

CHAPTER 12

PRODUCTIVITY

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CHAPTER 12

PRODUCTIVITY



Figure 1. *Pohlia wahlenbergii* var. *glacialis*, a wetland moss that is among the more productive of the acrocarpous mosses. Photo by Michael Lüth, with permission.

Productivity

It is within the framework of productivity that bryophytes are often considered unimportant as components of the ecosystem. As Martin and Adamson (2001) have pointed out, the photosynthetic capacity of mosses is generally considered to be much lower than that of the tracheophytes. However, they contend that this may be a misleading conclusion based on the method of calculating rates of net CO₂ uptake. Rather, they demonstrate that when productivity of bryophytes is calculated on the basis of chlorophyll, differences in rate disappear. It is only when dry mass is used to calculate productivity that bryophytes appear to have a much lower productivity rate than that of tracheophytes. And this depends on whether the senescent portions are included in the calculations.

Ecological Factors

Ability to Invade

There are so many ways in which to measure productivity that one must be careful to consider the purpose for which it is being measured. If it is measured to determine how soon it will grow enough to overtake the pebble path through the garden, a consideration of the linear growth of the stem pointed in that direction is most relevant. But if it is to determine what that particular species is capable of doing, in its own right, we would look at it quite differently, most likely at its biomass gain or CO₂ fixed on an hourly or annual basis. And if we want to know how soon it will fill in as ground cover, we need to know its lateral growth – the growth of its branches as well as its main stem. But it is even more complex than that.

New plants could arise from gemmae or fragments, requiring yet other measurements.

These measures are not easily convertible. For example, Gerdol (1996) expressed the linear growth of *Sphagnum magellanicum* (Figure 2) as 28-31 mm during the growing season, giving a sense of its ability to add to the depth of the peatland. Its dry matter production, however, was 12-13 mg per plant, giving us less of a mental picture of what effect it has on the ecosystem appearance. Does this latter measure reflect new capitula? How much has it increased the mat vertically? Despite these questions, for a peatland harvester, the biomass increase is of more value than the height of the plant.



Figure 2. *Sphagnum magellanicum*, a major peat accumulator. Photo by Michael Lüth, with permission.

Niche Differences

Conditions that favor one species of bryophyte may be detrimental to another. This permits the slow-growing bryophytes to co-exist for a long time, with one species, in this case *Pleurozium schreberi* (Figure 3), advancing more in one year and the other, *Dicranum polysetum* (Figure 4), advancing more in another (Zhang 1998). Arscott *et al.* (2000) demonstrated this with their 13-year experiment in two Arctic streams. An increase in phosphorus caused little difference in the clump-forming *Schistidium agassizii* (Figure 5), whereas the formerly rare mat-forming species of *Hygrohypnum* (Figure 6) increased rapidly. Furthermore, *Hygrohypnum* species had greater tolerance to elevated temperatures ($>20^{\circ}\text{C}$) than did *S. agassizii*, whereas the latter recovered easily from desiccation, while *Hygrohypnum* was susceptible to damage.



Figure 3. *Pleurozium schreberi*, a slow-growing forest floor species. Photo by Janice Glime.



Figure 4. *Dicranum polysetum*, a slow-growing species that competes with *Pleurozium schreberi* (Figure 3). Photo by Michael Lüth, with permission.



Figure 5. *Schistidium agassizii* forming clumps. Photo by Michael Lüth, with permission.



Figure 6. *Hygrohypnum ochraceum* forming mats. Photo by Michael Lüth, with permission.

Growth

Growth is one measure of productivity, but it has two components: **biomass gain** and **increase in length** (including branches). As Schwinning (1993) pointed out, unequal growth rates within a species can result from environmental and other factors independent of the productivity. She attributed these unequal rates to genetic differences, site differences, and competition (both intra- and interspecies).

Growth Measurements

Growth measurement is never easy in a non-linear subject such as a pleurocarpous moss. For example, several authors (Rincon & Grime 1989; Zechmeister 1995; Stark *et al.* 2001) have concluded that measuring stem elongation only may provide an inaccurate picture of true productivity. In fact, biomass accumulation and shoot elongation are uncoupled events and biomass is a better predictor of productivity than is elongation (Stark 2002). As a result, the methods used for measuring bryophyte growth are varied, each having its own purpose for a particular growth habit.

In larger, perennial mosses it is possible to determine growth because the plant provides natural markers (**innate** markers of Russell 1988; Figure 7). In their seminal papers on phenology of bryophytes, Longton and Greene (1969a, b) estimated annual growth rates using attached cotton markers to measure each stem, measuring distances between innate markers (inflorescence position), and measuring the length of the green apical portion of the stem. Hagerup (1935) used the alternating leaf sizes of taxa such as *Ceratodon purpureus* (Figure 8) to measure annual growth.

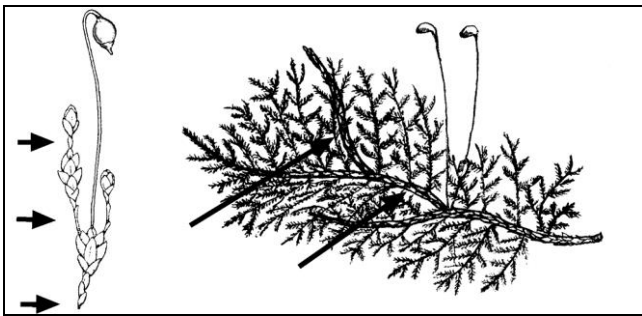


Figure 7. **Left:** Alternating regions of large and small leaves illustrating natural markers of growth on a species of *Bryum*, based on Hagerup (1935). **Right:** *Hylocomium splendens* – arrows indicate region markers for a new season of growth. Drawings by Margaret Minahan.



Figure 8. *Ceratodon purpureus*, a species with reduced leaf sizes marking the annual growth. Photo by Michael Lüth, with permission.

In others, such as *Philonotis fontana* (Figure 9) and *Aulacomnium palustre* (Figure 10), **innovations** (new

branches just below the apex) often mark new growth, but the first leaves of new growth also cause a constriction compared to the smaller (or larger) leaves ending the previous growing season. In other taxa, there is a wider spacing of the leaves at the beginning of each new season, again causing a clear demarcation between years.



