COMMENTARY

Life at the boundary: photosynthesis at the soil–fluid interface. A synthesis focusing on mosses

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Received 16 September 2015; Accepted 5 January 2016

Editor: Christine Raines, University of Essex

Abstract

Mosses are among the earliest branching embryophytes and probably originated not later than the early Ordovician when atmospheric CO₂ was higher and O₂ was lower than today. The C₃ biochemistry and physiology of their photosynthesis suggests, by analogy with tracheophytes, that growth of extant bryophytes in high CO₂ approximating Ordovician values would increase the growth rate. This occurs for many mosses, including Physcomitrella patens in suspension culture, although recently published transcriptomic data on this species at high CO₂ and present-day CO₂ show down-regulation of the transcription of several genes related to photosynthesis. It would be useful if transcriptomic (and proteomic) data comparing growth conditions are linked to measurements of growth and physiology on the same, or parallel, cultures. Mosses (like later-originating embryophytes) have been subject to changes in bulk atmospheric CO₂ and O₂ throughout their existence, with evidence, albeit limited, for positive selection of moss Rubisco. Extant mosses are subject to a large range of CO₂ and O₂ concentrations in their immediate environments, especially aquatic mosses, and mosses are particularly influenced by CO₂ generated by, and O₂ consumed by, soil chemoorganotrophy from organic C produced by tracheophytes (if present) and bryophytes.

Key words: ABA, bryophytes, C₃ biochemistry and physiology, decreased oxygen, adaptation to global change, hornworts, increased carbon dioxide, liverworts, mosses, photorespiration, transcriptomics.

Introduction

Bryophytes are the basal embryophytes, and probably evolved at the latest by the early Ordovician (Jones and Dolan, 2012; Pires and Dolan, 2012; Willis and McElwain, 2013; Proctor, 2014; Raven and Edwards, 2014; Edwards et al., 2015). The present-day bryophytes are all poikilohydric; while the sporophytes of hornworts, and most mosses, have some homoeohydric attributes, they are matrotrophic on the poikilohydric gametophytes (Proctor, 2014; Raven and Edwards, 2014). Many bryophytes are desiccation-tolerant, and while most live on land, a number are aquatic (Proctor, 2014; Raven and Edwards, 2014). Present-day bryophytes generally extend less than 0.1 m above the substrate (Raven, 1999a, b; Proctor, 2014; Raven and Edwards, 2014), and their spatial niche on land overlaps that of tracheophytes in the height range 10–100 mm (Raven, 1999a, b; Boyce, 2008; Proctor, 2014; Raven and Edwards, 2014). We focus here on mosses, but also...
mention other bryophytes (hornworts and liverworts) when necessary.

There seem to be no quantitative estimates of the biogeochemical role of mosses today, but there are qualitative discussions on the role of cryptogamic covers (liverworts, hornworts, mosses, lichens and free-living algae) (e.g. Cornelissen et al., 2007; Edwards et al., 2015), and quantitative data on the global productivity and biomass of cryptogamic covers today, including cryptogamic ground covers and cryptogamic plant covers, i.e. epiphytic on tracheophytes (Elbert et al., 2012; Porada et al., 2013, 2014; Edwards et al., 2015). Global primary production by these organisms is 0.32 Pmol C from CO$_2$ to organic carbon per year (7% of the net primary productivity of terrestrial vegetation), while global biomass is 0.41 Pmol C (about 1% of total terrestrial vegetation), in both cases with significant uncertainty (Elbert et al., 2012; Porada et al., 2013, 2014; Edwards et al., 2015). Edwards et al. (2015) and Porada et al. (2013, 2014) have used the data of Elbert et al. (2012) to estimate the global primary productivity due to cryptogamic covers in the Ordovician before there was a significant tracheophyte component, with even greater uncertainty than for the present-day estimates.

Here we focus on the ecophysiology of mosses, probably the latest-originating bryophytes (Willis and McElwain, 2013; Proctor, 2014; Raven and Edwards, 2014; Edwards et al., 2015), since the focus of this commentary is on Shinde et al. (2015) who worked on Physcomitrella patens. Shinde et al. (2015) compared the transcriptomes of P. patens protonemata grown under four gas phases related to the present day and to the atmospheric composition of the Ordovician in which the earliest mosses grew. The earliest mosses had no significant competition from tracheophytes for reproductively mature gametophyte in the 10–100 mm height range, though the protonematal mats had competition from terrestrial cyanobacteria and algae. The control treatment had 400 μmol mol$^{-1}$ CO$_2$ and 210 mmol mol$^{-1}$ O$_2$ to represent our present-day atmosphere, and the Ordovician treatment had 1500 μmol mol$^{-1}$ CO$_2$ and 130 mmol mol$^{-1}$ O$_2$. The other two treatments were: high CO$_2$ and current O$_2$ (1500 μmol mol$^{-1}$ CO$_2$ and 210 mmol mol$^{-1}$ O$_2$) and current CO$_2$ with sub-ambient O$_2$ relative to current levels (400 μmol mol$^{-1}$ CO$_2$ and 130 mmol mol$^{-1}$ O$_2$). References to estimates of Ordovician CO$_2$ and O$_2$ can be found in Willis and McElwain (2013), Raven and Edwards (2014) and Edwards et al. (2015). The extent to which there are non-atmospheric sources of CO$_2$ for terrestrial bryophytes living on soil or on respiring plant structures today, and the extent to which there may have been such sources in the Ordovician, are considered subsequently in this paper. This discussion suggests that soil, and phorophyte respiration for epiphytes, was probably a less important source of CO$_2$ in the Ordovician than it is today. The absence of tracheophytes meant there were no large phorophytes for use by epiphytes, and that there were only the short rhizoids of bryophytes as the means of supplying organic carbon for soil respiration, and not the much deeper-penetrating belowground structures of tracheophytes (see also the subsection ‘Bryophytes growing on land’ below). Use of a rock-dwelling bryophyte, rather than Physcomitrella, would have eliminated the alternative substrate-derived source of CO$_2$, but with the disadvantage of using a ‘non-model’ bryophyte.

