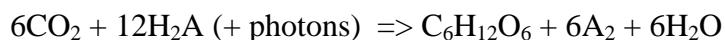# Photosynthetic bacteria

Authors: Literature review by Dr Sara Beavis with comments by Ken Bellamy, 19 July 2010

INTRODUCTION

Photosynthesis is a biochemical process involving the action of light and the formation of carbohydrates (with release of molecular oxygen) from carbon dioxide and water. This occurs in the chlorophyll tissue of plants and blue-green algae under the influence of light, and is expressed by the simplified, general formula:

$$6CO_2 + 6H_2O \text{ (+ photons)} => C_6H_{12}O_6 + 6O_2$$

A second form of photosynthesis - bacterial photosynthesis - has evolved independently from the more commonly known photosynthetic process. Photosynthetic bacteria synthesise carbohydrate energy from light using a similar mechanism to that used by plants and cyanobacteria, with one fundamental difference: bacterial photosynthesis actually produces water. Where chlorophyll-based photosynthesis requires the initial input of water to provide missing electrons to photon-absorbing pigments, bacteria use alternate electron donors other than water, and this process can be described by the general equation:

$$6CO_2 + 12H_2A \text{ (+ photons) } => C_6H_{12}O_6 + 6A_2 + 6H_2O$$

Here $H_2A\cdot$ is a generic term referring to a suitable reducing substrate where 'A' is not oxygen.

In short, rather than using water as an electron donor during photosynthesis, photosynthetic bacteria use any one of a suite of compounds as the source of electrons, for example, elemental sulfur, sulfide, other reduced sulfur compounds, and reduced iron, amongst others. The use of compounds other than water as electron donors distinguishes bacterial photosynthesis from all other forms of photosynthetic activity. This is the result of these bacteria not being capable of photochemically generating a sufficiently strong oxidant (Brune, 1995).

Anoxygenic photosynthetic bacteria are found in those environmental niches where the electron donor is abundant.   For example, sulfur reducing bacteria thrive in oxygen depleted environments (such as sediments in lakes and lagoons) where they reduce sulfate to sulfide. When light reaches such environments (such as during the drying of a lake or through disturbance), photoautotrophic sulfur bacteria will then proliferate.

Whilst photosynthetic bacteria do not require water to act as an electron donor during the initial stages of the photosynthetic process, they ultimately produce water and carbohydrates, resulting in a net production of molecular water via the photosynthetic process. This paper is aimed at providing an overview of the photosynthetic bacteria and identifies differences between the key groups which ultimately define the environments in which they may occur or dominate.

THE PHOTOSYNTHETIC BACTERIA

Photosynthetic bacteria are an incredibly diverse group, containing high levels of morphological, physiological and molecular variation. Traditionally, anoxygenic phototrophic bacteria have been classified according to their phenotypic properties, into the following key groups:
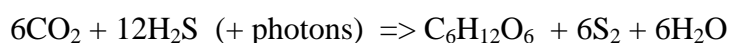
A. Chlorobiaceae: Green Sulfur Bacteria
B. The Proteobacteria: Purple Bacteria
C. The Heliobacteria
D. Anoxygenic Filamentous Phototrophic Bacteria

However, these traditional groupings are not supported by phylogenetic evidence, with DNA sequence data (from the gene 16S rRNA) supporting an alternative classification. Consequently, four major taxonomic groups have been proposed, based upon DNA sequence data. Below we provide a summary of the taxonomy, physiology and ecology of each of the main taxonomic groups of photosynthetic bacteria. We specifically focus upon intraspecific variation in the electron donors used, and the light spectrum accessed by the four key taxonomic groups of photosynthetic bacteria.

A. Chlorobiaceae: Green Sulfur Bacteria

The phototropic green sulfur bacteria form a closely related phylogenetic group, which exists to the exclusion of other phototrophic bacteria and chemotrophic bacteria (Gibson et al. 1985). Consequently, the Chlorobiaceae is considered to be a robust taxonomic group. The morphology of the group is characterised by spherical, oval or rod-shaped cells and the absence of flagella (Figure 1). All but one species is sessile, the exception being *Chlorherpeton thallassium*, which is motile via gliding. All green sulfur bacteria share similar physiological characteristics: they are strictly anaerobic and obligately phototrophic. They are commonly found in stratified and anoxic aqueous environments that receive light, as well as in sediments, and other sulfide-rich environments such as acid sulfate soils and hot springs. This group of bacteria is capable of growth at light intensities under which other phototrophs cannot survive and account for approximately 80% of the total annual productivity in some aquatic environments. Consequently, they can be the principal contributors of fixed carbon in some ecological niches. All strains are strictly anaerobic and obligately photoautotrophic in growth mode with CO_2 as the only carbon source exploited by the Chlorobiaceae. None are capable of dark respiratory or strictly fermentative metabolism. Green sulfur bacteria use sulfide as the primary electron donor, which is oxidised to sulfate, however, some strains of Chlorobiaceae use thiosulfate and hydrogen as alternative electron donors. The majority of species require vitamin B12 as a growth factor.