Figure 9. *Philonotis calcarea* showing multiple innovations just beneath the antheridial splash cup. Photo by Michael Lüth, with permission.



Figure 10. *Aulacomnium palustre* showing the branches near the tip. Photo by Kristian Peters through Creative Commons.

In males of **Polytrichaceae** (Figure 11, Figure 13) and others, new growth can arise from a splash cup so that one can trace back through a series of splash cups to measure growth (Figure 11). These various interruptions are useful in many of the acrocarpous moss taxa and at least some leafy liverworts. In pleurocarpous taxa, a new set of branches may arise, providing a marker, as is most exquisitely exhibited in the stair-step moss, *Hylocomium splendens* (Figure 7, Figure 12). But these markers tell us only the total growth for the year, and not the season of growth, and in many pleurocarpous mosses, more than one set of branches can arise in a single year, as in *Fontinalis* (Figure 14) (Glime 1982).



Figure 11. *Polytrichastrum* showing new growth from splash cups (arrows). Photo by Michael Lüth, with permission.



Figure 12. *Hylocomium splendens*, showing annual branching. Photo by Amadej Trnkoczy through Creative Commons.

Changes in color can demarcate the growth of the current season, but these are difficult to discern for more than one year (Figure 13).



Figure 13. *Polytrichum commune* showing change in color from dark green to light green where the current year's growth begins. Photo by Michael Lüth, with permission.

Hawes *et al.* (2002) determined the ages of mosses in a lake bed of the Canadian High Arctic by using annual **growth bands**. These bands were 10-30 mm in length and were apparent due to changes in leaf density and size. The most recent growth provided four – five bands with

recognizable leaves and measurable concentrations of chlorophyll *a*. Another twelve bands were recognizable from leaf scars. However, their attempt to correlate effects of ice cover with growth in a given year failed, and they suggested that the relationship of ice cover to growth (and growth bands) was more complex.



Figure 14. *Fontinalis* showing branching. Photo by Andrew Spink <www.andrewspink.nl>, with permission.

Russell (1988) described eight methods for measuring growth (Figure 15), including innate markers. The **cranked wire** technique is commonly employed for *Sphagnum* (Figure 2), but suffers from the problem of compaction of the mat, particularly as a result of snow, thus underestimating growth, particularly for more than one year. **Tags** can be used to mark a specific point on the moss from which future measurements are taken, but one must be careful not to injure the stem or interfere with water movement. A modification of this method works well for *Fontinalis* (Figure 16) and other aquatics (Glime 1980, 1982); narrow strips of white velcro are placed around the stem as markers (Figure 16) (black velcro seems to have a toxic dye); for terrestrial mosses, the velcro may interfere with water transport, spacing, and drying.

Nets placed over the mosses (Figure 15) likewise provide a starting point for measurements but suffer problems similar to the compaction problems with the cranked wire, although generally it is the older parts that get compacted most. And these might also interfere with water movement, hence giving unnatural readings. **Vital stains** that are not water soluble can serve as markers, including fluorescent dyes and powders; these must be selected not to interfere with photosynthesis or alter nutrient concentrations. **Bags** constructed of nylon mesh can be used to mark a starting point, with an initial measurement of the protruding stems. Russell (1988) recommends cutting the stems to a known length and putting them in the bag, neatly arranged upright; note that this is a flat bag, and the growing tip should not be removed. Gremmen *et al.* (1975) and Russell (1984) used a **coring** method in which they cut horizontally through the

soil beneath the bryophytes, then spread small pieces of polystyrene pellets or other marker before replacing the moss, thus providing a marker from which to measure. This method could again suffer from compaction problems, depending on the species of bryophyte. **Photography** can give rates of advancement of a colony but cannot provide details of growth and provides only horizontal growth (cover), not vertical assessment. Similarly, sheets of clear plastic can be placed over the moss patch and outlines drawn for future comparison. Zhang (1998) used the latter method to show that location of moss patches on the forest floor is quite dynamic.

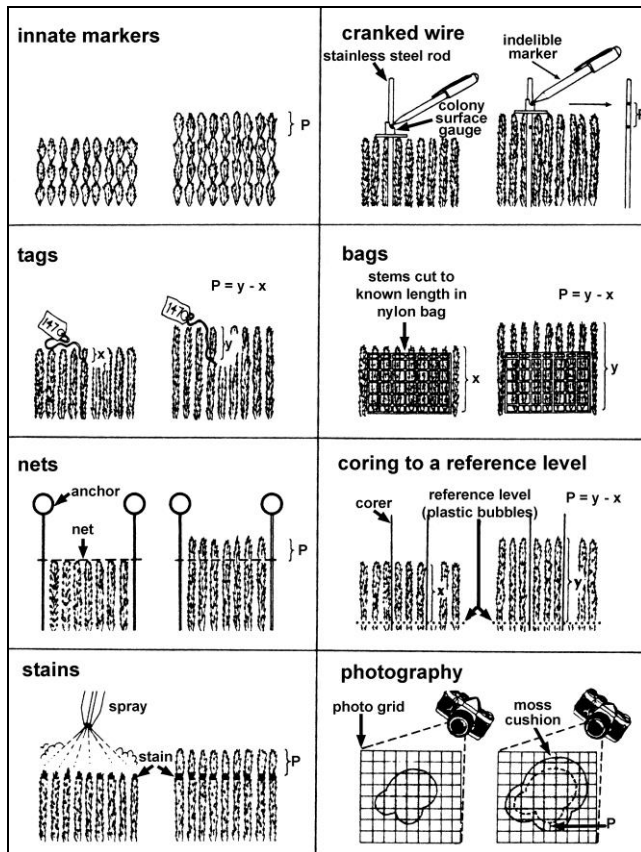


Figure 15. Methods usable for measuring bryophyte shoot extension growth. **Left** figure of each pair represents the starting condition and time; **right** figure represents end of measuring period. Modified from Russell 1988.



