**The fitness of the environments of air and water for photosynthesis, growth, reproduction and dispersal of photoautotrophs: an evolutionary and biogeochemical perspective**

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**Abstract**

Life has evolved to exploit aquatic and terrestrial environments, but these present very different challenges and opportunities for photoautotrophs. This paper outlines how the physical and chemical ‘fitness’ of air and water have interacted with the evolution of the physical structures and physiological properties of aquatic and terrestrial algae and plants and altered the biogeochemistry of the planet. The two environments are particularly different for photosynthesis and the consequences of water stress in air and potential carbon and light stress under water are discussed, as are the consequences of the lower density of air compared to water for investment in support. The properties of air and water also affect mineral nutrition, reproduction and dispersal of photoautotrophs and the nature of competition between different types of plants. Furthermore, the pivotal role of photoautotrophs in global biogeochemical cycles and major feedbacks are emphasized. They have altered the environment dramatically, changed the availability of essential resources and created niches that can be exploited by new or different species or types of organism. Recent rapid anthropogenic changes, particularly in CO2, are noted and discussed in relation to the security of human requirements.

**Keywords:** Aquatic plants; land plants; macroalgae; macrophytes; phytoplankton

1. **Introduction and evolutionary perspective**

Life on Earth is believed to have evolved in aquatic environments, around 3.5 Giga years ago (Ga; ([Mojzsis et al., 1996](#_ENREF_131)) marking the beginning of the ongoing intimate interaction between the biology and the geochemistry of the planet (Fig. 1). The characteristics or ‘fitness’ *sensu* Henderson ([Henderson, 1924](#_ENREF_78)) of the abiotic environment will have had a major effect on the evolutionary trajectory of life. Prokaryotic photoautotrophy appeared at least 2.4 Ga ([Rasmussen et al., 2008](#_ENREF_154)) but perhaps as early as 3.0 to 2.6 Ga ([Blank, 2013](#_ENREF_20)). Eukaryotic algae may have evolved as early as 2.3 to 2.0 Ga ([Blank, 2013](#_ENREF_20)). Interestingly, the earliest cyanobacteria probably evolved in freshwaters ([Blank and Sanchez-Baracaldo, 2010](#_ENREF_21)) and the same may also be true of the earliest photosynthetic eukaryotes ([Blank, 2013](#_ENREF_20)). Regardless of where the eukaryotes originated, there was a subsequent evolutionary explosion of different groups of endosymbiotically-formed algae, producing a huge phylogenetic diversity ([Falkowski et al., 2004](#_ENREF_57); [Raven et al., 2009](#_ENREF_159)). Aquatic photoautotrophs are found in all of the five major eukaryotic supergroups recognised by Keeling ([Keeling et al., 2005](#_ENREF_92)) if the second primary endosymbiotic event involved in the more recent acquisition of plastids in the amoeba *Paulinella* is included ([Marin et al., 2005](#_ENREF_121)). This has conferred on them fundamentally different biochemical and metabolic characteristics and a large variety in types of algal photoautotrophs. Some of the algal groups that are currently important ecologically, such as the haptophytes and diatoms, arose recently, around 0.26 to 0.20 and 0.55 to 0.13 Ga respectively ([Parfrey et al., 2011](#_ENREF_144)) (Fig. 1).

The algae, plus the cyanobacteria, will have dominated global productivity until the evolution of the Embryophytes (bryophytes and vascular plants) from charophyte green algae, which occurred between 0.82 and 0.57 Ga ([Lewis and McCourt, 2004](#_ENREF_104); [Clarke et al., 2011](#_ENREF_36)) (Fig. 1). In contrast to the great phylogenetic diversity of organisms responsible for aquatic productivity, the Embryophytes dominate terrestrial productivity ([Falkowski et al., 2004](#_ENREF_57)). The movement of plants between water and land is likely to have occurred very gradually, with transitional environments, such as the coastal intertidal region, estuaries, or areas with seasonally variable water tables, providing intermediate habitats and amphibious plants ([Maberly and Spence, 1989](#_ENREF_118)) acting as intermediate life-forms. Fossil records of the distinctive aquatic plants within the genus *Isoestes* (lycophyta) have been found at the start of the Triassic (around 0.25 Ga) and it has been hypothesized that they were weedy survivors of the Permian-Triassic extinctions ([Retallack, 1997](#_ENREF_170)). The most successful land plants, the angiosperms, arose maybe as early as 0.24 to 0.18 Ga ([Clarke et al., 2011](#_ENREF_36)) or even 0.43 Ga ([Parfrey et al., 2011](#_ENREF_144)). Some Embryophytes, particularly angiosperms, have returned to living in freshwaters, as macrophytes, and to the oceans as seagrasses, a process that has occurred independently around 100 times ([Les et al., 1997](#_ENREF_102)). Some freshwater macrophytes, such as those from the Nymphaeales, are ancient and close to the base of the angiosperms ~0.12 Ga ([Friis et al., 2001](#_ENREF_64)) although there is some uncertainty about the exact dates ([Yoo et al., 2005](#_ENREF_213)), while Hydrocharitacean seagrasses probably evolved more recently, around 0.06 Ga ([Chen et al., 2012](#_ENREF_35)) (Fig. 1).

Today, the aquatic and terrestrial environments contribute roughly equally to global primary productivity despite the smaller percent contribution of land (31%) to the global area ([Field et al., 1998](#_ENREF_60)). Most scientists study either aquatic or terrestrial botany. A few have straddled both environments, in part as a consequence of studying fundamental processes, such as photosynthesis e.g. ([Bowes et al., 1971](#_ENREF_25)).

1. **Environmental challenges and opportunities in air and water**

The two major environments for photosynthesis on Earth, liquid water and air, have very different physical and chemical properties ([Denny, 1993](#_ENREF_44)) and present very different challenges and opportunities for photoautotrophs; the relative ‘fitness of the environments’ ([Henderson, 1924](#_ENREF_78)) is different. Chemical and physical conditions in salty and fresh water also differ, and few photoautotrophs are able to thrive in both. These environmental differences have led to the evolution of plants with different structures and processes in each environment and the comparative study of these can produce important insights into the fundamental controls on biological fitness and the role of photoautotrophs in global biogeochemical cycles. The sections below outline some of the opportunities and constraints of each environment and how photoautotrophs have evolved to minimise the problems and maximise the advantages in order to photosynthesise, acquire mineral resources, grow, compete, reproduce and disperse.