**Contribution of the work of Shinde et al. (2015)**

Turning to the experiments on Physcomitrella patens of Shinde et al. (2015), as related to the C$_3$ physiology and biochemistry of the moss (see Supplementary Data S1 available at JXB online), the control treatment had a gas phase of 400 μmol mol$^{-1}$ CO$_2$ and 210 mmol mol$^{-1}$ O$_2$, i.e. present atmospheric levels. However, the P. patens was cultured on peat pellets which were presumably not sterile and so would have released CO$_2$ and increased the CO$_2$ concentration around the gametophytes to above the nominal 400 μmol mol$^{-1}$ CO$_2$. While this gives growing conditions closer to (but by no means identical with) those of present-day P. patens on damp mud (see discussion below) than would use of a growth substrate based on materials with no metabolisable organic carbon, it means that the CO$_2$ concentration around the mosses was not accurately known. However, in view of the large (3.75-fold) difference between the control (400 μmol mol$^{-1}$) and high CO$_2$ treatment (1500 μmol mol$^{-1}$), the effects of the CO$_2$ production from the peat substrate are probably negligible in the context of Shinde et al. (2015)’s work. The effect of O$_2$ consumption by the peat substrate on the low O$_2$ (130 mmol mol$^{-1}$) and the control O$_2$ (210 mmol mol$^{-1}$) are even less significant in the context of the work.

As pointed out by Shinde et al. (2015), work on C$_3$, largely flowering, tracheophytes comparing plants with an increased CO$_2$ treatment with those grown at ambient atmospheric CO$_2$ generally show an initial large increase in the photosynthetic rate with a subsequent smaller, sometimes insignificant, steady-state enhancement (e.g. Tuba et al., 1999; Long et al., 2004). The higher steady-state photosynthetic rate under elevated CO$_2$ occurs with a decreased stomatal conductance and with a lower level of Rubisco protein (Long et al., 2004). The decreased stomatal conductance still allows an increase in steady-state intercellular space CO$_2$ during photosynthesis, and this greater CO$_2$ availability allows a higher rate of photosynthesis despite the lower Rubisco content by decreasing the extent to which Rubisco activity is limited by CO$_2$ concentration. The complication of stomata is, of course, absent from moss gametophytes, so the prediction is that there would be a down-regulation of Rubisco with long-term exposure to high CO$_2$ while still allowing a higher photosynthetic rate. Even without a decrease in O$_2$ the higher CO$_2$ concentration means a low Rubisco oxygenase activity and hence a decreased activity of the photosynthetic carbon oxidation cycle (PCOC). The decreased O$_2$/increased CO$_2$ concentration combination should further decrease the Rubisco oxygenase and PCOC activities, although if (as is likely from the discussion above) photosynthesis is near or at CO$_2$ saturation at 1500 μmol mol$^{-1}$ the further stimulation of net photosynthesis by decreased O$_2$ should be smaller than when CO$_2$ is rate-limiting, as in the treatment with present-day CO$_2$/decreased O$_2$. 


These considerations must be set against the evidence on moss gametophytes showing that long-term growth in increased CO₂ can be greater, the same as, or less than that at present CO₂ levels, although some of the data sets showing no effect of increased CO₂ on growth rate could have been related to resource supply in the natural environment (Table 1; Tuba et al., 1999; Supplementary Data S1).

For the more readily explained cases of increases in photosynthetic and growth rates of mosses with elevated CO₂, such responses require an increased flux through the pathways of RuBP-regeneration including Benson-Calvin cycle enzymes and thylakoid reactions, with a decrease in the flux through the PCOC reactions, on a moss biomass basis. An increased steady-state net photosynthetic rate can only occur over the long term (several generation times at the specific growth rate in the original growth conditions) if there is either a large capacity for storage of photosynthetic products when there is no increase in growth rate, and/or growth can be increased under otherwise resource-replete conditions by increased supply of photosynthate (i.e. growth rate is not sink-limited). Since, from data discussed above (Tuba et al., 1999; see Supplementary Data S1), it is possible that the growth rate of *P. patens* is CO₂-limited in the present-day atmosphere under otherwise resource-replete conditions, there is the possibility of a higher specific growth rate (g dry biomass increase per g dry biomass per day) if there is a larger supply of organic carbon from photosynthesis. This requires an absence of sink limitation, i.e. the rate of photosynthesis is not limited by the capacity to use the resulting organic carbon for growth or storage. This would permit an increase in photosynthesis under high CO₂ conditions, which would, as mentioned above, require an increased flux through the pathways of RuBP-regeneration including Benson-Calvin cycle enzymes and thylakoid reactions. The high CO₂ would also decrease the flux through the PCOC reactions through the favouring of carboxylation over oxygenation when the CO₂:O₂ ratio is increased. The resulting increased specific growth rate would also require an increased flux on a biomass basis through all pathways on which growth using photosyntheate depends.