Figure 16. *Fontinalis novae-angliae* on velcro, permitting measurement of growth. Photo by Janice Glime.

Growth rates may include only the dominant stem, or the sum of all the branches as well. Smith (1982) found that the epiphytic *Isoetecium myosuroides* (Figure 17) in England never grew more than 16 mm per year. In an even drier habitat, on dry, exposed, granite ledges in northwestern Ontario, Vitt (1989) measured a yearly growth rate of 2.3-3.1 mm yr⁻¹ for *Racomitrium microcarpon* (Figure 18). Vitt (1990) also measured growth as lateral expansion of a clone. In clumps of *Pylaisia polyantha* (Figure 19) on the bases of poplars, the yearly increase was about 6-8 mm yr⁻¹.



Figure 17. *Isoetecium myosuroides* on tree. Photo by Michael Lüth, with permission.



Figure 18. *Racomitrium microcarpon*, a species of exposed granite ledges. Photo by Michael Lüth, with permission.



Figure 19. *Pylaisia polyantha* with young sporophytes. Photo by Michael Lüth, with permission.

Biomass measurements for living bryophytes are often meaningless because of their tremendous ability to sequester water, not only internally but also externally. Wet mass can be up to 20 times the dry mass of *Sphagnum* (Figure 2), making any wet mass measure meaningless for comparison purposes. Drying the moss, however, creates a new variable that necessarily terminates the experiment and may therefore not be practical. Furthermore, dry mosses can gain sufficient atmospheric moisture to show measurable mass gain during the short time required to weigh them (personal observation). In cases where light availability is the same for all members of a population, biomass and growth in length can be correlated and either might be chosen as a measure of productivity, depending on the goals of the study.

How does the growth occur within the plant and what are the sources of the needed resources? Bisang *et al.* (2008) investigated this question in *Pseudocalliergon trifarium* (Figure 20). This species has discrete annual segments. They found that growth in mass correlates with the segment mass of the previous two years. This relationship declines linearly for the older years. Hence, it appears that growth is limited by reallocation of resources.

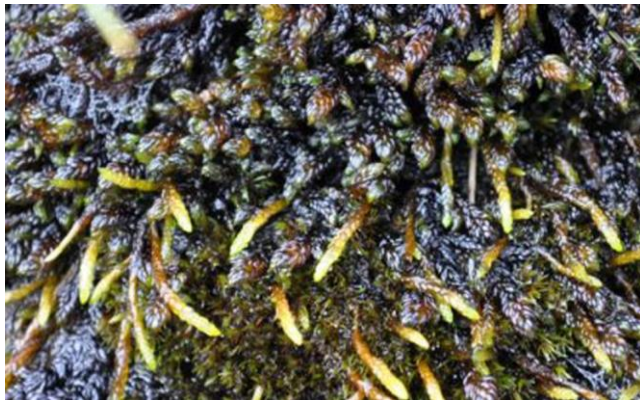


Figure 20. *Pseudocalliergon trifarium*, a species with discrete annual segments. Photo by Andrew Hodgson, with permission.



Figure 21. Annual growth marker of *Pseudocalliergon trifarium* showing end of a season of growth where leaves become smaller on left and remain small for new growth on right. Photo courtesy of Lars Hedenäs.

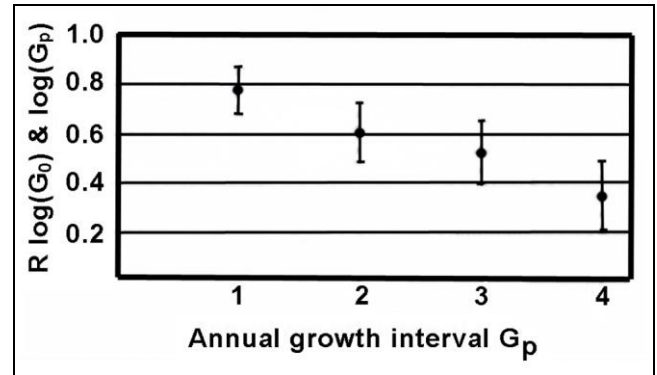


Figure 22. Pearson's Product Moment correlation coefficients R between the most recent growth interval (G_0) and consecutively older annual intervals, G_1 to G_4 . Shoots from 12 populations were pooled ($n=44$). Bars indicate ± 1 standard error of R . Data for biomass were log transformed prior to analyses. Redrawn from Bisang *et al.* 2008.

In *Bryum laevigatum*, growth bands are evident, marked by a dark brown color and smaller leaves (Rod Seppelt, Bryonet 16 February 2013). New growth exhibits light green, larger leaves. Rhizoids are often more prominent among the smaller leaves. Are these best referenced as growth bands, responsive to changes in the weather, or are they truly markers of annual increments?

Aquatic forms demonstrate markers that may be indicators of seasonal changes in water level, with cessation or near cessation of growth occurring when the water level is low in summer and they are stranded above water. These seasonal changes may be manifest as changes in leaf size or stem length or branching (Rod Seppelt, Bryonet 16 February 2013).

In Antarctica, *Bryum argenteum* (Figure 23) and *Ceratodon purpureus* (Figure 8) exhibit banding patterns (Rod Seppelt, Bryonet 16 February 2013). These may represent differences between the spring-summer growth and winter dormancy. The internode distance and hyaline leaf apex length differ between Antarctic populations of *B. argenteum* and those of Tasmania. Both produce clusters of branches.



Figure 23. *Bryum argenteum*, a species that exhibits banding patterns. Photo by Rui-Liang Zhu, with permission.

Annual Length Increase

Length increase is generally related to growth form, with acrocarpous mosses exhibiting slow rates of growth in length compared to pleurocarpous mosses (Table 1). The pleurocarpous taxa further increase their biomass by development of new branches, creating an exponential growth pattern. Among these pleurocarpous bryophytes, some can become very long and have high growth rates, with some *Fontinalis* (Figure 24) (Glime 1987b) and *Sphagnum* (Figure 2) species growing 400 mm in a season. *Taxiphyllum barbieri* (Figure 25; Java moss, often mistakenly called *Vesicularia dubyana*) can quickly fill a 50 gallon aquarium through extensive branching and length gain.



