Chapter 1

What Can We Learn From Bryophyte Photosynthesis?

David T. Hanson*
Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

Steven K. Rice
Department of Biological Sciences, Union College, Schenectady, NY 12308, USA

Summary

Bryophytes have been evolving in terrestrial and aquatic environments longer than any other group of land plants, surviving and thriving through an incredible range of climatic and environmental variation. Several of the bryophyte growth forms we find today closely resemble those found in ancient fossils whereas many of the other early land plant forms lack modern representatives. What is it about bryophyte growth form and physiology that has allowed them to persist through time and radiate into every terrestrial ecosystem, even dominating some of them? What can we learn from modern bryophytes to address this question and to predict how plants will respond to future environmental change? In this chapter, we briefly examine these questions as a preview to the volume as a whole.

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*Author for correspondence, e-mail: dthanson@unm.edu

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I. Introduction

Bryophytes have barely been tapped as a resource for understanding photosynthesis and respiration on land despite the fact that the bryophyte life form has achieved ecological success in varied environments that span every continent, occur across dramatic gradients of temperature and water availability and were present at the early stages of the transition from aquatic habitats to land, potentially as early as the Cambrian (see Chaps. 2 and 3). Critical aspects of life cycle evolution were involved in adapting bryophyte ancestors to life on land (e.g., protection of the embryo in protective maternal tissue, elaboration of two distinct multicellular stages specialized for different functions), but the colonization of land also required structural and physiological adaptations to succeed in habitats with high solar radiation, a drying atmosphere, high temperature fluctuations, and limited access to dissolved nutrients (Chaps. 4 and 7).

Although the primary architecture of the photosynthetic machinery was conserved from their algal ancestors, early land plants, as with contemporary bryophytes, likely facilitated carbon capture over short and long temporal scales in several ways. These include the reduction of external water films on leaf surfaces, which impede diffusion of carbon dioxide, the evolution of ventilated thalli or leaf structures, and the evolution of carbon concentrating mechanisms. In addition, they evolved desiccation tolerance, which allowed plants to equilibrate with a drying atmosphere and retain metabolic function upon rehydration along with adaptations to achieve positive carbon balance during wet—dry cycles. Bryophyte population and community structure also indirectly influences photosynthesis through alteration of canopy boundary layers and, thereby, retention of water and soil respired CO_2. The multiple scales over which bryophyte photosynthesis is measured (shoot, canopy, community) also raises the question of what is a functional photosynthetic unit in bryophytes, i.e. what can be treated as an analogue to the vascular plant leaf (Chaps. 5 and 9)? The amazing variation in form and function and the diverse range of micro-habitats that bryophytes occupy makes them an ideal, yet rarely utilized, system for studying the role of photosynthesis and respiration in the adaptive radiation of plants.

II. Terrestrialization

Terrestrialization is the adaptive radiation of aquatic organisms onto land. The organisms we consider here are grouped by function rather than by phylogeny. Interestingly, despite the existence of all major lineages of aquatic photosynthetic organisms, from cyanobacteria to green algae, being present when terrestrial photosynthetic organisms were becoming wide-spread, only one small corner of that aquatic diversity came to dominate land. For roughly the last 500 million years, descendants of Charophycean green algae, collectively called embryophytes, or land plants, have adaptively radiated onto land with greater success than any other lineage. Thus, the story of terrestrialization by photosynthetic organisms has been effectively limited to a single lineage. Bryophytes are at the base of this lineage, and in this volume we examine what features of bryophyte photosynthesis may have allowed them to be so successful.