There is no *a priori* way of knowing which of the enzymes, transporters and photochemical catalysts involved in these pathways would have an activity low enough to prevent the increased fluxes, and hence which might be expected to be upregulated. For C₃ flowering plants, studies with down-regulation of individual enzymes of the Benson-Calvin cycle using the formalism of control strength analysis shows that Rubisco, sedoheptulose-1,7-bisphosphate-1-phosphatase, aldolase and transketolase, can all contribute to the limitation of photosynthetic rate in the present atmosphere (Kacser and Burns, 1973, 1979; Heinrich and Rapoport, 1974; Heinrich et al., 1977; Stitt and Schulze, 1994; Raines, 2003, 2011), with variations in Rubisco control strength with CO₂ concentration (Stitt and Schulze, 1994). While it seems counterintuitive that reversible reactions such as those catalysed by aldolase and transketolase can exercise control of metabolic fluxes (Raines, 2011), such control is possible under some circumstances (Kacser and Burns, 1973; Fell and Sauro, 1986). Increased resource supply permitting an increased specific growth rate of a photosynthetic organism does not involve a parallel increase in the protein content of the biomass, so that there is an apparent excess of protein in the cells growing at low growth rates (Flynn et al., 2010; Raven, 2013a, b, 2015). Shinde et al. (2015) provide no data on either photosynthetic and respiratory rates or on specific growth rates, so it is not possible to determine if the high CO₂ treatments stimulate net photosynthesis and, if so, whether this leads to an increased specific growth rate rather than increased organic C storage. However, on the basis of short-term work on mosses (see above), an increase in photosynthetic rate in the high CO₂ treatments and an increased long-term photosynthetic rate are likely, as is an increased specific growth rate.

As discussed above, not all mosses show an increase in specific growth rate when acclimated to CO₂ concentrations in excess of the present atmospheric level (Table 1; Supplementary Data S1).

### Table 1. Effects on rates of photosynthesis or growth of high CO₂ relative to present CO₂ for weeks to months, in a range of moss species

See Supplementary Data S1 for more details, e.g. the possibility of limitation by resources other than carbon for observations in the field.

| Organism               | Location                          | Photosynthetic rate in high CO₂ relative to present CO₂ | Growth rate in high CO₂ relative to present CO₂ | References                        |
|------------------------|-----------------------------------|--------------------------------------------------------|-------------------------------------------------|-----------------------------------|
| Physcomitrella patens  | Submerged in culture medium        | Not measured                                           | Higher                                          | Hohe et al. (2002)                |
|                       | Submerged plants                  | Not measured                                           | Higher                                          | Cerff and Posten (2012)           |
| Sphagnum cuspidatum    | Submerged plants                  | Not measured                                           | Higher                                          | Paffen and Roelofs (1991)         |
| Sphagnum magellanicum  | Submerged plants                  | Not measured                                           | Higher                                          | Heijmans et al. (2001)            |
| Sphagnum spp.          | Submerged plants                  | Not measured                                           | Higher                                          | Smolders et al. (2001)            |
| Syntrichia ruralis (as Tortula ruralis) | Laboratory; shoot in air | Increase                                                | Not measured                                    | Tuba et al. (1998)                |
| Sphagnum spp.          | Field                             | Not measured                                           | No significant effect                           | Van den Heijden et al. (2000a, b); Berendse et al. (2001) |
| Syntrichia ruralis (as Tortula ruralis) | Shoot in air                       | Not measured                                           | No significant effect                           | Csintelen et al. (1997)           |
| Hylcomium splendens    | Shoot in air                       | Not measured                                           | Decreased                                       | Sonnenson et al. (1996)           |
| Sphagnum fallax        | Shoot in air                       | Not measured                                           | Decreased                                       | Mitchell et al. (2002)            |
| Polytrichum strictum   | Shoot in air                       | Not measured                                           | Decreased                                       | Mitchell et al. (2002)            |
Some mosses show no stimulation of growth with added atmospheric CO$_2$, although here the investigations use plants growing in their natural environment and thus are subject to the possibility of limitation by resources other than C, reliance on C supply from CO$_2$ from mineralisation of organic matter in the soil or sediment, or ‘sink limitation’ where the present CO$_2$ supply provides all of the organic carbon that can be consumed by growth or storage (see Supplementary Data S1). More difficult to explain are the cases where growth with additional CO$_2$ is less than in present-day CO$_2$ (Table 1; Supplementary Data S1). Careful analysis is needed of the measurements made in the data in Table 1 and Supplementary Data S1, since measurements of dry matter gain and of elongation (a better measure of differentiation) do not show parallel changes with seasonal variations of temperature and light (Fig. 3 of Rincon and Grime, 1989).

In the case of _P. patens_ in suspension culture there is an increased specific growth rate with enhanced CO$_2$. Hohe et al. (2002) found specific growth rates of 0.25 d$^{-1}$ with air and 0.57 d$^{-1}$ with 2 mmol CO$_2$ mol$^{-1}$ at 25°C, and Cerff and Posten (2012) found specific growth rates of 0.48 d$^{-1}$ for unbubbled control cultures and 0.78 d$^{-1}$ when bubbled with 2.5 mmol CO$_2$ mol$^{-1}$ at 23°C. Locumi et al. (2005) found specific growth rates of 0.864 d$^{-1}$ with 1.75 mmol CO$_2$ mol$^{-1}$ at 21°C, but did not provide data for (near) present-day CO$_2$ concentrations. Tamburic et al. (2015) point out the difficulties in establishing the extent to which the growth medium is in equilibrium with the gas stream, and especially in equilibrium with the overlying atmosphere when the medium is not bubbled. However, the data of Hohe et al. (2002) and Cerff and Posten (2012) clearly show that high, and most likely saturating, CO$_2$ gives substantially higher specific growth rates of this moss, than lower, near-present atmospheric CO$_2$ concentrations. The suspension culture apparently keeps the moss held in an undifferentiated protonemal condition with no sink limitation, which could account for the large increase in specific growth rate with additional CO$_2$ (see preceding paragraph and Supplementary Data S1).