Figure 24. *Fontinalis antipyretica*, a genus that branches multiple times in a growing season. Photo by Michael Lüth, with permission.



Figure 25. *Taxiphyllum barbieri*, a fast-growing species in an aquarium. Photo by Buchling through Creative Commons.

On Signy Island in the Antarctic, the upright *Polytrichum strictum* (Figure 26) grows 2-5 mm, whereas at Pinawa, Manitoba it grows 15-55 mm per year, exhibiting differences due to microclimate and habitat (Longton 1974, 1979). Pitkin (1975) showed wide variation in growth of *Hypnum cupressiforme* (Figure 27), depending on its height on the tree trunk, with mm of growth at 30-100 cm above ground doubling that at 150-200 cm from 23 May to 6 October. Not surprisingly, growth of the upper side of a sloping trunk was more than double that on the lower side.



Figure 26. *Polytrichum strictum*, a species that has 10X as much growth in Manitoba compared to that on Signy Island. Photo by Sture Hermansson, through online permission.



Figure 27. *Hypnum cupressiforme*, a species whose growth varies with height on the tree trunk. Photo by Jan-Peter Frahm, with permission.

Table 1. Comparison of growth in length of various mosses from a variety of locations and habitats.

Species	mm yr ⁻¹	Location	Reference
<i>Forsstroemia trichomitria</i>	3.85-4.45	Virginia	Stark 1986
<i>Calliergon</i>	10-30	Arctic	Hawes <i>et al.</i> 2002
lake species	10	Canadian Arctic	Sand-Jensen <i>et al.</i> 1999
<i>Leucobryum glaucum</i>	9.1	S. England	Bates 1989
<i>Meesia triquetra</i>	3.7-14.8	Devon Island	Vitt & Pakarinen 1977
<i>Ptilidium pulcherrimum</i>	3.5-6.3	N. Sweden	Jonsson & Söderström 1988
<i>Sphagnum magellanicum</i>	28-31	S. Alps, Italy	Gerdol 1996
<i>Sphagnum papillosum</i>	33		Gaberscik & Martincic 1987
<i>Sphagnum</i> spp.	4-24	northern Quebec	Moore 1989
<i>Polytrichum strictum</i>	2-5	Antarctic	Longton 1979
<i>Polytrichum strictum</i>	15-55 ¹	Pinawa, Manitoba, Canada	Longton 1979
<i>Fontinalis duriae</i>	400 (incl branches)	N. Michigan	Glime 1987a
<i>Rhynchostegium riparioides</i>	33.4-73.3	streams, Northern Pennines, England	Kelly & Whitton 1987
<i>Racomitrium lanuginosum</i>	5.4-6.7	Marion Island	Russell 1984
<i>Racomitrium lanuginosum</i>	2.3	Mt Fuji	Nakatsubo 1990
<i>Racomitrium lanuginosum</i>	5-15	England	Tallis 1959, 1964
<i>Racomitrium microcarpon</i>	2.3-3.1	NW Ontario	Vitt 1989

Uncoupling

In bryophytes, as in some other plants, the increase in height/length may not be well correlated with increase in biomass. For example, in loblolly pine, branching becomes denser in low-density populations, but in high-density populations the trees grow taller. Likewise, self shading or other causes of low light cause elongation without a concomitant gain in biomass, as illustrated by grass elongation under a board on your lawn. It is an interesting phenomenon that biomass increases and elongation may not occur at the same time. Rincon and Grime (1989) showed very clearly that growth in length and increase in biomass of *Brachythecium rutabulum* (Figure 28, Figure 31), *Thuidium tamariscinum* (Figure 29, Figure 31), and *Lophocolea bidentata* (Figure 30, Figure 31) may be almost inverse relationships. When dry matter production declined, there was an increase in length, causing a negative biomass production (Figure 31). This, however, is not true for all species, as seen by *Plagiomnium undulatum* (Figure 31, Figure 32) and *Pseudoscleropodium purum* (Figure 31, Figure 33).



Figure 28. *Brachythecium rutabulum* with capsules, a species in which growth in biomass and length do not occur together. Photo by Tim Waters, through Creative Commons.



Figure 29. *Thuidium tamariscinum* with capsules, a species in which growth in biomass and length do not occur together. Photo by Michael Lüth, with permission.



Figure 30. *Lophocolea bidentata*, a species in which growth in biomass and length do not occur together. Photo by Des Callaghan, with permission.

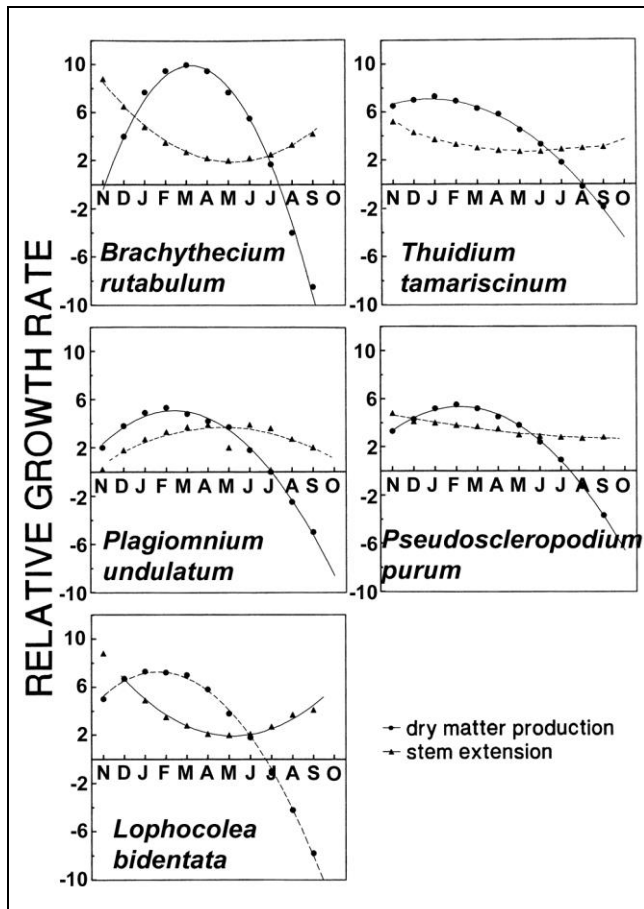


Figure 31. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime 1989.