The photosynthetic process for this group can be summarised as:

$$6CO_2 + 12H_2S \ (+ \text{photons}) => C_6H_{12}O_6 + 6S_2 + 6H_2O$$

$$6CO_2 + 12\,H_2\,(+ \text{ photons}) => C6H_{12}O_6 + 6H_2O$$

The Green Sulfur Bacteria contain both green and brown species, each of which is characterised by their light-harvesting pigments, which in turn determines the light absorption range of each of these groups. Green Chlorobiaceae species contain bacteriochlorophyll c or d and the carotenoid chlorobactene OH-chlorobactene (Gloe et al 1975; Schmidt 1978). In contrast, the brown species contain bacteriochlorophyll e and the carotenoids isorenieratene at beta-isorenieratene (Liaaen-Jensen 1965). The net result of these differences in pigments amongst types of Chlorobiaceae is that green bacteria have a light absorption range of 440 - 510 nm (Herbert & Tanner 1977), whilst brown bacteria have a broader absorption range of 480 - 550nm.
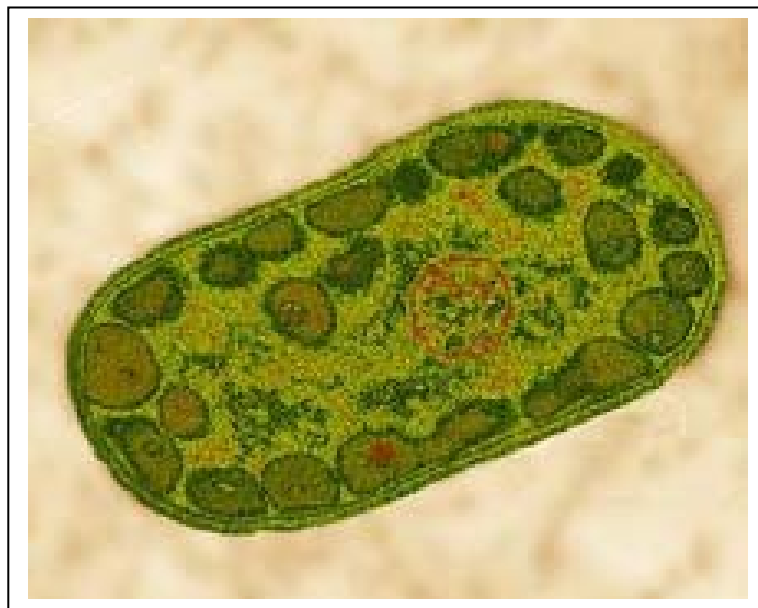

Figure 1 Green Sulfur Bacteria (Chlorobiaceae species)

B. The Proteobacteria: Purple Bacteria

The Proteobacteria may be divided into four subgroups: alpha, beta, gamma and delta. The delta subgroup consists of the families Chromatiaceae and the Ectothicrhodospiraceae (Figure 2). These bacteria occur in reducing environments such as stagnant water bodies, and anoxic subaerial and subaqueous sediments where hydrogen sulfide can be used. The remaining subgroups are grouped together as the Purple Nonsulfur Bacteria (Figure 4), however, this group is extremely heterogeneous as revealed by genetic analysis of 16S rRNA sequences, containing representatives of both the alpha and beta subgroups. Therefore, the identification of a true family group has been abandoned, and the common name "Purple non-sulfur bacteria" has been put forward as the "taxonomic" label for this group (Imhoff et al. 1984; Imhoff & Truper 1989). The environments in which these purple nonsulfur bacteria commonly occur include geothermal hot springs, tidal seawater pools, hypersaline environments, activated sludge systems and wastewater treatment plants (Montano et al, 2009).

The Chromatiaceae family is defined by the fact that, under proper growth conditions, species within this family deposit globules of elemental sulfur *inside* their cells (Imhoff 1984a). Many species grow under photoheterotrophic conditions. The principal photosynthetic pigments utilised by this group are bacteriochlorophylls a and b (which have a light absorption range of 375-590 nm in the visible spectrum, and 800-890 in the infrared spectrum) and carotenoids (which have a light absorption range of 400-600nm).
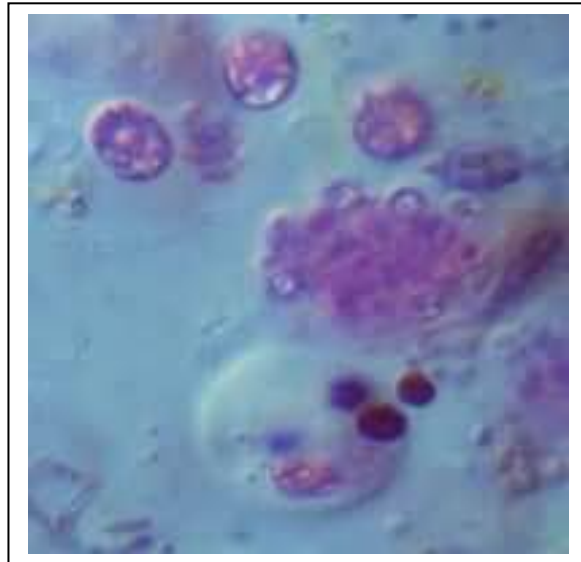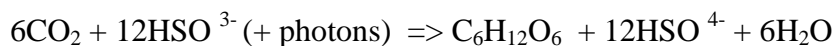

Figure 2 Purple Bacteria (Chromatiaceae)

The Ectothiorhodospiraceae family is distinguished by the fact that, during oxidation of sulfide, members of this family deposit elemental sulfur *outside* the cells. Unlike the Chromatiaceae, members of the Ectothiorhodospiraceae are dependent upon saline and alkaline growth conditions in which thiosulfate is stable (Imhoff 1989). Members of this family display a light absorption range of 775 to 850 nm.