Against this background, the transcriptomic data of Shinde et al. (2015) involved the growth of _P. patens_ under conditions described above (under ‘Contribution of the work of Shinde et al. 2015’). The elevated CO$_2$ treatments show down-regulation of the transcription of a number of genes for proteins involved in photosynthesis, although there are differences depending on whether O$_2$ was 210 mmol mol$^{-1}$ or 130 mmol mol$^{-1}$ (Shinde et al., 2015). If these differences in transcript abundances are related to changes in the proteome there is a decreased concentration of the corresponding proteins, and if these catalyse reactions that restrict the rate of photosynthesis (see above for the reverse argument) then the capacity for photosynthesis is decreased. Shinde et al. (2015) showed up-regulation of the gene regulating abscisic acid (ABA) synthesis under high CO$_2$ conditions; Wang et al. (2010) found that in proteomic analysis of _P. patens_ treated with external ABA, the Rubisco small subunit and some thylakoid proteins decreased in abundance, being consistent with ABA as part of a signalling pathway from high CO$_2$ to decreased expression of photosynthesis-related genes, although there is incomplete matching of the genes down-regulated in the transcriptomic analysis for CO$_2$ and proteomic analysis for ABA. If the proteome reflects the transcriptome in both cases, components in parallel to ABA must be involved in the signalling pathway of the high CO$_2$ response. Furthermore, no up-regulation of the key ABA synthesis gene was found in the high CO$_2$ and low O$_2$ treatment, although this also caused down-regulation of some photosynthesis-related genes. Clearly, further work is needed on the signalling and regulatory pathways of acclimation to high CO$_2$ and with experiments combining transcriptomic and proteomic approaches on the same (or parallel) samples.

As mentioned above, Shinde et al. (2015) did not measure rates of photosynthesis, respiration or growth under the four growth conditions, but the photosynthetic down-regulation suggested by the transcriptome data are not readily reconciled with the increased specific growth rate of _P. patens_ gametophytes in suspension culture bubbled with increased CO$_2$ relative to the rate in an approximation to equilibration with present-day atmospheric CO$_2$ (see above). Clearly the growth conditions in suspension culture differ from those in Shinde et al. (2015), and a direct comparison of metabolic and growth rates with transcriptomics with the same growth conditions for each treatment would be valuable.

**Photosynthesis in mosses since the Ordovician**

It is likely that variations in bulk atmospheric CO$_2$ and O$_2$ concentrations, and smaller-scale temporal and spatial variations through evolutionary time, have influenced photosynthesis in mosses, and other oxygenic photosynthetic organisms. An example is genetic adaptation of Rubisco. Positive selection of Rubisco has been shown for a range of oxygenic photolitho-trophs (Kapralov and Filatov, 2007; Miwa et al., 2009; Young et al., 2012; Galmés et al., 2014). This selection could influence Rubisco kinetics, e.g. carboxylase and oxygenase specific reaction rate at, respectively, CO$_2$ and O$_2$ saturation, affinity for CO$_2$ and O$_2$ in the absence of the other substrate, and CO$_2$-O$_2$ selectivity (Sage, 2002; Haslam et al., 2005; Tcherkez et al., 2006; Young et al., 2012). For mosses the occurrence of positive selection of Rubisco has only been analysed for a data set of four species, and the evidence for positive selection is weaker than for the tracheophytes examined (Kapralov and Filatov, 2007); however, this weaker evidence was also the case for algae, for which later, more detailed, analysis showed positive selection (Young et al., 2012). The evidence for liverworts is only available for species of the genus _Conocephalum_ where the recent divergences involved might account for the relative weakness of the evidence for positive selection (Miwa et al., 2009).

The early data on Rubisco kinetics of three moss species (Table 2 of Raven, 2000; e.g. Rintamäki and Aro, 1985) show that the affinities for CO$_2$ are within the range (from a much larger data set) for vascular plants, with a significantly lower value for an aquatic species than for the terrestrial species.
More complete evidence on the Rubisco kinetics of bryophytes (one species each of moss and liverwort) shows that, of the 28 species of C3 embryophyte examined, the bryophytes had the lowest CO2 affinity and the lowest rate of CO2 fixation per molecule of Rubisco protein at limiting CO2 concentrations (Galmés et al., 2014). While the data set as a whole shows evidence of positive selection on Rubisco, no specific data are available on positive selection for just the bryophytes (Galmés et al., 2014): see discussion of interpretation of data on the natural abundance of stable isotopes (Raven et al., 2002).

Variation in CO2 and O2 concentrations in space and time during bryophyte evolution

Bryophytes growing on land

The bryophytes evolved not later than the earliest Ordovician when atmospheric CO2 was several times higher that found today and the O2 was probably lower (Willis and McElwain, 2013; Raven and Edwards, 2014; Edwards et al., 2015; Gerhart and Ward, 2000). Subsequent variations involved very low CO2, and high O2, in the Carboniferous, and very low CO2 again in the Pleistocene. Over most of the last 450 Myr the CO2 level has been higher that it is today. As discussed above, these changes may have been involved in positive selection of Rubisco, although there is less evidence than is desirable on this topic for bryophytes.

Organic carbon in soils would have increased substantially since the early Ordovician, initially from the cryptogamic covers alone and subsequently from what would have been larger inputs from vascular plants. The diversification and spread of tracheophytes, beginning in the Silurian, for many habitats presumably dominated by cryptogamic covers, whose photosynthetic members were bryophytes, lichens and free-living cyanobacteria and (mainly green) eukaryotic algae (Raven and Edwards, 2014; Edwards et al., 2015), resulted in competition, new niche environments, and changes to the atmospheric composition as well as to soils. Below-ground parts of the tracheophytes (with the quantitatively less significant bryophytes and lichens) respire, secrete organic compounds and ultimately die and leave particulate organic carbon that act as growth, and hence respiratory, substrates for chemoorganotrophic microorganisms (bacteria, fungi, protists) and metazoans. This ‘soil respiration’ results in a CO2 concentration in the soil gas spaces that, with the diffusion coefficient of CO2 in the gas phase corrected for the fraction of soil occupied by gas and tortuosity of the path to the soil surface, gives CO2 flux to the atmosphere equal to the rate of CO2 production by soil metabolism (Simůnek and Suarez, 1993a, b). Between the soil surface and the turbulent bulk atmosphere is the soil-atmospheric diffusion boundary layer where the CO2 concentration decreases from the soil surface to the bulk (i.e. turbulent) atmosphere (Denny, 1993; Vogel, 1994; Nobel, 2005; Jones, 2014). Of course, soil respiration under bryophyte vegetation is also contributed to by respiration of below-ground parts of the bryophytes (e.g. rhizomes and rhizoids of Polytrichum spp., Sveinbjörnsson and Oechel, 1981) and decomposition of the bryophytes post mortem by bacteria, fungi, protists and invertebrates, and while this can be partly recycled by bryophyte photosynthesis, it cannot contribute to community net biomass increase by the bryophytes. Furthermore, the shallow ‘rooting’ depth of the rhizoids of bryophytes, and the low stature of above-ground parts that ultimately contribute to soil carbon, would have meant small flux of organic carbon into the soil in the Ordovician with minimal tracheophyte contribution. This contrasts with today when many bryophyte habitats are dominated by taller, deeper-rooted tracheophytes with a much greater flux of organic matter into the soil than in the Ordovician, with a correspondingly greater production of CO2 from respiration of below-ground plant parts, and post mortem by bacteria, fungi, protists and invertebrates, moving out of the soil and into the diffusion boundary layer of the atmosphere where much bryophyte photosynthesis occurs.