Figure 32. *Plagiomnium undulatum*, a species in which weight gain and elongation can occur together. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The uncoupling of growth rate in length with that of branches is not surprising. As branches elongate, more distance is available for branch buds to form. In *Leptodictyum riparium* (Figure 34), total growth and growth of branches increase together (Sanford 1979). The rate of main axis growth, on the other hand, decreases as the rate of branch growth increases.



Figure 33. *Pseudoscleropodium purum*, a species in which weight gain and elongation can occur together. Photo by Michael Lüth, with permission.



Figure 34. *Leptodictyum riparium*, an aquatic species in which total growth and that of branches occur together, but main axis growth rate decreases at that time. Photo by Michael Lüth, with permission.

At least in *Sphagnum* (Figure 36-Figure 37), this uncoupling seems to be reflected in seasonal carbohydrate content as well (Shiraishi *et al.* 1996). In the Hakkoda Mountains of Japan, the glucose content of three *Sphagnum* species was highest in summer. Shiraishi *et al.* (1996) attributed this to an uncoupling between the active periods of matter production and growth. Sucrose, however, peaked in autumn in *S. capillifolium* (*S. nemoreum*; Figure 35) and *S. papillosum* (Figure 36), presumably in preparation for winter, and the seasonal changes were different between these two hummock species and *S. tenellum* (Figure 37), a hollow species.



Figure 35. *Sphagnum capillifolium*, a hummock species in which growth and weight increase are uncoupled. Photo by Michael Lüth, with permission.



Figure 36. *Sphagnum papillosum*, a hummock species in which growth and weight increase are uncoupled. Photo by Michael Lüth, with permission.



Figure 37. *Sphagnum tenellum* with capsules, a hollow species in which growth and weight increase are uncoupled, but sucrose production differs from the timing of the two previous hummock species. Photo by Dick Haaksma, with permission.

Gaberscik and Martincic (1987) likewise found that net photosynthesis did not correlate with growth. In August, when photosynthesis was maximal, biomass accumulation actually decreased. Chlorophyll content correlated positively with this period of high net photosynthesis, and consequently did not correlate with growth. Rather, the most intensive dry mass increase was at the beginning of the growing season. Winter was a low period for both photosynthesis and growth.

Seasonal Differences

We have assumed maximum growth of most temperate bryophytes to be in the spring when moisture is usually abundant and temperatures are cool. In their study of standing crops, Al-Mufti *et al.* (1977) supported this premise, showing that the peak standing crop in bryophytes occurred in May, the culmination of spring growth, and again in December, following cooler and more moist weather of autumn. The lowest biomass was in August when bryophytes would have suffered respiratory loss in the heat of summer. Zotz and Rottenberger (2001) likewise found this for three moss species [*Grimmia pulvinata*

(Figure 38), *Schistidium apocarpum* (Figure 39), *Syntrichia ruralis* (Figure 40)] on an exposed limestone wall in temperate Europe, with a strong seasonal pattern showing highest carbon fixation in autumn and near zero in summer.



Figure 38. *Grimmia pulvinata*, a rock-dwelling species that is typically dormant in summer. This shows white awns that are common among xerophytic bryophytes. Photo by Michael Lüth, with permission.



Figure 39. *Schistidium apocarpum*, a rock-dwelling species that is typically dormant in summer. Photo by Christophe Quintin, with permission.



Figure 40. *Syntrichia ruralis*, a rock-dwelling species that is typically dormant in summer. Photo by Darkone, through Creative Commons.

However, we need more field studies to corroborate this assumption of spring growth on a broad scale. Growth in bryophytes has been difficult to measure because it is slow and increments are small, with yearly increments measuring in mm in many taxa.

Kershaw and Webber (1986) approached the seasonal behavior from a different angle, showing that in a forest habitat, chlorophyll was highest in *Brachythecium rutabulum* (Figure 28) in summer when light intensity was lowest. Low light, coupled with high temperatures, contributes to low summer productivity.

In a temperate, semi-arid, sandy grassland, *Syntrichia ruralis* (Figure 40) was strongly dependent on its microclimatic conditions and followed the same general principles I have suggested (Juhász *et al.* 2002). Its highest productivity, however, was in December and January, with carbon gain beginning in October. It was dormant throughout the hot, dry summer. In a different study where the temperate grassland had cover provided by *Juniperus communis* (Figure 41) shrubs, those species that occurred in the open exhibited a decline in photosynthetic efficiency from the humid spring to the hot, dry summer and exhibited lower efficiency (F_v/F_m) than those bryophytes growing in the shade of the shrubs (Kalapos & Mázsza 2001).



Figure 41. *Juniperus communis*, a species that provides shade for bryophytes, permitting them to have greater photosynthesis than plants in the open. Photo by Neva Micheva, through Creative Commons.

Using transparencies to map coverage, Jansová (2006) found that **epixylic** bryophytes in a Bohemian old-growth forest grow faster in winter (October – April) than they do in summer, although some species did not differ in percentage growth (Jansová 2006). Both expansion and local extinction were greater in winter, making stability greater in summer.

But not all habitats create such pronounced seasonal differences. In the subarctic, *Dicranum fuscescens* (Figure 42) exhibited no clear seasonal differences in daily CO_2 uptake, nor were there any apparent differences between lowland and highland sites (Hicklenton & Oechel 1977). Melick and Seppelt (1994) found no seasonal differences in carbohydrate levels in continental Antarctica, although chlorophyll levels did decrease during winter. One reason for this apparent lack of seasonality is the high degree of daily variation that is experienced by bryophytes in Arctic and Antarctic areas.