The photosynthetic process for this family can be summarised as:

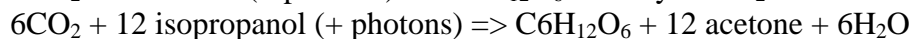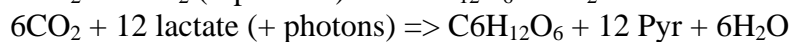$$6CO_2 + 12HSO^{3-} \text{ (+ photons) } => C_6H_{12}O_6 + 12HSO^{4-} + 6H_2O$$

The Purple Non-sulfur Bacteria (Figure 3) are extremely diverse, members of this group varying broadly in morphology, utilization of carbon sources and electron donors. In general, members of this group are photoheterotrophic, growing under anaerobic conditions in the light with various organic substrates as a resource. However, many species are also able to grow photoautotrophically with either molecular hydrogen or sulfide as the electron donor and CO2 as the sole carbon source. Furthermore, most representatives of the Purple Non-sulfur Bacteria can also grow under aerobic conditions in dark conditions as chemoheterotrophs: under these conditions, synthesis of photosynthetic pigments is repressed.

Figure 3 Purple Non-sulfur Bacteria

The diversity of the purple nonsulfur bacteria means that any estimate of the light absorption range utilised by group members will be based on single species studies, rather than an appreciation of the group as a whole. That being said, the majority of purple nonsulfur bacteria possess both bacteriochlorophyll a and carotenoid pigments, which permit light absorption at 800 - 890 nm.

$6CO_2 + 12 H_2$ (+ photons) $=> C6H_{12}O_6 + 6H_2O$

$6CO_2 + 12$ lactate (+ photons) $=> C6H_{12}O_6 + 12$ Pyr $+ 6H_2O$

$6CO_2 + 12$ isopropanol (+ photons) $=> C6H_{12}O_6 + 12$ acetone $+ 6H_2O$

C. The Heliobacteria

The Heliobacteria (Figure 4) are anoxygenic photosynthetic bacteria that primarily inhabit the soil substrate and share a relatively recent common ancestor with gram-positive bacteria. The family Heliobacteriaceae (Beer-Romero & Gest 1987) constitutes a distinct lineage and contains two genera: Heliobacterium and Heliobacillus. This group synthesises the simplest photosynthetic complexes of all known phototrophs.
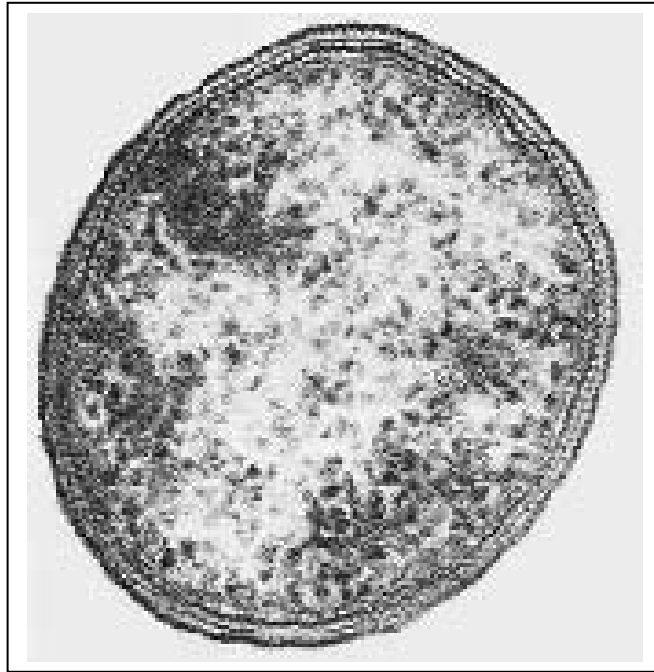
Figure 4 Heliobacteria

Heliobacteria can grow photoheterotrophically on a limited group of organic substrates and chemotrophically (anaerobically) in darkness by pyruvate or lactate fermentation; they are also active nitrogen fixers (Kimble and Madigan 1992a, b). Heliobacteria are widely distributed in rice soils and occasionally found in other soils, although some species have been obtained from hot springs. A study by Stevenson (1993) attempted to determine the optimal physiochemical soil environment for Heliobacteria, and found that the optimal habitat included relatively dry, acidic soils. Heliobacteria have been found in tropical soils (e.g. Far Eastern and African paddy fields), temperate soils (e.g. Minnesota, Arkansas, Texas [USA] and Italy), and soils from the Arctic region (e.g. Iceland).