The concentration of CO2 in moss canopies on soil under a tracheophyte canopy can, even in the photoperiod when the mosses are photosynthesising, exceed that in the bulk atmosphere (Tarnawski et al., 1994; Tuba et al., 1999; DeLucia et al., 2003), and there is usually a net CO2 flux from the soil to the atmosphere above the moss canopy in the light (Goulden and Grill, 1997; Tuba et al., 1999; Sommerkorn et al., 1999; DeLucia et al., 2003; Botting and Fredeen, 2006). Epiphytic mosses growing on non-photosynthetic parts of plants could be in a similar situation, with the potential to increase photosynthetic rate using CO2 built up in the diffusion boundary layer after efflux from the non-photosynthetic stem derived from stem respiration and, via xylem transport and (to a limited extent) diffusion through aerenchyma from root respiration (Tuba et al., 1999; Green, 2010; Muhr et al., 2013). Harwood et al. (1999) measured CO2 at 0.1 m, 9 m and 13 m above the soil in a Quercus petraea forest with moss (Leucobryum glaucum) pillows and vascular plants (Oxalis acetosella, Pteridium aquilinum) as the dense ground flora, and found higher CO2 concentrations at 0.1 m than at the two higher levels, even in the photophase. Variations over the diel cycle at 0.1 m were 345–405 μmol mol−1, while at 9 m and 13 m the range was 340–360 μmol mol−1. This would allow greater rates of photosynthesis in bryophytes exposed to substrate-derived CO2 than in the same bryophytes not so exposed, provided other growth conditions allow a response to the additional CO2. Another example is that 3500 μmol mol−1 CO2 occurs in the atmosphere in turfs of Grimmia antarctica in East Antarctica in the summer (Tarnawski et al., 1992), almost 10 times the present atmospheric level of CO2. The CO2 values in Tarnawski et al. (1992) are higher than those in the Ordovician, while those in Harwood et al. (1999) are much lower.

Harwood et al. (1999) also measured the vertical profile of atmospheric 13CO2/12CO2, and found values at 0.1 m that were lower than those at 9 m and 13 m, indicating the influence of 13CO2-depleted CO2 from soil respiration, with the 13CO2/12CO2 predicting an increased CO2 mol fraction in general quantitative agreement with the direct measurements of CO2 mol fraction by these workers. This decrease in 13CO2/12CO2
of substrate CO$_2$ would be expected to be reflected in the $^{13}$C/$^{12}$C of organic C in the bryophytes. A test comes from the work of Fletcher et al. (2005) who grew four species of thalloid liverwort on compost or on an organic matter-free 3:2 sand:vermiculite mixture. Despite the expected higher CO$_2$ concentrations near the compost surface owing to respiration of organic matter, Fletcher et al. (2005) found that the lower $^{13}$CO$_2$/$^{12}$CO$_2$ of CO$_2$ from soil respiration is not reflected in a lower $^{13}$C/$^{12}$C of organic matter in the liverworts, as shown by no significant difference in $^{13}$C/$^{12}$C between organic C of the liverworts of the thalli grown on the organic or on the inorganic substrates (Table 4 of Fletcher et al., 2005). This lack of a significant effect on liverwort $^{13}$C/$^{12}$C of organic C means no detectable effect of the soil-derived CO$_2$ on liverwort C accumulation, regardless of whether the thalli had pores on the upper surface with associated gas spaces (Conocephalum, Lunularia, Marchantia) or had a thallus without intercellular gas spaces (Pellia): Table 4 of Fletcher et al. (2005). Fletcher et al. (2005) do not say what level of fertilizer was used in comparing the substrate treatments, but presumably the liverworts were not nutrient-limited. Furthermore, the different morphology of mosses and of thalloid liverworts might allow a greater effect on mosses.

In view of the increase in soil organic carbon in semi-natural habitats seen over recent decades (Chen et al., 2015), it is likely that the CO$_2$ efflux from soils will be at least maintained under continuing global environmental change, so this CO$_2$ will be added to the increased atmospheric CO$_2$ in the atmosphere in the soil boundary layer as a CO$_2$ source for bryophytes (Tuba et al., 1999).

Sphagnum spp. that produce hummocks, with the upper parts with air rather than water between the plants, depend on high CO$_2$ concentrations in the acrotelm water, and the CO$_2$ concentration, even in the light, in the gas phase in the upper parts of the hummock is twice that in the outside atmosphere (Smolders et al., 2001; see also Rydin and Clymo, 1989; Lamers et al., 1999). It is significant that, despite the low content of photosynthetic light-harvesting pigments per unit area of moss leaves, the high leaf area index of moss canopies means very significant attenuation of photosynthetically active radiation (PAR) within the canopy (Niinemets and Tobias, 2014), giving large opposing gradients of PAR and CO$_2$ within the canopy.