A. Photosynthesis on Land

Despite their current dominance of terrestrial environments, land plants (embryophytes) are one of several groups of photosynthetic organisms that have terrestrial representatives. It is likely that cyanobacteria, many varieties of algae, and even lichens colonized land before or concurrently with land plants and each of these groups have extant terrestrial representatives

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Abbreviation: Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase

(Chaps. 2 and 3). Therefore, traits that allow persistence of photosynthetic organisms on land must be common to all these groups and be much broader than traits that allow photosynthetic organisms to thrive and compete successfully on land. Having low enough resistance to diffusion of CO_2 to provide adequate supply to the chloroplast interior and a mechanism for either maintaining water balance or dealing with the consequences of desiccation, seem to be the most basic criteria. Combining these traits with nutrient acquisition, photoprotection, thermotolerance and additions to C_3 biochemistry that improve CO_2 capture may be the adaptations that led to successful radiation into many habitats. These interactions among photosynthesis, phylogeny, climate, micro-habitat, and morphology clearly played important roles in generating the current situation where only the embryophyte lineage dominates land.

B. Tiny but Tenacious

So what is it about bryophytes that allowed them to succeed on land relative to other early photosynthetic organisms and that allows them to dominate the flora at high altitudes and latitudes today? The latter is much easier to answer as we can study extant organisms and their response to environmental conditions; however there are some intriguing patterns in fossil data that suggest the importance of scale to the organism's water and carbon economy. In Chap. 4, the author suggests that the successful photosynthetic organisms on land today are either small (<10 cm) and poikilohydric, or large (>10 cm) and homiohydric with few exceptions. Thus early bryophytes may have capitalized on their tiny size and the tenacious strategy afforded by poikilohydry, where harsh conditions are essentially avoided through desiccation-induced dormancy. This foothold could have then set the stage for evolution of the embryophyte lineage into the large, homiohydric strategy that works so well in less harsh environments.

C. Making Inferences from Extant Organisms

What made bryophytes more tenacious than other small early terrestrial photosynthetic organisms, leading to their ultimate success? Some of the other organisms, such as lichens, are also very tolerant of life on land but have been less successful. The answer to what features allowed the success of embryophytes over other lineages is probably unknowable as many of the early lineages have no extant relatives and there is a fairly poor fossil record. Perhaps the combination of multicellularity, protected sexual reproduction, and desiccation tolerance were the key for surviving through dramatic climate changes, or maybe UV and thermotolerance were essential. These speculations bring up three critical issues that affect our interpretation of historical events and we need to keep in mind that the farther back in time we go, the larger these issues become.

First, extant organisms are the product of evolution through time. We can observe the physiological properties of these organisms and can make predictions of the age of a lineage and the large-scale climate changes that occurred through that time range. However, evolution through natural selection occurs in response to local competition and local habitats acting on populations of individuals. When local conditions follow the larger-scale patterns, then our predictions are more meaningful, the problem is that we have no way of knowing when the large and small scale conditions align. Even for time periods and localities where we have a high degree of confidence about the environment and ecosystem, we still do not know the ancestral physiology.

Second, inferring ancestral physiology from phylogeny and comparative physiology of extant organisms is inherently problematic. Unlike gross morphology, there is very little information in the fossil record that informs us about photosynthetic physiology. Stable isotopes, chemistry, biophysics and in some cases even anatomy can put some reasonable bounds on physiology assuming that the physiology of the ancient organism falls within the realm of known organism function. However, there is another fundamental issue, that of phylogeny itself. We are working from the tips of a tree to infer what organisms are at the base and how they branch. Even if we assume that we get the branching order correct, we do not have information about the evolutionary patterns along each branch so we do not know the physiological properties of a common ancestor between two groups. Also, fossils that could represent common ancestors or extinct lineages are highly variable, with older ones generally lacking DNA and often lacking much internal structure. As the number of characters decrease, our ability to even assess their relationships to extant plants becomes more difficult.

Third, historical data are inherently sparse as we only have material that was preserved, found, and analyzed. Molecular clock data help us predict what should have existed in the past in terms of ancestors of extant organisms, but that does not predict what other organisms might have existed and gone extinct. To quote Donald Rumsfeld (Feb. 12, 2002, Department of Defense news briefing), “As we know, there are known knowns. There are things we know we know. We also know there are known unknowns. That is to say we know there are some things we do not know. But there are also unknown unknowns, the ones we don’t know we don’t know.”