Figure 42. *Dicranum fuscescens*, a species with no clear seasonal differences in CO_2 uptake. Photo by BBS, with permission.

Nevertheless, seasonal water availability can impose seasonal differences, even in these northern regions. In peatland habitats, productivity may respond to greater water availability in summer, but decrease if the moss becomes submerged (Suyker *et al.* 1997), increasing again as they achieve greater CO_2 exchange with receding water. Skré and Oechel (1981) demonstrated, in their two years of study of the Alaskan taiga, that increased amounts of young, photosynthetically active tissue near the end of the growing season in the mosses *Polytrichum commune* (Figure 13), *Pleurozium schreberi* (Figure 3), *Hylocomium splendens* (Figure 12), and *Sphagnum subsecundum* (Figure 43) accounted for their highest maximum net photosynthesis occurring in August. Williams and Flanagan (1998) reported maximum photosynthetic rates of boreal *Sphagnum* in summer ($14 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared to spring ($5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and autumn ($6 \mu\text{mol m}^{-2} \text{s}^{-1}$). In the same habitat, however, *Pleurozium schreberi* had no seasonal variation, with mean rates of 7, 5, and $7 \mu\text{mol m}^{-2} \text{s}^{-1}$ during spring, summer, and autumn, respectively.



Figure 43. *Sphagnum subsecundum*, a fen species with maximum photosynthetic rates in August. Photo by Jean Faubert, with permission.

Asada *et al.* (2003) showed that winter growth was important for the *Sphagnum* species [*S. austini* (Figure 44), *S. fuscum* (Figure 45), *S. rubellum* (Figure 46), *S.*

papillosum (Figure 36), *S. lindbergii* (Figure 47), *S. tenellum* (Figure 37), and *S. pacificum* (Figure 48)] in the hypermaritime coastal peatland of British Columbia, Canada. Position in the hummock seemed to be important, with lower productivity on the hummocks than in the hollows, again emphasizing the importance of water availability.



Figure 44. *Sphagnum austinii*, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.



Figure 45. *Sphagnum fuscum* hummock, a species that has important winter growth in coastal British Columbia. Photo by Oscar Gran, through Creative Commons.



Figure 46. *Sphagnum rubellum*, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.



Figure 47. *Sphagnum linbergii* in Lapland, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum pacificum*, from Alaska, a species that has important winter growth in coastal British Columbia. Photo by Vita Plasek, with permission.

In the maritime Antarctic (Figure 49), respiration in *Brachythecium* (Figure 50) is highest in summer and lowest in winter, regardless of temperature, whereas in *Chorisodontium* (Figure 51-Figure 52) and *Andreaea* (Figure 53), there is little difference, perhaps relating to their drier habitats (Davey & Rothery 1996). Photosynthesis rates are generally higher in summer. The optimum temperature for photosynthesis does not change between summer and winter.



Figure 49. Maritime Antarctic and mosses. Photo by Matt Amesbury, through Creative Commons.



Figure 50. *Brachythecium glaciale*, a species with greater in summer than in winter in the Antarctic. Photo by Michael Lüth, with permission.



Figure 53. *Andreaea depressinervis*, an Antarctic genus in which respiration rate differs little between summer and winter. Photo by through Creative Commons.



Figure 51. *Chorisodontium aciphyllum*, an Antarctic species in which respiration rate differs little between summer and winter. Photo by Peter Convey, with permission.



Figure 52. *Chorisodontium aciphyllum*, an Antarctic species in which respiration rate differs little between summer and winter. Photo by Jan-Peter Frahm, with permission.

False Growth Markers

Growth markers come in many types. C. Robin Stevenson (pers. comm.) reports using sand as a marker in *Campylopus introflexus* (Figure 54-Figure 56). Each growth increment was demarcated by a layer of sand; changes in leaf size also marked the same increments. But are these truly growth markers? Stevenson suggests that they might also be triggered by heavy rain events. This could supply multiple markers in one year, or it could represent the winter growth surge.

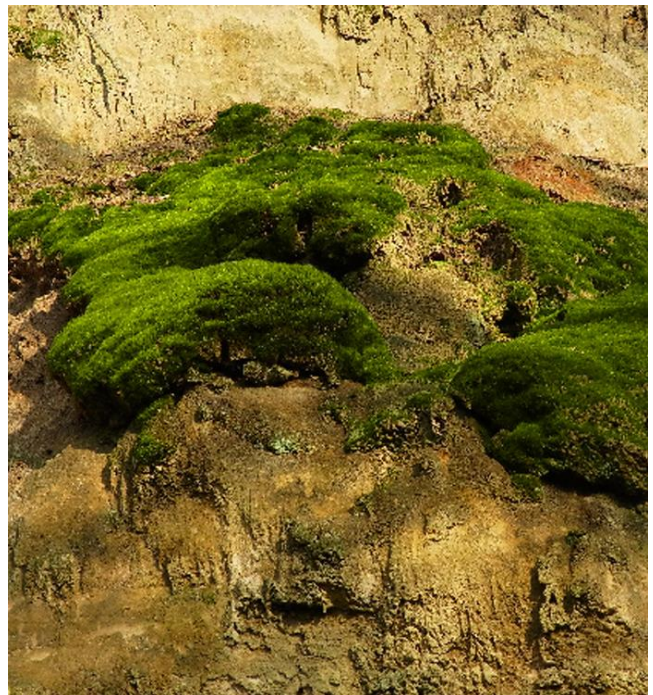


Figure 54. *Campylopus introflexus*, a species that shows definite growth markers. Photo courtesy of C. Robin Stevenson.



Figure 55. *Campylopus introflexus* showing growth markers. Photo courtesy of C. Robin Stevenson.



Figure 56. *Campylopus introflexus* showing growth markers. Photo courtesy of C. Robin Stevenson.