Heliobacteria produce a unique photosynthetic pigment, BChl g, which distinguishes them from all other anoxygenic phototropic bacteria (Madigan 2001; Madigan & Ormerod 1995b). This novel bacteriochlorophyll is responsible for the light absorption characteristics. Heliobacteria absorb light in the infrared component of the light spectrum, specifically around 788nm. This light absorption range is distinct from those regions of the spectrum absorbed by green bacteria (705-740 nm) or purple bacteria (830-1199 nm) (Oelze 1985). The use of BChl g to exploit an under-utilized section of the light spectrum constitutes a distinct ecological niche that is occupied by Heliobacteria alone, which is thought to contribute to the ecological success of the heliobacteria (Madigan 1988; Pfennig 1989).

D. Anoxygenic Filamentous Phototrophic Bacteria

The Anoxygenic Filamentous Phototrophic Bacteria constitute a large and diverse family known as the Chloroflexaceae (Figure 5): all members of this group are genetically similar (according to 16S rRNA sequence-based phylogenetic analysis), however, the finer details of the taxonomy of the group are uncertain. The family Chloroflexaceae includes the genera Chloroflexus, Oscillochloris, and Chloronema, however, only a single species - Chloroflexus aurantiacus, has been studied in any detail. As a result, much of what is known of the Chloroflexaceae is based upon Cf. Aurantiacus.

Members of the Chlorofleaceae occupy a diverse range of habitats including freshwater lakes, saline lakes and marine habitats. They are also abundant in wastewater treatment plants. The group is usually associated with cyanobacteria and is predominantly found as visible components of microbial mats growing on mud or within water in both saline and freshwater habitats as well as hot springs. Within these mats, members of the family Chloroflexaceae are found in sympatry with representatives of the cyanobacteria as well as purple and green sulfur bacteria. Members of the Chloroflexacea are primarily photoheterotrophs, meaning that whilst they derive energy from light, they cannot use carbon dioxide as their only source of carbon. Instead, photoheterorophic organisms extract organic compounds from their environment in order to satisfy their carbon requirements. The Chloroflexaceae grow best when grown anaerobically in light upon complex organic media. That being said, members of this group do survive in the absence of light, that is, as chemotrophs, growing in the dark under aerobic conditions.

The Chloroflexaceae are known to use both sulfide (Madigan & Brock 1977a) and hydrogen (Holo & Sirevag 1986) as electron donors for CO_2 fixation. Unlike all other photosynthetic bacteria the Chloroflexaceae do not engage in nitrogen fixation, which suggests that this group diverged from all other photosynthetic bacteria before the evolution of nitrogenase in the phototrophs.

The Chloroflexaceae displays enormous diversity in the pigments used for harvesting light as a part of the photosynthetic process. It is thought that most species contain variants of BChl in their chlorosomes as the primary light-harvesting pigment, however, the light absorption properties of this pigment vary. For example, hot springs species have been found to access absorption bands at 740, 805 and 865 nm via BChl c and light-capturing pigments. Similarly, marine and hypersaline species contain BChl c (which absorbs light between 747 and 755 nm) or BChl d or e (which absorbs light between 710 and 725 nm). In contrast species found in Yellowstone National Park (USA) contain BChl a, which absorbs light between 807 and 910 nm (Boomer et al, 1990). Ongoing research has suggested that some species of Chloroflexaceae may undergo enzymatic methylation of BChl pigments, with the result that the light absorption abilities of individuals may change significantly. This is of particular interest because Cf. aurantiacus and other species of Chloroflexaceae occupy habitats that are subject to significant levels of environmental flux. It has been suggested that alterations to the pigments contained within individuals may occur in response to changes in environmental parameters (Pierson & Castenholz 1974b; Kharchenko 1992).
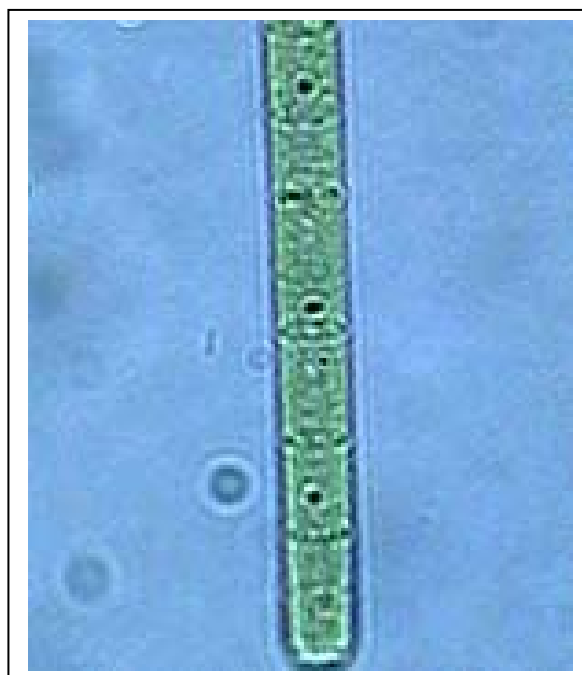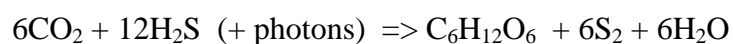
Figure 5 Green filamentous bacteria