Despite the uncertainties and problems with making past inferences, it is very important that we try because these inferences provide a platform for predicting plant responses to future climate change and environmental perturbations. In addition, understanding how plants have adapted to various environments gives us clues to the metabolic potential that exists in plants and how it could be tapped for agriculture, restoration of damaged ecosystems, and other uses. In the case of predicting future responses, we have the starting organisms to work with. Thus, we can test if these organisms can survive predicted past and future climates through plasticity. We can also initiate long-term selection experiments and track critical ecosystem responses using historical data to generate theory and inform experimental design. In the end, only tracking changes through time will truly show how plants evolve and adapt to life on land.

III. Biochemical and Cellular Biology

As extant representatives of the earliest land plants, modern bryophytes have an interesting mix of algal and seed plant features that are evident in their biochemistry and cellular biology. However, we have only scratched the surface of the potential diversity possessed by this group of organisms. The likelihood for discovering novel pathways and mechanisms for cellular function is high as bryophytes are not simply a mixture of algal and seed plant biology. The combination of pathways from algae and seed plants is itself unique and almost certainly requires novel mechanisms to maintain cell function. In addition, the long lineage of bryophytes has provided ample time and environmental variation to allow large divergences to have evolved from the common ancestors of bryophytes and other plants.

A. Are Bryophytes C_3?

To answer this, we have to first be clear what is meant by this deceptively simple question. Confusion often arises because the two well-known CO_2 concentrating mechanisms in plants, CAM and C_4, both initially form a stable four-carbon compound that is subsequently decarboxylated for fixation through the Calvin-Benson-Bassham cycle. Therefore, CAM and C_4, which initially fix CO_2 into a four-carbon intermediate, are seen as having biochemical add-ons to the C_3 pathway. However, in algae and cyanobacteria, it is common to have a CO_2 concentrating mechanism without the formation of a four-carbon intermediate. In these instances, the photosynthetic pathway is only C_3, while the function of CO_2 concentration is provided through the pumping of CO_2 and bicarbonate into the cell along with locating carbonic anhydrase where it can facilitate CO_2 diffusion and availability for ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco).

To date, there is no clear evidence for C_4 metabolism in bryophytes despite a few attempts to find it (Chap. 12). In light of recent work identifying single-cell C_4 metabolism in seed plants and in some algae, a more concerted effort may be warranted. It is not clear if a common property of bryophyte biology, such as desiccation tolerance and the effects it has on cell structure, has constrained the evolution of single-cell C_4 metabolism. Currently, it appears that a few bryophytes have developed CO_2 concentrating mechanisms more like those in algae, with adaptations that control localization of carbonic anhydrase, utilize bicarbonate, and form pyrenoids (Chaps. 2, 6, and 12). It is also possible that the high CO_2 from respiration found in the soil boundary layer (Chap. 13) significantly reduces the benefits of investing in a CO_2 concentrating mechanism, and potentially even a role for mixotrophy assisting with positive carbon balance (Chap. 2).

B. The Terrestrial Pyrenoid: Unique Among Plants

The pyrenoid is a structure within the chloroplast, primarily composed of Rubisco and dissected by thylakoid membranes. The presence of a pyrenoid has been correlated with CO_2 concentrating mechanism function in algae and hornworts (Chap. 6), and is thought to function as a location where bicarbonate can be transported and subsequently converted into CO_2. This process elevates CO_2 around Rubisco, and disruption of the pyrenoid slows the rate of photosynthesis at ambient levels of CO_2. Interestingly, pyrenoids are common and wide-spread among algae but nearly absent in plants. Hornworts are the only group of land plants that contain pyrenoids, but the reason for this is not clear as pyrenoids have evolved and been lost multiple times in both algae and hornworts (Chap. 6). Recent discoveries regarding the role of the Rubisco small subunit in the formation of pyrenoids is spurring research into expressing them in seed plants to improve photosynthesis. However, there may be unique properties of hornworts, such as few, very large chloroplasts per cell, that may be necessary for the pyrenoid to properly function and it will be imperative to resolve such questions in the near future.