*2.1 Photosynthesis*

The contrasting physical properties of air and water impose different problems and provide different opportunities for photosynthesis, particularly with regard to the availability of the key resources of water, carbon and light.

*2.1.1 Water availability*

Water availability would have been the biggest obstacle to overcome in the colonisation of land by aquatic plants and algae for all but the most low-growing of species, in the wettest of terrestrial habitats. By definition, pure water has a water potential of zero and sea water with a salinity of 34 has a water potential of about -1.5 MPa. In contrast, the water potential of air depends on relative humidity and can vary between close to zero at 100% humidity and as low as -200 MPa for very dry air, creating a major challenge to minimise water loss while permitting sufficient exchange of CO2 and O2 to allow photosynthesis to take place. Some photoautotrophs can tolerate extreme desiccation, such as many intertidal algae ([Schonbeck and Norton, 1978](#_ENREF_189); [Maberly and Madsen, 1990](#_ENREF_114)) or poikilohydric ‘resurrection plants’ from arid environments ([Oliver et al., 2000](#_ENREF_141)). This is unlikely to have been the case for early land plants from the Silurian and Lower Devonian (0.44 to 0.39 Ga) which had a cuticle based on two polymers, cutin and cutan, to restrict uncontrolled water loss ([Edwards et al., 1996](#_ENREF_50); [Raven, 2000](#_ENREF_157)). They also possessed stomata which evolved more than 0.4 Ga ([Ruszala et al., 2011](#_ENREF_175); [Chater et al., 2013](#_ENREF_34)) (Fig. 1) to control exchange of CO2 and O2 while minimising the risk of desiccation ([Edwards et al., 1998](#_ENREF_51); [Raven, 2000](#_ENREF_157)). These early plants had a relatively low stomatal density that might be linked to the atmospheric concentrations of CO2 which were higher than today ([Edwards et al., 1998](#_ENREF_51)) and the high atmospheric CO2 will also have promoted a high water-use efficiency which will have declined as levels of atmospheric CO2 fell ([Franks and Beerling, 2009](#_ENREF_63)).

Most terrestrial plants are rhizophytic with roots that supply soil water to the plant. Tracheids and vessels evolved as a means of transmitting water from the roots to the photosynthesising leaves ([Edwards, 2003](#_ENREF_49)). Some bryophytes possess simpler hydroids for water transport but these are probably not homologous to the structure in tracheophytes ([Ligrone et al., 2000](#_ENREF_105)). The competitive success of the angiosperms on land after around 0.14 to 0.10 Ga (the behavioural phase of land plant evolution *sensu* Bateman ([Bateman et al., 1998](#_ENREF_13)) may be linked to a high leaf vein density with a high hydraulic capacity to deliver water to their photosynthesising leaves ([Brodribb and Feild, 2010](#_ENREF_29)). Despite these evolutionary innovations, however, global earth observation data show that water availability is still a major factor controlling terrestrial plant productivity today ([Hsu et al., 2012](#_ENREF_83)).

Secondarily-derived freshwater macrophytes and seagrasses have retained many features derived from their terrestrial ancestors. However, they have adapted to their environment and tend to lack, or possess non-functional, stomata and the cuticle is substantially reduced in thickness to less than 100 nm ([Sculthorpe, 1967](#_ENREF_191); [Frost-Christensen et al., 2003](#_ENREF_65)). Although they lack the transpiration stream of terrestrial plants, aquatic macrophytes do have acropetal mass flow of water from the roots to shoots that will promote translocation of nutrients from the sediment to the growing apices ([Pedersen, 1993](#_ENREF_145)) (see section 2.3).

*2.1.2 Carbon availability*

Potential benefits of a lack of water stress in aquatic habitats are replaced by potential problems of obtaining a key resource for photosynthesis, inorganic carbon. The concentration of CO2 in freshwater is similar to the concentration in air at a given temperature ([Henderson, 1924](#_ENREF_78)); the Bunsen absorption coefficient is close to one. For example, air with 400 ppm of CO2 has a concentration of CO2 of 18 mmol m-3, while freshwater at 20°C in equilibrium with this partial pressure has a similar concentration of about 16 mmol m-3. However, the diffusion coefficient (a constant determining the effect of a concentration gradient on the rate of flux) of CO2 through boundary layers in water is about 10,000 times lower than through boundary layers in air ([Raven, 1970](#_ENREF_155)) because of the greater density and viscosity of water. Consequently, the external transport resistance of aquatic photosynthesis is much greater in water than in air ([Black et al., 1981](#_ENREF_19)) and half-saturation concentrations of CO2 for macrophytes are high, typically between 100 and 200 mmol m-3 roughly six- to eleven-times air-equilibrium ([Maberly and Spence, 1983](#_ENREF_117); [Bowes and Salvucci, 1989](#_ENREF_27); [Maberly and Madsen, 1998](#_ENREF_115)). In contrast, terrestrial C3 plants are much closer to CO2 saturation at atmospheric levels depending on other environmental conditions ([Lloyd and Farquhar, 1996](#_ENREF_106)). As an average over a year, most freshwaters are oversaturated with CO2 as a result of input of organic and inorganic carbon from the catchment ([Cole et al., 1994](#_ENREF_37); [Sand-Jensen and Staehr, 2009](#_ENREF_182); [Maberly et al., 2013](#_ENREF_113)). This may be insufficient to overcome transport limitation of macrophytes but can stimulate photosynthesis of freshwater phytoplankton 10-fold compared to air-equilibrium concentrations ([Jansson et al., 2012](#_ENREF_86)). Marine phytoplankton productivity may also be limited by availability of CO2 ([Hein and SandJensen, 1997](#_ENREF_77)).