Terrestrial mosses today are also subject to low atmospheric CO$_2$ at high altitudes and this low CO$_2$ habitat is considered here because, in contrast with the antiparallel behaviour of CO$_2$ and O$_2$ just above the soil, there is a proportional decrease in the mole fraction, and the partial pressure, of CO$_2$ and O$_2$ (Körner, 2007; Jones, 2014; see below in this paragraph). This naturally-occurring contrast deserves further investigation; the four sets of experimental conditions used by Shinde et al. (2015) represents a beginning to such comparisons. The decrease in total atmospheric pressure increases the mean free path of gas molecules, and thus the diffusion coefficients of gases, which partly offsets the decreased concentration of gases in limiting the flux to the surface of a moss; this pressure effect does not offset the decreased concentration for diffusion in the aqueous phase of moss leaf or in carboxylation in the chloroplast (Jones, 2014). There are various complicating factors; e.g. at a given latitude, the higher altitudes have a lower temperature that decreases the gas diffusion coefficients in the atmosphere as well as in the aqueous phase of leaves, and the capacity for CO$_2$ assimilation by chloroplasts (Körner, 2007; Jones, 2014).

Tracheophytes and bryophytes extend to altitudes of just over 6 km, such as in the Himalaya (Chopra, 1975; Webster, 1961; Swan, 1990; Grau et al. 2007; Crawford, 2008). Grau et al. (2007) show that the species richness of liverworts, mosses and flowering plants all peak at intermediate altitudes in the Himalaya, but their meta-analysis does not extend to altitudes higher that 5 km, and species richness does not necessarily equate to area covered by each clade. It is, of course, not possible to say that bryophytes do not occur above 6 km, just that the hypothesis that there are no bryophytes above 6 km has not been falsified to our knowledge in a scientific publication.

At 5.5 km altitude the atmospheric pressure is just under half (0.05 MPa) that at sea level (0.1 MPa), so the partial pressure of CO$_2$ at 5.5 km altitude is 20 Pa rather than 40 Pa at sea level, and O$_2$ is 10.5 kPa rather than 21 kPa (Jones, 2014). The parallel decrease in the concentration of CO$_2$ and O$_2$ means that the proportional effect of photosynthesis on net photosynthesis is, to a first approximation, the same at high altitude as at sea level. Among confounding factors in determining altitudinal limits of species may be the high UV-B flux at high altitudes (Arróniz-Crespo et al., 2006; Sonesson et al., 1996; Turnbull and Robinson, 2009; Robinson and Erickson, 2015).

Submerged bryophytes and other rhizoid-bearing submerged rhizophytes

Mosses (and liverworts) also occur as submerged benthic primary producers in freshwater lakes, ponds and rivers (Glime, 2007, 2011, 2014). The submerged aquatic mosses and liverworts almost always function as haptophytes, i.e. with rhizoids adherent to stones and rocks (Luther, 1949; Raven, 1981), but occasionally as rhizophytes, i.e. with rhizoids ramifying in fine-grained sediments (Luther, 1949; Raven, 1981; Hawes et al., 2002). Common macroagal rhizophytes include the Charales (freshwater and euryhaline charophycean green algae, i.e. close to the ancestors of the embryophytes) and the marine Caulerpa (ulvophycean green alga).

In waterlogged soils and in submerged freshwater sediments, CO$_2$ produced by the roots of emergent or submerged rooted (rhizophytic) vascular plants is retarded from escaping to the soil, or in some soils CO$_2$ becomes very high and enters roots (Greenway et al., 2006). The tracheophytes also supply dead root and shoot material and, in freshwaters, particulate and dissolved organic carbon is supplied from terrestrial productivity in the catchment, as is dissolved inorganic carbon from soil respiration in the catchment (Neal et al., 1998; Maberly et al., 2013; Catalán et al., 2014). Another source of particulate organic carbon to sediments is sedimentation of phytoplankton and zooplankton from the overlying water body. Respiration of this organic matter in aerated sediments...
producing CO\textsubscript{2} with, in anoxic sediments, anaerobic respiration and fermentation producing CO\textsubscript{2}, and some CH\textsubscript{4} from methanogenesis which can be oxidised by methanotrophs in oxygenated water to produce CO\textsubscript{2} \citep{Gruc-Rokosz2010, Gruc-Rokosz2015}.

There is a net diffusive flux of CO\textsubscript{2} (and CH\textsubscript{4}) down the concentration gradient from the sediment to the bulk water body, at least for the case of no oxygenic photosynthetic microorganisms at the sediment surface \citep{Gruc-Rokosz2010, Gruc-Rokosz2015}. As for the case of soil and the atmosphere, mixing of the fluid phase does not extend to the surface of the sediment; the thickness of the diffusion boundary layer in water is less than that in air \citep{Denny1993, Vogel1994, Nobel2005, Jones2014}, but the diffusive coefficient of CO\textsubscript{2} and O\textsubscript{2} in water is 10,000 times lower than in air, so steep concentration gradients are present across these aqueous boundary layers. For the reverse flux of O\textsubscript{2} into the sediment the effective thickness of the diffusion boundary layer, at the top of which the concentration of the diffusing species is equal to that in the mixed water above, is not more than 1 mm even in the calmest water \citep{Jorgensen1985, Gunderson1990, Jorgensen1990b}. The effective diffusion boundary layer thickness for CO\textsubscript{2} efflux from the sediment would be expected to be similar, although complicated by the presence of the other components (HCO\textsubscript{3}\textsuperscript{-}, CO\textsubscript{3}\textsuperscript{2}\textsuperscript{-}, H\textsuperscript{+}, OH\textsuperscript{-}) of the inorganic carbon system. The distance above the sediment at which CO\textsubscript{2} supply to rhizophtic macrophytes, including a few submerged mosses, is supplemented by the CO\textsubscript{2} supply from the sediment cannot be directly related to the values cited above for macrophyte-free sediment. This is because the macrophytes will increase the sediment diffusion boundary layer as a function of the macrophyte morphology. While the effective diffusion boundary distance is more than 1 mm thick in a macrophyte bed, account needs to be taken of removal of CO\textsubscript{2} within the diffusion boundary layer by macrophyte photosynthesis. Even then, substantial gradients of dissolved CO\textsubscript{2} and O\textsubscript{2} with water depth (or distance above the soil/sediment) can occur over much larger distances within the water column e.g. as recorded in deepwater rice fields \citep{Setter2012}.