C. Drying Without Dying

A defining, though far from ubiquitous, property of bryophytes is their ability to tolerate desiccation (drying to equilibrium with air) and rapidly recover net positive photosynthesis in a matter of minutes (Chaps. 4 and 16). This is associated with expression of proteins important for managing both dehydration and re-hydration (dehydrins and re-hydrins, respectively). As one might expect, there is also a respiratory burst associated with repair that contributes to the overall carbon balance of the plant. This rapid recovery is essential for maximizing carbon uptake in the good times where water content is high enough for optimal cellular function, but not so high that diffusion of CO_2 is severely limited. Both plant form and community/canopy structure contribute significantly to the balance of water and carbon, making moss photosynthesis more structurally complex than higher plants over small scales, i.e. what one typically places in a measurement chamber (Chaps. 5, 10, and 13).

D. Tolerating Light

Managing high light is essential for the adaptive radiation of plants onto land and remains a major issue in many open habitats dominated by bryophytes today. The combination of cold and high light in polar and alpine regions and in peatlands (Chaps. 7, 13, 15, and 17) and the drying and re-hydrating in high light and often hot environments (Chap. 16) present some of the greatest challenges for a photosynthetic organism. Some tolerance of high light can be accomplished through simple, rapid avoidance mechanism such as chloroplast movements (Chap. 8), production of UV absorbing compounds (Chap. 7), and longer-term dormancy through desiccation. However, bryophytes also have the land plant style xanthophyll cycle for dissipating excess light energy and algal-derived methods for dissipating heat (Chap. 7). In addition, most bryophytes lack multi-cell layer leaves so photoprotection mechanisms need to be active in all cells. Also, the combination of stresses experienced by bryophytes has likely led to the evolution of novel physiological mechanisms that we have yet to discover.

E. Bryophyte Genomics

The genomic era is upon us and bryophyte research is both leading and lagging. The genomic sequence of *Physcomitrella patens* was the first non-seed land plant to have its genome sequenced, and it can be transformed via homologous recombination as easily as yeast (see Chap. 11). Despite this remarkable toolbox for understanding fundamental properties of photosynthesis, this system has only been capitalized upon by developmental biologists. This presents an opportunity for readers of this volume as there is so much basic knowledge to be gained by applying the *P. patens* system to study photosynthesis and respiration.

IV. Organization of the Bryophyte Photosynthetic System

All bryophytes evaluated thus far utilize the Calvin-Benson-Bassham cycle, yet given their small stature that restricts their ability to maintain constant cellular water, their extra-cellular water pools that limit diffusion of carbon dioxide and their high rates of dark respiration relative to photosynthesis, achieving a positive carbon balance presents unique challenges. In order to do so, bryophytes have evolved physiological traits across multiple scales from biochemical through canopy-level that have allowed them to succeed ecologically in many habitats not suitable to other land plants.

Leafy bryophytes are organized hierarchically with leaves (i.e., phyllids), shoots or shoot systems (i.e., canopies) serving as the principal unit of gas exchange or light acquisition, depending on the species (Chaps. 5, 9 and 10). In shoots with large, well-spaced leaves as in the Polytrichaceae or Mniaceae and also in some aquatic species (e.g., *Fontinalis antipyretica*, *Sphagnum macrophyllum*), leaves may function individually enough to be considered appropriate photosynthetic units and are satisfactorily large enough to measure some physiological activity. At this scale, there has been much interest in understanding the physiological significance of leaf modifications like hair points (reduce rates of evaporation and affect carbon balance), papillae (enhance diffusion of carbon dioxide to chloroplasts contained within them), lamella (enhance photosynthetic leaf area and allow diffusion of carbon dioxide in gas phase) and leaf shape (long linear leaves enhance CO_2 uptake in aquatic species), and more recently comparative studies suggest that allocation to features like leaf costa or water storage cells present trade-offs in terms of carbon balance with rates of net photosynthesis (Chaps. 5 and 12).