However, although on average most lakes and rivers are oversaturated with CO2 compared to the atmosphere ([Rebsdorf et al., 1991](#_ENREF_165); [Cole et al., 1994](#_ENREF_37)) concentrations of CO2 can approach zero in some sites such as small productive lakes ([Talling, 1976](#_ENREF_199); [Maberly, 1996](#_ENREF_111)) where photosynthetic demand for inorganic carbon can outstrip environmental supply. For example, rates of CO2 influx from the atmosphere for a maximum inwardly directed concentration difference of 400 ppm and a high gas piston velocity of 0.15 m h-1 driven by wind stress and surface cooling-derived buoyancy flux ([MacIntyre et al., 2010](#_ENREF_119)) would be about 0.7 µmol m-2 s-1. In contrast, phytoplankton with a chlorophyll *a* concentration of 50 mg m-3, roughly equivalent to maximum concentrations in a eutrophic lake ([OECD, 1982](#_ENREF_138)), in a water column 5 m deep and with an average rate of photosynthesis of 100 µmol CO2 mg-1 chlorophyll *a* h-1, would have an approximately 10-times greater areal demand for CO2 at the lake surface of about 7 µmol m-2 s-1. Although chemical enhancement of CO2 input from the atmosphere ([Emerson, 1975](#_ENREF_54)) will increase the atmospheric input, it is clear that low rates of gas transfer have the potential to constrain photosynthesis in aquatic habitats ([Jansson et al., 2012](#_ENREF_86)).

Compared to CO2, oxygen is less soluble in water and its concentration is around 30-times lower in water than in air. Like for CO2, the oxygen diffusion coefficient in water is about 10,000 times lower in water than in air, although when the concentration difference between air and water is taken also taken into account, the rate of supply is 300,000 times lower in water ([Verberk et al., 2011](#_ENREF_206)). As for CO2, rates of oxygen production or consumption can exceed rates of exchange with the atmosphere which can lead to substantial over- or under-saturation in aquatic ecosystems, especially in dynamic inland waters. Oxygen concentrations that exceed air-equilibrium, as a consequence of rapid photosynthesis, will tend to favour photorespiration and exacerbate carbon limitation.

These potential problems have led to a range of avoidance, exploitation and amelioration strategies *sensu* ([Klavsen et al., 2011](#_ENREF_95)) in aquatic plants. Avoidance involves restriction of the occupied niche to locations where CO2 concentrations are high- such as immediately above the sediment surface ([Maberly, 1985](#_ENREF_109); [Weyhenmeyer et al., 2012](#_ENREF_211)). Exploitation involves anatomical or morphological features such as floating leaves ([Maberly and Spence, 1989](#_ENREF_118)) or large root to shoot biomass with continuous lacunae that permit sedimentary CO2 to be exploited ([Wium-Andersen, 1971](#_ENREF_212); [Madsen et al., 2002](#_ENREF_120)). Although it is possible that strategies can change over geological time, these two strategies will probably have been involved in the early colonisation of freshwaters by terrestrial plants since bryophytes have the former strategy ([Maberly, 1985](#_ENREF_109)) and *Isoetes* (lycophyta) can exploit sedimentary CO2 ([Wium-Andersen, 1971](#_ENREF_212)). These strategies are therefore potentially ancient since lycophytes probably evolved around 0.42 Ga ([Rickards, 2000](#_ENREF_172)) and the Nymphaeales near the base of the angiosperms can have floating or aerial leaves with access to atmospheric CO2 as well as submerged leaves. Amelioration involves physiological and biochemical processes that concentrate CO2 around the primary carboxylase enzyme, Ribulose-bisphosphate carboxylase-oxygenase (RuBisCO), enhancing carbon fixation and minimising photorespiration; a so-called CO2 concentrating mechanism (CCM; Gontero & Salvucci; Raven & Beardall, this issue). About 90% of terrestrial embyrophytes lack a CCM, but three types of biochemically-based CCM occur. These include Crassulacean Acid Metabolism (CAM) which, on the basis of species number, is present in about 6% of terrestrial vascular plants ([Silvera et al., 2010](#_ENREF_192)), and C4 carbon fixation which occurs in about 3% of terrestrial plants ([Sage et al., 2012](#_ENREF_176)). These are based on pre-fixation of inorganic carbon (bicarbonate) by phosphoenolpyruvate carboxylase (PEPC), that is not sensitive to oxygen, followed by decarboxylation of a C4- compound to produce CO2 around RuBisco. In addition, C2 photosynthesis or photorespiration (also known as C4-C3 intermediate photosynthesis), ([Sage et al., 2012](#_ENREF_176)) which is known from about 40 species in 21 lineages, concentrates CO2 around RuBisCO following decarboxylation of glycine within adjacent mitochondria. All terrestrial CCMs are polyphyletic having evolved many times: in the case of C4 at least 66 times ([Silvera et al., 2010](#_ENREF_192); [Sage et al., 2012](#_ENREF_176)). Although they both maximise the carbon economy of a plant, particularly in hot climates, CCMs are also extremely important in maximising the efficiency of use of water, nitrogen and phosphorus, e.g. ([Hocking and Meyer, 1991](#_ENREF_79); [Leakey et al., 2009](#_ENREF_100); [Raven, 2013](#_ENREF_158)).

In contrast to the relatively low frequency of CCMs in terrestrial plants, about 60% of freshwater plants have a biochemical or biophysical CCM ([Maberly and Madsen, 2002](#_ENREF_116)) consistent with the potentially greater carbon-limitation in aquatic environments. Aquatic CAM, first described in the lycophyte *Isoetes howelli* ([Keeley, 1981](#_ENREF_91)); Keeley this issue), is a mechanism that maximises net carbon uptake. It does this by minimising respiratory carbon loss by allowing carbon re-fixation at night and also exploits the generally higher nocturnal concentrations of CO2 generated by community respiration. As in terrestrial plants with CAM, aquatic CAM plants are found in phylogenetically disparate groups. It is present in all the tested species of *Isoetes* (ca. 150 species are present in the genus) as well as in aquatic species from the genus *Crassula* such as *C. helmsii*, ([Newman and Raven, 1995](#_ENREF_137); [Klavsen and Maberly, 2010](#_ENREF_94)) and also in widespread species such as *Littorella uniflora* in the Plantaginaceae ([Madsen et al., 2002](#_ENREF_120)) and the invasive *Ottelia alismoides* (Hydrocharitaceae) ([Zhang et al., 2014](#_ENREF_214)). In contrast to the polyphyletic nature of terrestrial C4 metabolism, aquatic C4 metabolism appears to be largely restricted to the Hydrocharitaceae, a family of about 100 species within the Alismatidae ([Les and Tippery, 2013](#_ENREF_103)). The best known aquatic C4 species is *Hydrilla verticillata* which possesses PEP carboxylase and a NADP-ME decarboxylase pathway that are induced at high temperature, high light and carbon-limitation ([Van et al., 1976](#_ENREF_204); [Holaday and Bowes, 1980](#_ENREF_82); [Bowes et al., 2002](#_ENREF_26); [Bowes, 2011](#_ENREF_24)). The closely related *Egeria densa* ([Casati et al., 2000](#_ENREF_33)) and *Otellia alismoides* ([Zhang et al., 2014](#_ENREF_214)) also show evidence for aquatic C4 metabolism. Also within the Alismatidae, the seagrasses *Cymodocea nodosa* and possibly *Halophila stipulacea* (Hydrocharitaceae) show some evidence for C4 metabolism ([Koch et al., 2013](#_ENREF_96)).