Growth Control

Using the open-habitat moss *Physcomitrella patens* (Figure 57), Chodok *et al.* (2010) determined that pH and temperature significantly affected both biomass and a number of polyunsaturated fatty acids (linoleic acid, LA; γ -linolenic acid, GLA; α -linolenic acid, ALA; eicosadienoic acid, EDA; di-homo- γ -linolenic acid, DHGLA; arachidonic acid, ARA; eicosapentaenoic acid, EPA). Sucrose, CaCl_2 , and MgSO_4 affected only some of the polyunsaturated fatty acids. Higher concentrations of sucrose positively affected LA, ARA, and EPA production; higher concentrations of the metals CaCl_2 and MgSO_4 negatively affected ARA and EPA.

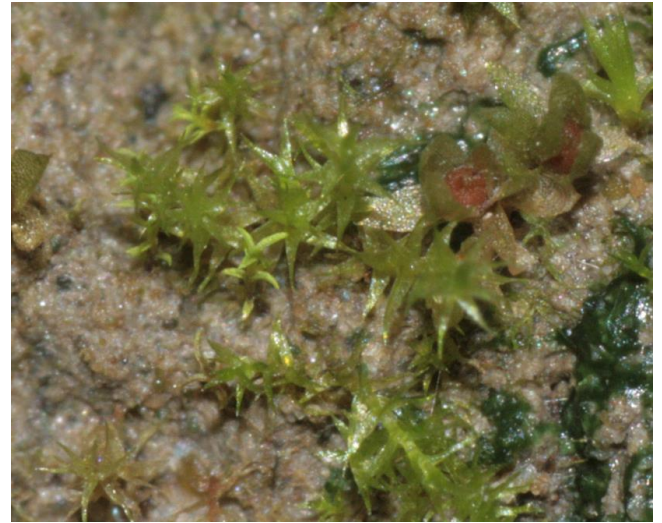


Figure 57. *Physcomitrella patens* with capsules, a species in which pH and temperature affect both biomass and polyunsaturated fatty acids. Photo by Hermann Schachner, through Creative Commons.

Growth Tradeoffs

Horsley *et al.* (2011) demonstrated that the allocation to asexual vs sexual reproduction in *Bryum argenteum* (Figure 23) is under genetic control. The allocation to asexual reproduction is negatively correlated with vegetative growth. Protonemal growth rate, on the other hand, is positively correlated with both asexual and sexual reproduction. The sexes did not differ in growth traits, asexual traits, sexual induction times, or biomass, but female sex-expressing shoots were longer than the males. Males, on the other hand, had a much higher number of reproductive structures, causing a much greater rate (24X) of investment in prezygotic tissue in males compared to females.

Etiolation

Elongation can be misleading. Low radiation causes greater elongation, with the highest elongation in *Dicranum majus* (Figure 58) from various polluted areas occurring at the lowest irradiance ($20 \mu\text{M m}^{-2} \text{s}^{-1}$) (Bakken 1995). **Etiolation** (excessive elongation and loss of chlorophyll due to insufficient light) can easily be observed if mosses are collected fresh, then put into a sealed plastic bag and stored in a nearly dark place. More on this phenomenon is discussed in the chapter on light.



Figure 58. *Dicranum majus* exhibiting a large plant size typical of low light conditions. Photo by Michael Lüth, with permission.

Belowground Productivity

It is rather presumptuous to title anything related to bryophytes as "Belowground Productivity" because data reporting such values are woefully lacking. Yet, bryophytes have rhizoids, and much of that biomass exists below ground, so such a title is not absurd. Furthermore, bryophytes have underground rhizomes, particularly in the **Polytrichaceae** (Figure 60). Sveinbjörnsson and Oechel (1981) have shown the respiration in the rhizome relative to whole plant CO_2 gain (Figure 59). Nevertheless, this is but an indirect indication that biomass is in place and active there with no indication of the carbon needed to put it there.

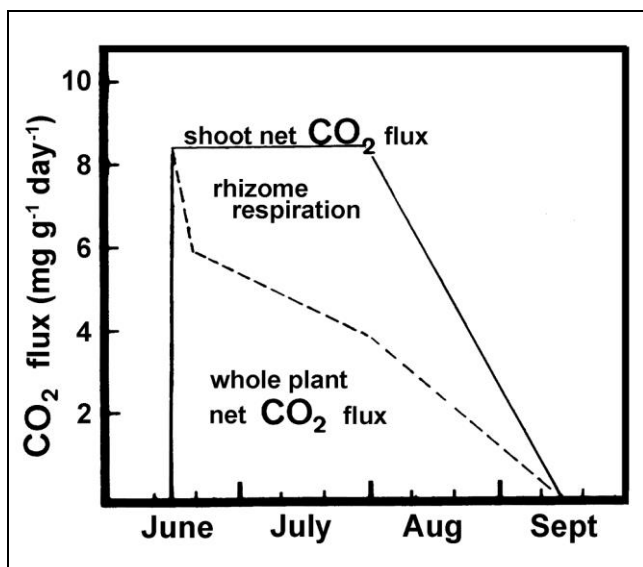


Figure 59. Relationship of aboveground and belowground CO_2 flux in *Polytrichum alpinum* (Figure 60) and *Polytrichum commune* (Figure 13) in the Alaskan tundra. Redrawn from Sveinbjörnsson & Oechel 1981.



Figure 60. *Polytrichastrum alpinum* with capsules. Photo by Michael Lüth, with permission.

Sporophyte Productivity

A discussion of the ability of the sporophyte to carry out photosynthesis is in Chapter 2-7, Bryopsida, and in Chapter 5-9, Ecophysiology of Development: Sporophyte. We know that bryophyte sporophytes have chlorophyll, even in thallose liverworts (Bold 1948), but few independent measurements of their rates of productivity seem to exist. These are further complicated by the photosynthetic capacity of the spores inside and the ability of the gametophyte to transport photosynthate to the sporophyte.

Nevertheless, Paolillo and Bazzaz (1968) demonstrated in *Funaria* (Figure 61) and *Polytrichum* (Figure 61) that the shape of the light saturation curve of the sporophyte is close to that of the gametophyte. For *Polytrichum*, the weight of the gametophyte decreases as that of the sporophyte increases and there is no net photosynthetic gain by the sporophyte, but such is not the case in *Funaria*. In *Funaria*, there is a net photosynthetic gain. In *Funaria* the calyptra is perched at the end of the capsule and covers little of it, whereas in *Polytrichum* the capsule is completely covered (Figure 61). The authors conclude that the seta serves as a reservoir for the developing capsule.



