to the intrinsic rate of increase (of the population). Generally large values of both of these parameters imply greater probability of colonization success and less probability of the population size fluctuating to extinction.

and the other without, but both with conditions potentially supporting photosynthesis, might be explained by a lack of transfer of photosynthesis. The discovery of two planets with such a signature in the same system would be more ambiguous, as this might be explained by the transfer of oxygenic photosynthesis or two independent origins of oxygenic photosynthesis. In both cases we would need to know what the chances are for the evolution of photosynthesis and its interplanetary transfer to assess the likelihood of two independent origins. The experiments reviewed in this paper, however, show the low probability of the transfer of photosynthesis.

The discovery that there are no extrasolar planets with atmospheric oxygen anywhere in the galaxy would render the discussion here practically obsolete (although potentially not theoretically irrelevant as oxygenic photosynthesis might be so rare as to be only present infrequently in other galaxies). The notion of the potential exchange of photosynthesis between two planets within a single system may not be entirely optimistic speculation. In our own Solar System, if Mars had been more massive and retained a thicker atmosphere, extending the period during which bodies of standing liquid water persisted on its surface, it is plausible that habitable surface conditions on both Earth and Mars would have overlapped with the period after the evolution of photosynthesis on Earth. The search for extrasolar planets will reveal how statistically likely such situations are. Finally, if indeed we ultimately never find photosynthesis on another planet in the Universe, we will have, at the very least, ascertained that the Earth is a unique and isolated island of photosynthesis. This in itself would be a remarkable conclusion in island biogeography.

Conclusion

The exogenous arrival of oxygenic photosynthesis on a planet would profoundly change the direction of biological evolution on its surface. However, the likelihood of the transfer of photosynthesis between planets is less than for chemotrophy or heterotrophy. The primary dispersal filter against photosynthesis is atmospheric transit on account of the requirement that photosynthetic organisms must grow near to the surface of a rock. This dispersal filter is universal; it is not specific to organismal biochemistry or physiology (Table 1). Impact shock acts as an additional, but weaker, dispersal filter against vegetative organisms during planetary ejection and it is influenced by cell physiology. Certain evolutionary innovations could allow for these dispersal filters to be survived and a consideration of these factors allows for generalised characteristics of organisms that would be successfully transferred between planets to be defined (Table 2). If oxygen biosignatures are eventually detected in the atmospheres of extrasolar planets, understanding the mechanisms and likelihood of the interplanetary transfer of photosynthesis will assist in the interpretation of their origins.

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