Within the algae, there is some indication of C4 or C4-C3- intermediate metabolism within the marine diatom *Thalassiosira weissflogii* ([Reinfelder et al., 2000](#_ENREF_167); [Roberts et al., 2007](#_ENREF_174); [Reinfelder, 2011](#_ENREF_166)). It is probably absent in the marine diatoms *T. pseudonana* ([Roberts et al., 2007](#_ENREF_174)) and *Phaeodactylum tricornutum* ([McGinn and Morel, 2008](#_ENREF_125)) where it is possible that potentially C4- carboxylating enzymes act to dissipate excess light energy via futile cycling ([Haimovich-Dayan et al., 2013](#_ENREF_73)). This is discussed more fully in Raven & Beardall (this issue). There is, however, strong evidence for C4 metabolism in the coenocytic marine chlorophyte *Udotea flabellum*. Various lines of evidence suggest that it has C4 physiology and biochemistry based on phospho*enol*pyruvate carboxykinase which acts as a carboxylase in the cytosol and a decarboxylase in the chloroplast ([Reiskind et al., 1988](#_ENREF_169); [Reiskind and Bowes, 1991](#_ENREF_168)).

Bicarbonate is derived from dissolution of calcareous rocks and weathering of silicates on land ([Pagani et al., 2009](#_ENREF_143)). In the ocean, the concentration of bicarbonate is about 100-times higher than CO2 at air-equilibrium. In freshwaters, it is the dominant form of inorganic carbon when the pH lies between the two carbonate dissociation constants corresponding roughly to pH 6.3 and 10.1, depending on temperature and ionic strength. Concentrations of bicarbonate typically range from zero to around 5 mol m-3, but they can be even higher in soda lakes ([Talling, 1985](#_ENREF_200)). About 55% of the freshwater plants tested have a biophysical CCM based on bicarbonate use ([Maberly and Madsen, 2002](#_ENREF_116)), although species from tropical regions, which often have lower bicarbonate concentrations, have been under-sampled. The majority of marine macroalgae also have the ability to use bicarbonate, although some appear to be restricted to CO2, such as subtidal rhodophyta that grow at low light ([Maberly, 1990](#_ENREF_110); [Murru and Sandgren, 2004](#_ENREF_133)), or rhodophyta that are high in the intertidal with extensive access to atmospheric CO2 ([Mercado and Niell, 2000](#_ENREF_127)). Chrysophytes as a phylogenetic group appear to lack the ability to use bicarbonate and lack a CCM ([Maberly et al., 2009](#_ENREF_112)).

Although carbon availability is likely to be a major driver for the possession of a CCM, in the case of the hornworts, bryophytes that are in the sister group to Embryophytes, the possession of a CCM appears to have evolved and been lost several times in evolutionary history and cannot be directly related to periods of low atmospheric CO2 ([Villarreal and Renner, 2012](#_ENREF_208)). Clearly, other ecological factors are involved, including perhaps local environmental conditions in these low-growing plants, in a similar way to the existence of aquatic mosses that lack a CCM but can survive episodes of low CO2 concentration in surface waters by exploiting the elevated concentration of CO2 just above the sediment surface ([Maberly, 1985](#_ENREF_109)).

*2.1.3 Light availability*

The energy source for photosynthesis is another important environmental variable affecting productivity which can be strikingly different in aquatic and terrestrial environments ([Maberly and Spence, 1989](#_ENREF_118)). Pure water attenuates photosynthetically available light and UV-B radiation much more rapidly than air. Its greater density than air allows particulate material, often eroded from land, especially in inland waters, to remain in suspension and attenuate light. Coloured dissolved organic matter, often largely produced in the catchment, can cause substantial attenuation of blue wavelengths of light and UV-B radiation. Finally, the phytoplankton themselves can substantially reduce underwater light when they are present at high density ([Talling et al., 1973](#_ENREF_201)) as can floating, submerged and emerged macrophytes. Most submerged plants are shade adapted ([Spence and Chrystal, 1970](#_ENREF_196)), macrophyte productivity is often light limited ([Sand-Jensen et al., 2007](#_ENREF_179)) and maximum colonisation depth is limited largely by light availability, restricting the aquatic zone inhabitable by photoautotrophs ([Krause-Jensen and Sand-Jensen, 1998](#_ENREF_98)). Even in low nutrient environments, light availability can be a major control on plankton productivity when concentrations of coloured dissolved organic matter are high ([Jones et al., 1996](#_ENREF_87); [Karlsson et al., 2009](#_ENREF_90)). While light quantity clearly has important effects on aquatic photosynthesis, there is little evidence for chromatic adaptation by benthic algae found at different depths, i.e. an ecological advantage from matching the accessory pigment complement of different phylogenetic groups of algae to the spectral characteristics of light at different depths resulting from variable attenuation of different visible wavelengths ([Raven and Hurd, 2012](#_ENREF_163)).