Another possible input of sediment inorganic carbon to photosynthesis is via CO\textsubscript{2} uptake by rhizoids and roots; see \cite{JonesDolan2012} and \cite{PiresDolan2012} for the evolutionary relationships of rhizoids, root hairs and roots. There are data for inorganic \textsuperscript{14}C uptake by the rhizoids, and translocation to the shoot by cytoplasmic streaming with diffusion through plasmodesmata in cross-walls of the submerged freshwater charophycean macroalga Chara hispida \citep{Andrews1984}. The contribution of \textsuperscript{14}C inorganic carbon entering though the rhizoids to whole-plant photosynthesis of the alga is negligible \citep{Andrews1984}, although rhizoids have a significant role in the whole-plant acquisition of phosphate \citep{Box1985, Box1986} and ammonium and nitrate \citep{Box1987}. The rhizoids of the marine submerged macroalga Caulerpa spp. have a role in accessing ammonium and organic N, and phosphate \citep{Williams1984, WilliamsFisher1985, Chisholm1996}, but there are no data on inorganic \textsuperscript{14}C uptake. There seem to be no data for inorganic \textsuperscript{14}C uptake by rhizoids of submerged mosses or liverworts. The absence of a significant supply of inorganic carbon through the rhizoids from the sediment is not surprising since there is a net efflux of CO\textsubscript{2} from the respiring rhizoids. However, the high CO\textsubscript{2} concentration in the sediment means that the steady-state CO\textsubscript{2} concentration in the rhizoids is increased, so that CO\textsubscript{2} concentration in the streaming cytoplasm entering the shoots is significantly higher than that in the streaming cytoplasm moving from the shoots into the rhizoids of Chara. However, the small size of this flux to the shoot can be seen from the \textsuperscript{14}C labelling studies of \cite{Andrews1984}, and there is a large net CO\textsubscript{2} efflux from the rhizoids, the higher CO\textsubscript{2} in the medium around the rhizoid meaning a corresponding increase in steady-state internal CO\textsubscript{2} if the CO\textsubscript{2} efflux is to equal the CO\textsubscript{2} production. Analogous arguments apply to O\textsubscript{2} transfer through rhizoids from the oxygenated shoot to the lower O\textsubscript{2} concentration in the rhizoids and sediment. These arguments mean that it is most unlikely that there is a net movement of CO\textsubscript{2} from the rhizoid to the shoot or of O\textsubscript{2} from shoot to rhizoid; respiration in rhizoids using organic carbon from the shoot predominates. There are no intercellular gas spaces in the Charophyceae so gas phase diffusion of CO\textsubscript{2} and O\textsubscript{2} through the thallus cannot occur. \cite{JonesDolan2012} point out that there was little direct evidence on nutrient uptake by bryophyte rhizoids; as indicated above, there is no evidence on CO\textsubscript{2} uptake by these bryophyte rhizoids.

These sediment-derived CO\textsubscript{2} inputs to freshwaters, and outputs from them by flow-through, are moderated by metabolism by photolithotrophs, including mosses functioning as haptothyes (rhizoids adherent to stones and rocks) or, much less commonly, rhizophytes (rhizoids ramifying in fine-grained sediments) in the water body, and by CO\textsubscript{2} exchange with the atmosphere. Interactions of these sources and sinks for CO\textsubscript{2} are reflected by periods of CO\textsubscript{2} well above air-equilibrium in the epilimnion of lakes through most of the year but with drawdown to well below air equilibrium at times of the year when phytoplankton productivity is highest \citep{Maberly1996}. The CO\textsubscript{2} availability to the shoots of freshwater rhizophytic (i.e. not the haptothptic Podostemaceae; \cite{Raven1981}) submerged tracheophytes can be higher near the sediment surface. Mosses (and liverworts) can, like some benthic macroalgae, live deeper in the water column than tracheophytes i.e. not deeper than 10 m, the depth limit of freshwater tracheophytes at sea level. Laboratory experiments show that this limit for freshwater tracheophytes is not determined by the inability to withstand more than 0.2 MPa total pressure \citep{Dale1984} and so the depth limit must be related to some other factor, such as light penetration. However, there is not necessarily a higher concentration of CO\textsubscript{2} at the sediment surface deeper in the water column than on nearer-surface sediments, although obviously the deep-water bryophytes must be able to gain sufficient CO\textsubscript{2} to explain the observed growth rates. A rare input of CO\textsubscript{2} to deep water in lakes is through geothermal activity, supporting the growth of the moss Fontinalis \citep{Lovalvo2010}. Some freshwaters and wetland habitats in industrialised areas and those with intensive animal production are, or
were, acidifying through anthropogenic atmospheric inputs. These inputs are of SO$_2$ from fossil fuel combustion, of NH$_3$ from low temperature combustion of fossil fuels and from intensive animal husbandry, of NO$_x$ from high-temperature fossil fuel combustion, and of NH$_4$/NH$_4^+$ from low temperature combustion of fossil fuels and from intensive animal husbandry, the latter producing H$^+$ after nitrification to NO$_3^-$; there are also effects from eutrophication (Roelefs, 1983; Roelefs et al., 1984; Beltmans et al., 2001). This increases the CO$_2$ concentration, as a fraction of total inorganic carbon and in absolute terms, and leads to an increased significance of bryophytes, e.g. Polytricum, Riccia and Sphagnum, among the macrophytes (Roelefs, 1983; Roelefs et al., 1984; Beltmans et al., 2001). Some of these effects can be reversed by liming, which increases total and carbonate alkalinity, increasing the pH and the HCO$_3^-$:CO$_2$ ratio (Roelefs, 1983; Roelefs et al., 1984; Beltmans et al., 2001). Increasing atmospheric CO$_2$ has a global influence in increasing both CO$_2$ concentration and CO$_2$:HCO$_3^-$ ratio in freshwater bodies through dissolution from the atmosphere in water bodies with relatively less catchment influence, often increasing CO$_2$ input to the water body (Maberly et al., 2013). These effects might also be expected to favour aquatic bryophytes over those tracheophytes that use HCO$_3^-$.