$6CO_2 + 12 H_2 (+ \text{photons}) => C6H_{12}O_6 + 6H_2O$

$6CO_2 + 12H_2S (+ \text{photons}) => C_6H_{12}O_6 + 6S_2 + 6H_2O$

FACTORS CONTROLLING BACTERIAL PHOTOSYNTHESIS

Light absorption

The principal limiting factors for bacterial photosynthesis include light, oxygen, and for the sulfur bacteria, redox conditions. Wavelength of light is a critical factor due to the range of light absorbing pigments which occur across the anoxygenic photosynthesising bacteria. In contrast to light absorbance by green plants, where absorbance maxima occur at 430 and 662nm (chorophyll *a*) and 453 and 642 (chlorophyll *b*) (Figure 6), light absorbance by bacterial pigments occurs at wavelengths between 375 and 1199 nm. With reference to Figure 7, this demonstrates that bacterial photosynthesis can occur in the presence of not only irradiation as visible light but also infrared, and to a lesser extent, ultraviolet. Multiple absorbance maxima characterise the bacterial photosynthetic pigments, and therefore the range over which these maxima occur for each major bacteria group are shown in Table 1. The wide range of irradiation wavelengths in which photosynthesis can occur by anoxygenic bacteria has important

implications for the ecological niches they can inhabit, such as in waterbodies at depths greater than 5m and within buried sediments.

Figure 6 Light absorbance spectra for green plants[1]. (source: http://www.uic.edu/classes/bios/bios100/lecturesf04am/absorption-spectrum.jpg)

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[1] Note that the low absorbance of green wavelengths demonstrates that in this part of the spectrum, most light is reflected explaining why plants are usually perceived as green

Figure 7 Wavelengths of ultra-violet, visible light and infrared radiation (source: http://www.21stcip.com/images/em_spect.jpg)

	Wavelength range (nm)	
Green sulfur bacteria		
green species	440-510	visible light
brown species	480-550	visible light
Green non-sulfur bacteria	705-740	visible light
Purple sulfur bacteria	375-590 775-850	ultraviolet, visible light, infrared
Purple non-sulfur bacteria	830-1199	infrared
Heliobacteria	788	infrared
Green filamentous bacteria		
hotsprings	740-805;865	visible light, infrared
marine hypersaline	747-755	visible light, infrared

Table 1 Wavelength range for bacteria phototrophs

Oxygen

An interesting characteristic of phototrophic bacteria is their capability of deriving energy using a number of metabolic pathways. When oxygen is available, they perform aerobic respiration, but in its absence, ATP can be produced through photosynthesis, anaerobic respiration or fermentation. (Gregor and Klug, 1999). In order that these bacteria can use light as a source of energy, pigments, specialised proteins and significant quantities of metabolic energy are all required to synthesise and assemble all the different parts of the photosynthetic apparatus. As a result, photosynthetic complexes are not created if oxidative respiration can be performed. In addition, when both oxygen and pigments are present, there is a risk to the organism from the generation of toxic oxygen species. Consequently, under certain environmental conditions, the formation of photosynthetic complexes under high oxygen tension is repressed (Leegood et al, 2000).

If the oxygen tension in the environment drops below a threshold value and the bacteria become energy-depleted, the formation of the photosynthetic apparatus is induced, even in the *absence of light.* (Gregor and Klug, 1999). By contrast, in the absence of oxygen and the simultaneous *presence of light*, photosynthetic bacteria perform an anoxygenic photosynthesis using a single photosystem with cyclic electron transport. Under these growth conditions, the number of photosynthetic complexes formed is dependent on light intensity.

Redox

Phototrophic bacteria are widely distributed in both natural and anthropogenic environments under conditions where oxygen is either absent or present only at low concentrations. In addition, there will be overlapping, but opposing, gradients of light (and in the case of sulfur

bacteria, sulfide). Sulfide required as the electron donor during anoxygenic photosynthesis is generated as an end-product of dissimilatory sulfate reduction by sulfate-reducing bacteria, which are dependent on a supply of organic matter as a source of energy and carbon (Ke, 2001). In contrast to the marine environment, where there is an abundant supply of sulfur, microbial sulfate reduction in freshwater habitats is often supply limited. However, high levels of sulfate can be found in industrial settings, some soils (including those where gypsum dissolution has occurred), and composting materials, in wastewaters and activated sludges, and irrigation tailwaters (Kobayashi et al, 1983; Kim et al, 1991) .

Most of the photosynthetic bacteria (excluding the cyanobacteria) grow as photoheterotrophs, using light as the source of energy by which organic nutrients are converted to metabolic products. The sulfur bacteria (such as the green sulfur bacteria and purple sulfur bacteria) occupy ecological niches in which sulfur, for example as elemental sulfur or thiosulfate, are available. Within such niches, sulfide is generated by sulfate reducing bacteria in an anoxic (reducing) environment.

These sulfur compounds are concentrated sources of electrons at a range of redox potentials. Table 2 shows the redox potentials of different sulfur compounds, where it is apparent that sulfide is oxidised to sulfate at an intermediate redox potential of -215mV, whilst thiosulfate is oxidised to sulfate at a higher redox potential of -245mV. The tabulated data also indicate low redox potentials for oxidation of sulfide and thiosulfate, suggesting that a significant amount of energy can also be obtained through aerobic oxidation of these electron donors (Bruns, 1995).