*2.2 Structural investment*

The density of air, freshwater and seawater is about 0.001, 1.00 and 1.03 Mg m-3 respectively, and in the Dead Sea it is as high as 1.24 Mg m-3 ([Steinhorn, 1983](#_ENREF_197)). These differences have several consequences for photoautotrophs. A major one is that land plants require a greater investment in structural material for support. One of the key evolutionary steps in the colonisation of the terrestrial environment by photoautotrophs was the evolution of the ability to produce lignin. Lignin is widespread in tracheophytes where it cross-links with cell wall polysaccharides to increase mechanical strength, thereby providing supporting for the plant. Lignin also helps resist the negative pressure caused by the transpiration stream within tracheids and vessels and increases hydrophobicity. It is based on phenylpropanoid metabolism that may have played an earlier role in the production of aromatic compounds that absorb UV-B radiation; replacing the attenuation caused by water ([Boerjan et al., 2003](#_ENREF_23); [Weng and Chapple, 2010](#_ENREF_210)). The final enzymatic step in the production of monolignin involves the cinnamyl/sinapyl alcohol dehydrogenase gene family. Cinnamyl alcohol dehydrogenase is monophyletic and present in the terrestrial lycophyte *Selaginella* but not in bryophytes ([Guo et al., 2010](#_ENREF_71)). Although lignin has been found in the intertidal red macroalga *Calliarthron cheilosporioides* ([Martone et al., 2009](#_ENREF_123)) this appears to have arisen independently ([Guo et al., 2010](#_ENREF_71)) as a response to physical stress within the intertidal zone.

Some terrestrial plants have a large reliance on silica to provide rigidity. Well known examples include the, sometimes amphibious, pteridophyte *Equisetum*, and many grasses, but silica can also be present in large amounts in freshwater species such as *Ceratophyllum demersum*, *Sagittaria sagittifolia* or *Myriophyllum* *spicatum* ([Schoelynck et al., 2010](#_ENREF_188)). In these aquatic species there appears to be an inverse correlation between silica and cellulose content that could be related to the flexibility of plants and their ability to respond to water flow and the drag and lift forces it generates ([Schoelynck et al., 2010](#_ENREF_188)). In terrestrial vegetation, silica may act as a grazing deterrent for some groups of invertebrates such as the Coleoptera ([Cooke and Leishman, 2012](#_ENREF_39)) and this could also apply to aquatic plants.

Terrestrial and aquatic plants have to withstand aerodynamic and hydrodynamic forces, caused by wind and water-flow respectively, that can cause parts of the plant or alga to break or the whole organism to become dislodged. For a given air or water velocity, the drag and lift forces are approximately 29-times greater in water because of its greater density ([Denny, 1993](#_ENREF_44)).Tall terrestrial plants, such as trees, are relatively inflexible because they need to be strong enough to support their own weight in a low density fluid ([Ennos, 1999](#_ENREF_55)). In contrast the greater density of water allows many submerged plants to invest less in structural materials and to be much more flexible. This is advantageous in overcoming drag forces because it allows them to ‘reconfigure’ their shape, thus reducing drag ([Sand-Jensen, 2003](#_ENREF_178); [Albayrak et al., 2012](#_ENREF_3)). Macrophytes around a lake shore, and even more so ntertidal marine macroalgae, face some of the most extreme forces of any organism and may experience water velocities up to 34 m s-1 (equivalent to the drag forces in air at a wind speed of nearly 1000 m s-1) as a wave breaks ([Gaylord et al., 1994](#_ENREF_66); [Denny et al., 2013](#_ENREF_43)). Some are highly flexible, such as many macroalgae, and so can reduce drag by reconfiguration ([Harder et al., 2004](#_ENREF_74)). A different strategy is shown by corraline algae where drag is reduced by changing projected area ([Martone et al., 2012](#_ENREF_124)). Many species use a combination of these two approaches to reduce the effects of drag. Of course a certain level of water movement is beneficial in reducing boundary layers, and hence promoting exchange of material, in both macroalgae and macrophytes ([Hurd, 2000](#_ENREF_85); [Miler et al., 2012](#_ENREF_128)).

*2.3 Mineral nutrition*

The mineral requirements of aquatic and terrestrial photoautotrophs are broadly similar ([Sardans et al., 2012](#_ENREF_185)) and in approximately descending order of importance comprise H, C, O, N, P, K, S, Mg, Ca, Cl, Fe, Mn, Cu, Zn, Mo, Ni, Co, and in some species Si ([Raven and Maberly, 2009](#_ENREF_164)), although there are differences linked to the evolutionary background of different prokaryotic and eukaryotic algae ([Quigg et al., 2003](#_ENREF_152)). In addition to supplying water, roots also provide essential minerals ([Raven and Edwards, 2001](#_ENREF_161)). Thus most terrestrial plants are rhizophytic and obtain the bulk of their mineral requirements from the soil, although atmospheric deposition, especially of nitrogen, can be important ([Bobbink et al., 1998](#_ENREF_22)). In aquatic plants there is the possibility of direct uptake of mineral nutrients from water. The charophytes (Characeae) possess simple rhizoids that penetrate the sediment and can take up nutrients ([Andrews, 1987](#_ENREF_6); [Vermeer et al., 2003](#_ENREF_207)). The secondarily derived aquatic angiosperms and lycophytes that evolved roots to cope with water stress on land, have often retained an extensive root system. This gives them access to nutrients in the sediment ([Barko et al., 1991](#_ENREF_11)) and in some cases to CO2 (see section 2.1.2) and also anchors them effectively ([Schutten et al., 2005](#_ENREF_190)).

However, aquatic and water-logged sediments are frequently anoxic as the supply of oxygen can be low, caused low rates of oxygen supply ([Verberk et al., 2011](#_ENREF_206)) and high rates of oxygen demand, caused by high concentrations of degradable organic carbon. This can limit root respiration, lead to the build-up of toxic by-products such as ethanol and the formation of potentially toxic concentrations of sulphide and heavy metal ions ([Colmer et al., 2014](#_ENREF_38)). Survival of roots in these environments is partly achieved by biochemical tolerance of anoxia, based on production of alternative end-products of glycolysis such as malate ([Crawford, 1992](#_ENREF_40)). Many aquatic and wetland species can also oxygenate the sediment around roots via high rates of oxygen diffusion from leaf to roots via internal lacunae that are continuous with the photosynthesising shoot leading to radial diffusion of oxygen into the local sediment ([Sand-Jensen et al., 1982](#_ENREF_180); [Lemoine et al., 2012](#_ENREF_101); [Moller and Sand-Jensen, 2012](#_ENREF_132); [Soana and Bartoli, 2013](#_ENREF_193)). Forced ventilation occurs in some species with floating or aerial leaves ([Dacey, 1980](#_ENREF_41); [Dacey, 1981](#_ENREF_42); [Grosse et al., 1991](#_ENREF_70)), providing access to atmospheric, not just photosynthetic, oxygen and a pathway for loss of volatile toxins such as ethanol.