However, even in species with large, well-spaced leaves, shoot system organization affects total leaf area, boundary layer properties that control water flux, microclimate, plant water status and light intensity and quality at the shoot surface, and thereby influences carbon dynamics of individual shoots as well as whole canopies. Consequently, in bryophytes, shoot-systems (i.e., the canopy) are normally considered the primary unit in studies of function (Chaps. 5, 9 and 10). Within the canopy, light gradients can be quite steep with light attenuating to levels below the light compensation point within the first few centimeters, although canopies with less dense shoot arrangements have thicker active canopies (Chap. 9). The branching structure of the canopy also influences canopy light interception. In some pleurocarpous species like *Pleurozium schreberi*, new branches can form from buds within the canopy interior and take advantage of light if it is available, although it is not known if these are acclimated to low light, thereby optimizing whole-canopy photosynthetic rates (Chap. 9). Newly developed imaging techniques that measure physiological states based on thermal emission, spectral reflectance or fluorescence analyses can be used to evaluate variation in physiological activity across and within bryophytes canopies (Chaps. 9 and 10) and present exciting opportunities to understand how processes are integrated in two- and, even, three-dimensions within the canopy. At ecosystem scales, eddy covariance methods allow estimates of carbon and water fluxes, which allows linkage of small-scale physiological processes with large and long-term patterns of photosynthesis and respiration (Chap. 14).

V. Ecophysiology of Bryophyte Photosynthesis: Adapting to Environmental Stress

In habitats ranging from Antarctic pavements to boreal forests, arid temperate crusts and tropical ecosystems, the photosynthetic performance of bryophytes is dictated by achieving positive carbon balance over wet—dry cycles (Chaps. 13, 14, 15, 16 and 17) within the context of diverse stresses that vary among environments. Given the poikilohydric nature of their water relations, bryophyte carbon dynamics are affected by the respiratory demands of desiccation and rehydration as well as by the photosynthetic performance of active tissues when hydrated. The relative importance of environmental stresses varies from habitat to habitat mostly along gradients of radiation exposure, the intensity and duration of desiccation stress, and temperature, the latter of which has asymmetrical effects on respiration and photosynthesis (Chap. 15).

In habitats that cannot support a full cover of vascular plants, bryophytes can occupy openings and be subject to visible light intensities great enough to cause photodamage as well as exposure to high energy UV-B radiation (Chap. 7), which may alter DNA structure. Although many bryophytes possess mechanisms to dissipate excess energy once it is absorbed in photosystems, others also reduce radiation levels at the chloroplast by manufacturing cell wall pigments (Chaps. 7, 15 and 17) or by cellular mechanisms like chloroplast movement (Chap. 8) avoiding photodamage rather than tolerating its effects. In high latitude environments, plants are subject low solar angles minimizing the potential for photodamage from visible light, but are exposed to increased UV-B and bryophytes appear to possess mechanisms to avoid damage from the latter. When subject to elevated levels of UV-B light, bryophytes increase concentrations of photoprotective pigments and photosynthetic activity is often unaffected (Chap. 17). In boreal peatlands, light intensities are higher and species do not avoid light stress as they often maintain hydration during exposure to high light intensities. In these systems, *Sphagnum* species may dissipate excess absorbed light energy using photorespiration, which reduces net rates of photosynthesis and production and by energy-dependent quenching mechanisms, in addition to producing cell wall pigments that reduce light levels at the chloroplast (Chap. 13). Species of dryland environments escape potential damaging effects of high light by tolerating exposure in a desiccated state, which alters shoot structure and shades chlorophyll from high light. When hydrated, dryland species also possess photoprotective and energy dissipating mechanisms (Chap. 16) as found in more mesic species described above.

VI. Conclusion

In this volume, we have brought together experts on bryophyte photosynthesis that focus on scales that range from biochemistry to whole ecosystem with those interested in physiological issues associated with the early terrestrialization by plants. We hope that these diverse perspectives provide the reader with a context to better understand the significance of the bryophyte functional syndrome in the past and in the present, how this understanding may direct biotechnological solutions to crop improvements, and to help predict responses of land plants to climate change scenarios.

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