Redox couple	Redox potential (mV)
SO_4^{2-}/ SO_3^-	-515
$S_2O_3^{2-}/HS^- +HSO_3^-$	-400
S^0/HS^-	-260
$2SO_4^{2-}/S_2O_3^{2-}$	-245
SO_4^{2-}/ HS_-	-215
SO_4^{2-}/S^0	-200
HSO^{3-}/HS^-	-115
HSO_3^-/S^0	-40
$S_4O_6^{2-}/2S_2O_3^{2-}$	+25

Table 2   Redox potentials of sulfur compounds (higher negative values of redox potential indicate increasingly anoxic or reducing conditions, whilst positive values indicate oxidising conditions) (Bruns, 1995)

The sulfur oxidising capabilities of the different anoxygenic phototrophs can be summarised as follows (Bruns, 1995):

Green sulfur bacteria

- Chlorobiaceae
    - Oxidise H_2S (hydrogen sulfide) and S^0 (elemental sulfur) to SO_4^{2-} (sulfate)
    - Oxidise H_2S, S^0 and $S_2O_3^{2-}$ (hydrogen sulfide, elemental sulfur and thiosulfate) to SO_4^{2-} (sulfate)

Proteobacteria (Purple bacteria)
- Chromaticaea
  - Oxidise H_2S (hydrogen sulfide) and S^0 (elemental sulfur) to $\mathbf{SO_4^{2-}}$ (sulfate)
  - Oxidise H_2S, S^0 and $S_2O_3^{2-}$ (hydrogen sulfide, elemental sulfur and thiosulfate) to $\mathbf{SO_4^{2-}}$ (sulfate)
  - Oxidise H_2S, S^0, $S_2O_3^{2-}$ and SO_3^{2} (hydrogen sulfide, elemental sulfur, thiosulfate, and sulfite) to $\mathbf{SO_4^{2-}}$ (sulfate)
- Ectothiorhodospiraceae
  - Oxidise H_2S (hydrogen sulfide) to S^0 (elemental sulfur)
  - Oxidise H_2S and S^0 (hydrogen sulfide, elemental sulfur) to $\mathbf{SO_4^{2-}}$ (sulfate)
  - Oxidise H_2S, S^0 and $S_2O_3^{2-}$ (hydrogen sulfide, elemental sulfur and thiosulfate) to $\mathbf{SO_4^{2-}}$ (sulfate)
  - Oxidise H_2S, S^0, $S_2O_3^{2-}$ and SO_3^{2} (hydrogen sulfide, elemental sulfur, thiosulfate, and sulfite) to $\mathbf{SO_4^{2-}}$ (sulfate)

Purple Non Sulfur Bacteria
  - Oxidise H_2S (hydrogen sulfide) to $\mathbf{S^0}$ (elemental sulfur)
  - Oxidise H_2S (hydrogen sulfide) to $\mathbf{S_4O_6^{2-}}$ (tetrathionate anion: an oxidation product of thiosulfate)
  - Oxidise $S_2O_3^{2-}$ to $\mathbf{S_4O_6^{2-}}$ (thiosulfate to tetrathionate anion)
  - Oxidise H_2S and $S_2O_3^{2-}$ to $\mathbf{SO_4^{2-}}$ (hydrogen sulfide and thiosulfate to sulfate)
  - Oxidise H_2S, S^0 and $S_2O_3^{2-}$ (hydrogen sulfide, elemental sulfur and thiosulfate to $\mathbf{SO_4^{2-}}$ (sulfate)

Filamentous Bacteria
- Chloroflexaceae
  - Oxidise H_2S to S^0 (hydrogen sulfide to elemental sulfur)

This indicates that some groups of photosynthesising bacteria have very diverse sulfur oxidising capabilities whilst others are more limited. Consequently, we can expect that certain groups of phototrophic bacteria will be able to inhabit a wider range of habitats than others, with redox potential as well as light being limiting factors.

IMPLICATIONS OF PHOTOSYNTHESIS IN BACTERIA

This paper highlights the diversity of photosynthetic bacteria, specifically the broad range of ecological niches exploited by different taxa, as defined by the light absorption properties, redox potential, and oxygen potential, of these groups. The light-harvesting pigments utilised by each of the four main groups of photosynthetic bacteria are diverse, and result in each group having a specific set of environmental conditions under which they can successfully undergo photosynthesis.

The controlling factors of light, oxygen and redox all have significance for the relative abundance or absence of bacteria groups in particular environments. Under given conditions, certain groups will have selective advantage over others due to their ability to absorb light within

specific wavelength ranges, or to utilise specific electron donors. For example, purple sulfur bacteria can thrive in deep anoxic water where only infrared light can penetrate. In addition, photosynthesising bacteria can respond opportunistically to favourable environmental conditions. Within lakes and reservoirs, pronounced vertical movement of bacterial populations occurs in response to seasonal changes in the depth of the thermocline. In summer months, the warming of surface waters causes the thermocline to rise to its highest point. This results in the upwards vertical movement of bacteria, as well as optimal growth due to the relatively high light intensity at these depths. Vertical movement has also been observed in experimental environments where 'bioconvection' occurs within sealed containers. Bioconvection involves upward movement of micro-organisms, in an aqueous medium, as a response to external biochemical stimuli such as a gradient in gravity, light or oxygen concentration (Czirok et al, 2000).