The bulk of marine macroalgae are haptophytic, attaching to solid substrate but relying on the water column for mineral resources. This also applies to aquatic bryophytes and one angiosperm family of freshwater macrophytes, the Podostemaceae, that is adapted to living on rocks in fast-flowing water including waterfalls, ([Koi and Kato, 2003](#_ENREF_97); [Tippery et al., 2011](#_ENREF_203)). Some species of freshwater macrophyte have roots but do not normally obtain mineral resources directly from the sediment. Examples include planophytic species at the water surface such as the angiosperm *Lemna* or the aquatic pteridophyte *Azolla*. Others, such as the aquatic angiosperm *Ceratophyllum*, are largely pleustophytic, i.e. free-floating within the water column. Both free-floating life-forms require relatively high nutrient concentrations in order to thrive. Some unrooted freshwater macrophytes, such as species within the genera *Utricularia* (Lentibulariaceae) and *Aldrovanda* *vesiculosa* (Droseraceae), supplement their mineral requirements by trapping small animals within bladders on the shoots ([Adamec, 1997](#_ENREF_2)). Aquatic plants represent about 10% of all known carnivorous plants ([Ellison and Adamec, 2011](#_ENREF_52)). Consortia within the bladders may provide as much advantage to the plant by nutrient recycling as by the trapping of animals ([Richards, 2001](#_ENREF_171)).

The plankton also rely entirely on the water column to supply their nutrient requirements (see Giordano & Raven, this volume), although resting stages of cyanobacteria and other algae at the sediment surface can take up nutrients from the sediment and then use them to support subsequent growth in the water column ([Barbiero and Welch, 1992](#_ENREF_10)). Nutrient availability is also one of the most frequent factors controlling phytoplanktonic abundance in marine and freshwater environments. While phosphorus is often limiting ([Vollenweider and Kerekes, 1980](#_ENREF_209); [Phillips et al., 2008](#_ENREF_148); [Schindler et al., 2008](#_ENREF_187)), nitrogen limitation is also common in freshwaters and marine environments ([Elser et al., 2007](#_ENREF_53)) often only partly overcome by nitrogen-fixing cyanobacteria e.g. ([Karl et al., 1997](#_ENREF_89)). In ocean regions remote from the input of terrestrial material, iron can also be an important resource that limits phytoplankton productivity ([Martin and Fitzwater, 1988](#_ENREF_122)) as has been shown by large-scale ocean fertilization experiments ([Boyd et al., 2007](#_ENREF_28)). On occasions, many of the essential elements listed above may become rate or yield limiting. Silica is a particular example as it is an absolute requirement for the cell walls of diatoms and in productive lakes the silica resource can limit diatom growth ([Lund, 1950](#_ENREF_107); [Neal et al., 2005](#_ENREF_135)).

*2.4 Reproduction and dispersal*

Differences between air and water have implications for the reproduction and dispersal of photoautotrophs. Common vectors of pollination for terrestrial plants, such as air and insects, are largely unavailable to secondarily evolved macrophytes when submerged, many of which consequently rely on access to the air for flower production and pollination ([Philbrick and Les, 1996](#_ENREF_147)). A few species such as those within the subgenus Eucallitriche ([Philbrick and Anderson, 1992](#_ENREF_146)), and *Najas* ([Les et al., 1997](#_ENREF_102)) and *Zostera* ([Ackerman, 1997](#_ENREF_1)) within the Alismatidae, have evolved methods to allow transfer of pollen underwater (hypohydrophily). Within the Hydrocharitaceae, other forms of pollination also occur including pollen-epihydrophily where pollen grains float on the water surface and pollinate stigmas of female flowers, and male-flower epihydrophily where male flowers float on the water surface and directly pollinate the stigmas of female flowers ([Tanaka et al., 2013](#_ENREF_202)). The pollen of hypohydrophilous species typically has little exine structure ([Tanaka et al., 2013](#_ENREF_202)) and this appears to be adaptive and possibly linked to the lack of desiccation stress. Similarly the exine sculpture of pollen-epihydrophilous species such as *Elodea nuttalli* and *Hydrilla verticillata* also appears to be adaptive allowing them to float on the water surface ([Tanaka et al., 2013](#_ENREF_202)). It has been speculated that the relative scarcity of marine angiosperms is linked to the problems of pollination underwater and the absence of marine insects to promote co-evolution ([vanderHage, 1996](#_ENREF_205)).

Although sexual reproduction in water is less straightforward than in air, the lack of water stress allows plant fragments that lack roots to survive for long periods of time, favouring asexual reproduction. This, in conjunction with high connectivity in aquatic environments ([Amoros and Bornette, 2002](#_ENREF_4)), driven by gravity or wave-driven water movement, provides an effective dispersal mechanism for vegetative propagules ([Riis, 2008](#_ENREF_173)), Li Wei this issue). Many aquatic plants also produce specialized vegetative structures, turions; above-ground based on modified shoots or below-ground based on modified roots or rhizomes, that act as resting stages and can also aid in dispersal ([Sculthorpe, 1967](#_ENREF_191)). Many aquatic macrophytes are rhizomatous ([Sosnova et al., 2010](#_ENREF_195)) and this along with asexual reproduction tends to result in clonal populations ([Grace, 1993](#_ENREF_68)) and in general lower population genetic diversity in many populations ([Barrett et al., 1993](#_ENREF_12)) although not in all ([Harris et al., 1992](#_ENREF_75)). The most obvious example of low genetic diversity in freshwater macrophytes occurs with invasive species, especially in dioecious species such as *Elodea* ([Lambertini et al., 2010](#_ENREF_99)).