For rhizophytic submerged tracheophytes, inorganic $^{14}$C supply to the roots generally show very small inputs of inorganic carbon to the shoots relative to the photosynthetic capacity of the shoot (see Raven et al., 1988). Here the pathways for any such axial CO$_2$ transport within the plant include intercellular gas spaces that are involved in O$_2$ supply to root respiration, and in rhizosphere oxygenation, and the xylem although the speed of movement and hence the flux are small for submerged plants (see Raven, 1984). A major exception to the generalisation of a minimal role for roots in CO$_2$ supply to shoots of submerged aquatics (but see also Winkel and Borum, 2009) is plants of the isoeid life form. Plants of the isoeid life form are not invariably aquatic, e.g. those Isoetes spp. that are amphibious. Consideration here is limited to those isoeids that typically grow fully submerged and, if amphibious with some leaf portions emergent above water retain submerged characteristics of no functional stomata in their leaf epidermes (Raven et al., 1988; Keeley, 1998). Almost all of the inorganic carbon used in photosynthesis enters as CO$_2$ through the roots and leaf bases buried in sediments (based on the very limited data on inorganic C entry in non-photosynthetic parts of tracheophytes: Johnson and Rayle, 1976), supplied from the high CO$_2$ concentrations produced by mineralisation in the sediment, with very little entering through the heavily cuticularised photosynthetic part of the leaf (Raven et al., 1988; Keeley, 1998; Maberly and Madsen, 2002; Pedersen et al., 2011a, b). This major role in CO$_2$ uptake for roots, and chlorophyll-free, less-cuticularised, leaf bases situated in sediments, is independent of whether the isoeids use C$_3$ or CAM photosynthesis (Raven et al., 1988; Maberly and Madsen, 2002; Keeley, 1998, 2014). The roots of these isoeids are also the main sites of exit from the plant body of O$_2$ produced by photosynthesis in the leaves (Raven et al., 1988; Maberly and Madsen, 2002; Keeley, 1998, 2014), with losses also presumably from the less-cuticularised leaf bases to the surrounding sediment; this internal diffusion of O$_2$ from shoots to roots and radial O$_2$ loss to the rhizosphere influences root functioning and sediment biogeochemistry (e.g. Armstrong, 1979).

Conclusions

Mosses are among the earliest branching embryophytes, originating before the tracheophytes. They probably originated not later than the early Ordovician when atmospheric CO$_2$ was higher and O$_2$ was lower than is the case today.

The C$_3$ biochemistry and physiology of their photosynthesis suggests, by analogy with the effects of free-air carbon enrichment experiments on C$_3$ tracheophytes, that growth of extant bryophytes in high CO$_2$ approximating Ordovician values would increase their growth rate. Such an increased growth rate has been shown for many mosses, including Physcomitrella patens in suspension culture, although in some work on mosses grown on substrates with increased CO$_2$ in the surrounding air, the elevated CO$_2$ either had no effect on the growth rate or decreased the growth rate.

The work of Shinde et al. (2015) provides transcriptomic data on P. patens grown at high CO$_2$ and present-day CO$_2$, in each case with either present-day O$_2$ or decreased O$_2$. Acclimation to elevated CO$_2$ of photosynthetic biochemistry is expected to occur in mosses, as has been documented for terrestrial C$_3$ tracheophytes, including down-regulation of Rubisco with long-term exposure to high CO$_2$ while still allowing higher photosynthetic rates than under present-day atmospheric CO$_2$, and with reduced photorespiration owing to increased CO$_2$:O$_2$ at Rubisco. The results of Shinde et al. (2015) show down-regulation of the transcription of several genes related to photosynthesis, including those encoding Rubisco and light-harvesting apoproteins, in the high CO$_2$ treatments. Down-regulation of light harvesting contrasts with the increased growth rate at high CO$_2$ in P. patens in suspension culture, although a direct comparison with transcriptomic data is difficult since the growth conditions for the growth rate measurements were very different. It would be useful if transcriptomic (and proteomic and metabolomic) data comparing growth conditions are linked to measurements of growth rate and physiology on the same, or parallel, cultures.

Mosses have been subject to changes in bulk atmospheric CO$_2$ and O$_2$ through their evolution and there is limited evidence for positive selection of moss Rubisco. Extant mosses are subject to a large range of CO$_2$ and O$_2$ concentrations, especially in the water body in aquatic environments, and also in very close to the soil,which generates CO$_2$ and takes up O$_2$ by chemoorganotrophy in both aquatic and terrestrial environments. The extent of variation from the present atmospheric concentrations of CO$_2$ and O$_2$ in the microenvironment of mosses and its implications for their functioning, needs more investigation.
Supplementary data

Supplementary data is available at JXB online.

Data S1. Pathway of photosynthetic inorganic carbon assimilation in mosses.

Acknowledgements

Discussions with David Beering, Richard Clymo, Jeff Duckett, Dianne Edwards, Howard Griffiths, David Hanson, Jon Keeley, Stephen Maberly, Geoff MacFarlane, Barry Osmond, Michael Proctor and Steven Rice were very helpful. The comments of two anonymous reviewers have been very helpful in improving the paper. The University of Dundee is a registered Scottish charity No SC015906.

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