Selective advantages for specific bacterial groups can be used strategically in industrial applications. Green sulfur bacteria, for example, have absorbance wavelengths that are different to other groups so they can be selected for simply by controlling the spectral composition of the delivered radiant energy (Van Germerden and Mas, 1995). They are best adapted to dim light, and are the most efficient users of radiant energy with a minimum requirement of photons per unit of fixed CO_2 (Hurse and Keller, 2003), Because of these attributes and their use of sulfur as an electron donor during photosynthesis, they are increasingly being recognised as useful in removing sulfide from wastewater. A further advantage in their use is due to their deposition of sulfur externally as elemental sulfur (S^0), and the consequent ease by which sulfur can be separated without the need to kill the cells (*ibid*). Photosynthetic bacteria have also been shown to: remove or detoxify aromatic compounds in the treatment of industrial wastewater (Khanna et al 1982); process caustic wastewater from offshore natural gas production (Khanna et al, 1996); and, provide a second stage process to dark-fermentation of palm oil residues by further metabolising volatile fatty acids to produce hydrogen and consume CO_2. (Suwansaard et al, 2008). It is evident, therefore, that physiology (in terms of pigments), photosynthetic apparatus (and consequent electron donors), and ecology of the different groups of anoxygenic bacteria have implications for anthropogenic applications.

A further characteristic of these bacteria is the production of molecular water as an output of photosynthesis. The impact of this attribute or its influence on the moisture content of soils has not been identified in the available peer reviewed literature. Moreover, its significance for anthropogenic use remains unclear as there is nothing, currently, in the peer reviewed literature that suggests agricultural or industrial advantages that could be exploited from this attribute. At the time of writing, few writers have noted the characteristic production of molecular water during photosynthesis and peer reviewed literature does not contain any significant study noting this attribute or its potential benefits. However, soil bacterial diversity in agricultural systems has been associated with organic matter formation and decomposition, as well as improvement in soil aggregation, aeration and water infiltration. All of these specific functions of soil bacteria improve the water holding capacity of soils. Therefore, the presence of diverse soil microbial populations should correlate with higher water holding capacity relative to soils with depleted microbial biomass. Partitioning the role of molecular water production from improved water holding capacity due to the presence of anoxygenic bacteria represents a research challenge for the future.

There is a prevalent assumption that any photosynthesis by soil-based bacteria will take place at or very near the surface of the soil. This arises because depth at which bacterial photosynthesis occurs will be a function of light penetration of the substrate, the measurement or estimation of which varies across the literature. A review by Tester and Morris (1987) concluded that physiologically or ecologically significant amounts of light rarely penetrate soil to a depth exceeding 4-5mm. By contrast, earlier workers found that a zonation of algal growth within aerated soils suggested a maximum depth of light penetration to 10mm (Tchan and Whitehouse, 1953; Stewart and Harbott, cited in Fogg 1973), whilst light sensitive geotropism in plant roots has been used to infer penetration of light to a depth of 15mm (Briggs pers comm.cited in Tester and Morris, 1987). Transmittance of light is controlled by particle size, moisture content, and aeration (as a function of soil fabric and texture). Although all light spectra are absorbed, there is greater absorbance of longer wavelengths (ie towards and including infrared) (Figure 8).
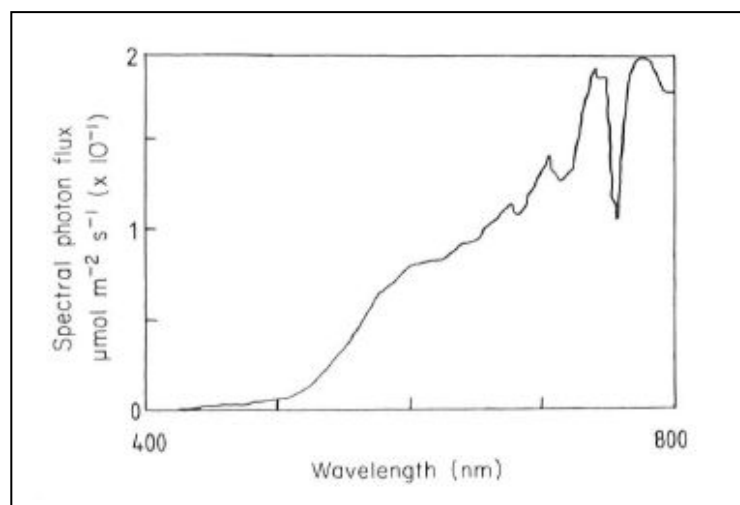

Figure 8 Spectral absorption in soil (source: Tester and Morris, 1987)

Recent studies indicate that light penetration depth and the spectral absorbance will vary according to clay mineralogy (Ciani et al, 2005) with air dried soils typically transmitting light to a depth <200μm at wavelengths of 275-500nm, but in goethite light transmission occurs to a depth of <10 µm at wavelengths of 275-700nm and in montmorillonite light transmission occurs to a depth of <180 µm at wavelengths of 275-700nm. In all of these studies, light penetration is based on the assumption that the soil substrate is dry, homogeneous, and without structural discontinuities. However, light will penetrate deeper in moist soils. Moreover, in deeply cracking montmorillonitic clays, it could be expected that light penetration and associated photosynthesis by anoxygenic bacteria would be occurring at significant depths (~10-40cm), but as very thin zones immediately adjacent to exposed surfaces. This suggests that any research into the implications of bacterial photosynthesis for soil moisture regime should focus on very shallow soil zones in both the vertical and, for cracking soils, horizontal planes. It also suggests that discrete soil niches will be filled by different groups of anoxygenic bacteria as a function of light transmittance, absorbance and reflectance of the substrate, together with the spectral absorbance of the bacteria.