Phytoplankton populations can be present in astronomical numbers at a given site and this, plus the presence of resting stages or spores in some species, produces a large propagule pressure which can promote dispersal. This has led microbial populations to have, generally, a much more widespread global distribution than larger plants ([Fenchel et al., 1997](#_ENREF_59); [Finlay, 2002](#_ENREF_61)) perhaps also helped by the relative ubiquity of their environmental requirements. The high dispersal potential of aquatic photoautotrophs ([Santamaria, 2002](#_ENREF_183); [Kinlan and Gaines, 2003](#_ENREF_93)) makes aquatic systems, especially inland waters, one of the most susceptible ecosystems to invasion by alien species ([Millennium Ecosystem Assessment, 2005](#_ENREF_129); [Strayer, 2010](#_ENREF_198)). The increased movement of human populations and goods around the globe has increased the propagule pressure on ecosystems. This, facilitated further by environmental, and in particular climate, change has lead to an increasing number of biological invasions in freshwater ([Santos et al., 2011](#_ENREF_184)) and marine systems ([Meinesz and Hesse, 1991](#_ENREF_126)). While there could be some benefits of increased species richness, they often trigger negative effects on the food web and on ecosystem function, at least in the short term.

*2.5 Competition*

The higher density of water compared to air, along with the lack of a water deficit and the solubility of essential nutrients in water, allows aquatic planktonic organisms to develop substantial populations. In contrast, although propagules such as spores, pollen and seeds can disperse in air, potentially over large distances ([Nathan, 2006](#_ENREF_134)), the low density and lack of resources prevent the formation of large populations of aerial planktonic photoautotrophs. There is therefore a potential for competition between microscopic planktonic photautotrophs and large multicellular rhizophytes in aquatic environments that is absent in terrestrial environments. Rhizophytes have an advantage over plankton in low nutrient systems as they can obtain nutrient resources from the sediment (see section 2.3). However in systems, particularly freshwaters, that are affected by anthropogenic eutrophication, the disadvantage of the planktonic life-form in relying on water for nutrient acquisition is reduced or removed. Planktonic photoautotrophs, prokaryotic and eukaryotic, can have volumes as small as 0.1 µm3 ([Raven, 1998](#_ENREF_156); [Raven et al., 2013](#_ENREF_160)). Given the relationship between size and growth rate ([Brown et al., 2004](#_ENREF_30)) these photoautotrophs can achieve 2 divisions per day under optimal conditions ([Raven et al., 2013](#_ENREF_160)) compared to around one division per day for large phytoplankton and 5 or 6 days to double biomass under optimal conditions for freshwater macrophytes ([Olesen and Madsen, 2000](#_ENREF_140)). These rates are, however, substantially lower than chemoautotrophs of equivalent cell volume that do not require photosynthetic machinery ([Raven et al., 2013](#_ENREF_160)).

Planktonic algae therefore have the obvious ability to outcompete macrophytes when nutrient resources are high. This may occur by shading ([Jupp and Spence, 1977](#_ENREF_88)) especially in deeper-water systems. Light competition is also a typical cause of biodiversity loss in terrestrial plant communities in response to nutrient enrichment, caused by shading ([Hautier et al., 2009](#_ENREF_76)). In addition, and largely restricted to aquatic systems, there may also be substantial competition for inorganic carbon. Phytoplankton, by virtue of their small size, have lower transport resistances and thus their rate of photosynthesis saturates at lower concentrations of CO2 than do macrophytes. Many, especially cyanobacteria, have a very effective CCM ([Badger and Price, 2003](#_ENREF_8)) which also allows them to outcompete macrophytes for inorganic carbon, especially those macrophytes restricted to CO2 as a carbon source and lacking avoidance or exploitation strategies (section 2.1.2). The lack of water stress can also allow dense epiphyte populations to develop which can also have negative consequences for photosynthesis of freshwater and marine macrophytes by reducing the supply of light and inorganic carbon ([Sand-Jensen, 1977](#_ENREF_177); [Phillips et al., 1978](#_ENREF_149); [Sand-Jensen and Sondergaard, 1981](#_ENREF_181); [Orth et al., 2006](#_ENREF_142)). The consequence, especially in shallow systems, can be a dramatic switch between benthic productivity dominated by rhizophytic macrophytes when nutrient availability is low and pelagic productivity dominated by plankton when nutrient availability is high. Each of these two stable-states has feed-back processes, involving the whole food web, that maintains the current state. Consequently there is hysteresis in the switching between states in both directions of nutrient availability ([Scheffer et al., 1993](#_ENREF_186)).

There is also, like in terrestrial environments, substantial competition between different life-forms. Thus isoetids that often dominate oligotrophic lakes tend to be outcompeted for light, and possibly inorganic carbon by taller elodeids, in lakes affected by nutrient enrichment ([Mjelde et al., 2012](#_ENREF_130)). In coastal waters, nutrient enrichment typically causes a switch from slow-growing seagrasses and macroalgae that are efficient at utilizing nutrient resources to faster growing macroalgae that outcompete the slower growth forms for light ([Duarte, 1995](#_ENREF_47)).

The high solubility of many organic compounds in water allows them to be excreted into the environment by photoautotrophs with potential for an additional mechanism of competition as well as population signalling. In terrestrial environments, allelopathy, the negative effect of one organism on others mediated by chemicals, can be important, especially in resource-poor environments, where it can affect seed germination and root processes. In aquatic environments, allelochemicals can also act on photosynthetic cells and tissue and may influence competition between macrophytes and phytoplankton ([Gross, 2003](#_ENREF_69)). They may also, in the case of charophytes which produce sulphur-containing compounds ([Anthoni et al., 1980](#_ENREF_7)), affect insect populations that may graze on them. Finally, there is evidence that cyanotoxins produced by *Aphanizomenon ovalisporum* may trigger eukaryotic algae, such as *Chlamydomonas reinhardtii*, to generate external phosphatases that release inorganic phosphate that can then be used by the cyanobacteria ([Bar-Yosef et al., 2010](#_ENREF_9)).

1. **A biogeochemical perspective and anthropogenic environmental change**

The biological processes that acquire, sequester, transform and release material and energy, interact strongly with the chemical and physical properties of the planet. This section illustrates two of the larger scale feedbacks linked to the biogeochemical cycling of oxygen and carbon and the consequences that have occurred over evolutionary time and highlights major anthropogenic changes and the present and future challenges they pose for mankind’s survival.

Perhaps the clearest example of the fundamental effect of biology on the planet is the production of oxygen as a by-product of splitting water to obtain hydrogen in order to produce reduced organic carbon in photosynthesis, which led to the ‘great oxidation event’ around 2.3 Ga ([Canfield, 2005](#_ENREF_32); [Anbar et al., 2007](#_ENREF_5); [Lyons et al., 2014](#_ENREF_108)) (Fig. 1). This had a fundamental effect on the biogeochemical properties of the planet and the biological opportunities it provided. Most organisms rely on oxygen as an electron acceptor and aerobic respiration is more efficient at generating energy than anaerobic respiration. Oxygenation of the oceans affected the availability of essential resources such as combined nitrogen, iron and phosphorus ([Planavsky et al., 2010](#_ENREF_151); [Planavsky et al., 2011](#_ENREF_150)). The production of atmospheric oxygen influenced the evolution of other groups by, for example, allowing mega-insects to evolve ([Dudley, 1998](#_ENREF_48)). The conversion of oxygen to ozone in the atmosphere reduced the flux of UV radiation to the surface of the Earth, affecting aquatic ([Hader et al., 2007](#_ENREF_72)) and particularly terrestrial organisms ([Caldwell et al., 2007](#_ENREF_31)).

The evolution of land plants occurred when atmospheric concentrations of CO2 were high, ([Raven et al., 2012](#_ENREF_162)) which will have ameliorated the balance between carbon gain and water loss ([Beerling, 2012](#_ENREF_15)). The subsequent draw-down of atmospheric CO2 and increase in atmospheric oxygen concentrations ([Berner, 2006](#_ENREF_18)) increased the potential for photorespiration relative to photosynthesis ([Ogren and Bowes, 1971](#_ENREF_139)), favouring the evolution of alternative photosynthetic mechanisms ([Sage et al., 2012](#_ENREF_176)) and affecting the evolution of plant leaf form ([Beerling et al., 2001](#_ENREF_16)).

Turning to carbon-cycling, lignin, produced to increase the mechanical strength of terrestrial plants (section 2.2) is a relatively difficult molecule to degrade and represents 30% of the biomass produced by plants ([Boerjan et al., 2003](#_ENREF_23)) leading to substantial reserves of stored organic carbon being produced. Only one phylogenetic group, the white rot family within the Agaricomycetes, has the ability to degrade lignin. The evolution of lignin degradation enzymes (fungal class II peroxidases) around 0.3 Ga (Fig. 1), led to a large reduction in rates of organic carbon burial and accumulation and of coal formation ([Floudas et al., 2012](#_ENREF_62)) with implications for the global carbon cycle. There is another potential feedback from the evolution of lignin degradation enzymes to global biogeochemical cycles. Lignin degradation releases aromatic acids that stimulate rock weathering ([Neaman et al., 2005](#_ENREF_136)). This may have increased the availability of minerals, including nutrients, to photoautotrophs on land and in receiving waters, with consequences for mineral nutrition. The development of forests about 0.35 Ga (Fig. 1) and the symbiotic association with mycorrhizal fungae also promotes weathering of rock and release of silica ([Quirk et al., 2012](#_ENREF_153)) potentially increasing the availability of this resource for diatom evolution ([Falkowski et al., 2004](#_ENREF_57)).

In the Anthropocene, growing populations and technological developments have increasingly directed the Planet’s resources towards Man’s use which has caused an unprecedented rate of planetary changes, many of which were unforeseen and which involve several systems. For example, terrestrial land cover as forest and natural grassland has been converted to agricultural use, reducing biodiversity and ecosystem complexity and often reducing precipitation where deforestation has occurred ([Millennium Ecosystem Assessment, 2005](#_ENREF_129)). Global biogeochemical cycles have been disrupted by release of organic carbon stored over geological time which has rapidly increased atmospheric concentrations of CO2 ([Hofmann et al., 2009](#_ENREF_81)) and methane ([Dlugokencky et al., 2011](#_ENREF_45)), altering the heat-balance of the planet; causing recent, rapid warming with a plethora of direct, indirect, unforeseen and long-term effects ([Solomon et al., 2009](#_ENREF_194)). Around a third of the CO2 produced has dissolved in the ocean causing surface pH to decrease, with negative consequences, most directly for organisms that produce skeletons based on calcium carbonate ([Hoegh-Guldberg et al., 2007](#_ENREF_80); [Doney et al., 2009](#_ENREF_46)). The invention and widespread use of the Haber-Bosch process to produce nitrogen fertilizers and the combustion of fossil fuels, has dramatically increased the global availability of nitrogen ([Erisman et al., 2008](#_ENREF_56)), with possible increases in forest productivity and in regions with high atmospheric N-deposition shifting the nutrient limiting phytoplankton productivity away from nitrogen towards phosphorus ([Bergstrom and Jansson, 2006](#_ENREF_17)). The thinning of the ozone layer over Antarctica ([Farman et al., 1985](#_ENREF_58)) and elsewhere as a result of production of chlorofluorocarbons has consequences for ecosystem function and Human health that required international legislation. Water use by humans exceeds the capacity to supply it, especially in regions experiencing climate change and relying on groundwater reserves that have accumulated over centuries ([Millennium Ecosystem Assessment, 2005](#_ENREF_129)). The large increase in the number of rivers which are dammed for water supply, hydro-power, flood-control and navigation reduces the silica load to the coast ([Humborg et al., 2000](#_ENREF_84)) and may alter coastal phytoplankton and fish productivity ([Gong et al., 2006](#_ENREF_67)).

Finally, the productivity and carrying capacity of the planet itself is being challenged by human populations and there are serious concerns over food security in many parts of the world ([Beddington, 2010](#_ENREF_14)). The production of more photosynthetically-efficient terrestrial crop plants based in part on learning from processes in aquatic plants (see von Caemmerer, this issue) may ameliorate this shortage, but longer-term, sustainable solutions are required to balance the flow of energy and resources through human populations and natural ecosystems within global biogeochemical cycles.

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**Figure legend**

Figure 1. Approximate time of appearance of key organisms or events.