Analysis of the penetration of light of frequencies other than visible light into soil profiles and its absorption by organisms able to perform photosynthesis using frequencies outside the visible light spectrum is not readily available in peer reviewed literature. The penetration of visible light frequencies (400—750nm) into soil is the primary focus of current literature. Several families of photosynthetic bacteria operate outside this range of frequencies and are able to conduct photosynthesis in environments which have limited or no visible light penetration (such as at depths greater than 5 metres in water and in buried sediments). While this is established in studies which concern wet sedimentary media, no peer-reviewed literature to date specifically discusses the impacts of photosynthesis by these groups of bacteria in a soil environment or their ability to utilise frequencies of light other than visible light in the soil media. The presence of photosynthetic bacteria in soils is established, yet the literature does not currently contain specific reference to anthropogenic use of their photosynthetic capacity or to benefits arising from that capacity.

As such the identification of specific anthropogenic benefits which may arise from the presence and cultivation of these organisms in agricultural and other soils (including any benefit arising from their capacity for production of molecular water, fixation of nitrogen and capture of CO_2) represents an enticing future challenge.

GLOSSARY

Anaerobic bacteria: Bacteria that do not require oxygen for survival and growth.

Chemoheterotroph: A chemotrophic organism that is unable to fix carbon or form their own organic compounds. Instead, these organisms utilize inorganic (e.g. sulfur) or organic (e.g. carbohydrates) energy sources.

Chemotrophic bacteria: Bacteria that acquire energy via the oxidation of electron donors (either organic or inorganic).

Chlorosome: A large enclosure of aggregated pigment, typically bacteriochlorophyll c (BChl c), that acts as a light-harvesting antenna structure and is characteristic of green photosynthetic bacteria (e.g. Chlorobiaceae)

Geotropism: any positive (or negative) movement or growth of a plant or sessile animal in response to (or against) the force of gravity

Goethite: a hydrated iron oxide, $HFeO_2$ or $Fe^{3+}O(OH)$ (known as lepidocrocite). Goethite often forms through the weathering of other iron-rich minerals, and is therefore a common component of soils.

Heterogeneous: A term used to describe a (taxonomic) group containing a large amount of variability, for example, genetic or morphological variability. It is the opposite of homogeneous, which means that a group contains very little variation.

Montmorillonite: is a very soft mineral that typically forms a clay. Montmorillonite's water content is variable and it increases greatly in volume when it absorbs water. Chemically it is hydrated sodium calcium aluminium magnesium silicate hydroxide $(Na,Ca)_x(Al,Mg)_2(Si_4O_{10})(OH)_2 \cdot nH_2O$.

Obligate: restricted to one particularly characteristic mode of life or way of functioning, for example, obligate anaerobes are microorganisms that can grow only in the complete absence of molecular oxygen; some are killed by oxygen.

Phenotype: the physical manifestation of an organism, including the physical parts, the sum of the atoms, molecules, macromolecules, cells, structures, metabolism, energy utilization, tissues, organs, reflexes and behaviors; anything that is part of the observable structure, function or behavior of a living organism.

Phenotypic properties: the observable properties of an organism that are produced by the interaction of the genotype (internally coded, inheritable information) carried by all living organisms and the environment

Photoautotroph: An organism that produces complex organic compounds (e.g. carbohydrates) from simple inorganic molecules (e.g. carbon) via photosynthetic processes.

Photoheterotroph: An organism that photosynthesizes carbohydrate energy from solar energy, but that cannot use carbon dioxide as their sole source of carbon. Instead, photoheterotrophs satisfy their carbon requirements using organic compounds extracted from their environment.

Phototrophic bacteria: Bacteria that – similarly to plants – acquire energy via photosynthesis. These bacteria use solar energy to convert carbon dioxide and an electron donor into carbohydrate energy and water.

Phylogenetics: The study of the evolutionary relationships existing amongst species or species lineages. Phylogenetic research is based upon DNA sequences and morphological data.

Redox potential: a measure of the affinity of a substance for electrons its electronegativity — compared with hydrogen, which is set at zero. Substances more strongly electronegative than hydrogen (i.e., capable of oxidising) have positive redox potentials. By contrast, substances less electronegative than hydrogen (i.e., capable of reducing) have negative redox potentials.

Sympatry: In evolutionary biology, sympatry refers to organisms whose geographic ranges overlap or are identical, such they may be found in the same location.

Thermocline: the region in a thermally stratified body of water which separates warmer surface water from cold deep water and in which temperature decreases rapidly with depth

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