Figure 61. **Left:** *Polytrichum* calyptra covering capsule completely. Photo by Janice Glime. **Right:** *Funaria* calyptra covering only the end of the capsule. Photo by Michael Lüth, with permission.

Polytrichum (s.l.) species in particular depend on the gametophyte for their carbon nutrition (Renault *et al.*

1992). The members of this group have large calyptrae (Figure 61) that completely cover the capsule and they are densely covered with hairs. This permits little light to reach the capsule. In *Polytrichastrum formosum* (Figure 62) sucrose is the primary soluble sugar in both generations, with the highest concentrations (~230 mM) occurring in the **haustorium** (cells at base of sporophyte foot; functions in absorption of nutrients from gametophyte to sporophyte). The **vaginula** (part of archegonium of moss enveloping base of embryo or seta after upper part has been torn away), on the other hand, has primarily hexoses.



Figure 62. *Polytrichastrum formosum*, a species that uses sucrose in both generations. Photo by Martin Grimm, through Creative Commons.

Productivity and Aging

The current year's tissues seem to be the primary site of photosynthesis for most mosses. Collins and Oechel (1974) found that early in the season, the photosynthesis of Alaskan mosses relied on tissues produced the previous year, or even previous two years, but those rates were lower than for tissues produced in the current year (75% and 40% for 1 and 2 years earlier, respectively). Callaghan and coworkers (1978) found an even greater reduction in Swedish Lapland mosses. One-year-old tissues had rates 55% lower in *Hylocomium splendens* (Figure 12) and 58% lower in *Polytrichum commune* (Figure 63) than those tissues produced in the current year.



Figure 63. *Polytrichum commune*, a species that has less productivity in the tissues formed the previous year than in that of the current year. Photo by A. J. Silverside, with permission.

Life Span

We have expressed productivity in measurements from seconds to annual, but in consideration of the ecosystem, it is also appropriate to speak in terms of a lifetime. Although our knowledge of life spans is still meager, we do have indications in some species, although they may be minimal rather than maximal ages. For example, Frye (1928) found specimens of *Eurhynchium oreganum* (Figure 64) that were up to six years old. Ulychna (1963) reported mean ages for *Polytrichum commune* (Figure 63) of 3-4 years, with dead parts of 15-17 years age, although if they were not growing in hummocks the dead parts seemed to be only 4-5 years old. (Perhaps that is the age when it starts to become a hummock?)

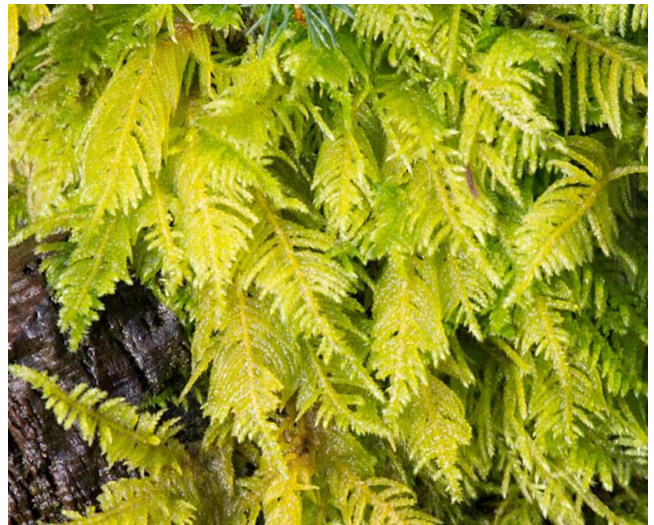


Figure 64. *Eurhynchium oreganum*, a species that has tissues at least six years old. Photo by Matt Goff <www.sitkanature.org>, with permission.

Corollary to the importance of life span is the effect that age has on growth rate. Ulychna (1963) found no effect in *Hylocomium splendens* (Figure 12) or *Polytrichum commune* (Figure 63). In the same two species, Callaghan *et al.* (1978) found that *Hylocomium splendens* grows its fronds for two years, then produces new segments, a factor that would be misleading in determining its age by its branching. Other factors can mislead age determinations based on growth markers. *Polytrichum commune* continues to have photosynthesis in dry conditions, whereas in *H. splendens* it ceases.

New growth may keep pace with dying portions (Callaghan *et al.* 1978). In *Hylocomium splendens* (Figure 12), normally the new shoot replaces the decomposing distal portion, but if the young segment is damaged, the whole shoot dies. On the other hand, *Polytrichum commune* (Figure 63) has a finite life expectancy which may differ with geographic area, but it also has an underground proliferation that can give rise to new shoots and compensate for lack of branching and death of aboveground parts.

In the maritime Antarctic, *Polytrichum strictum* (Figure 65) can have the extremely high annual mortality rate of 32% in young turfs (Collins 1976). However, in pure older turfs it is closer to 13%.



Figure 65. *Polytrichum strictum* illustrating the protection plants give each other in older tufts. Photo by Michael Lüth, with permission.

In the Arctic, longevity may compensate for the slow growth rates. Sand-Jensen *et al.* (1999) found that the slow, but steady-growing lake bottom mosses could persist for up to 17 years, retaining green leaves for several years, and decomposing slowly. Their growth rate, however, was only 10 mm per year, a relatively slow rate compared to pleurocarpous aquatic mosses elsewhere.

Leaf Production and LAI

Vitt (1990) decided to investigate the number of leaves and other leaf parameters that have been ignored for bryophytes. He did this to illustrate the complexity of moss populations, a fact often not realized by ecological observers. Using *Drummondia prorepens* (Figure 66), a small moss with large leaves, he found about 90 stems per cm^2 . The stems averaged *ca.* 65 leaves each, resulting in 6000 leaves per cm^2 . Considering the available leaf area for photosynthesis, he determined that one cm^2 has $\sim 15 \text{ cm}^2$ of photosynthetic moss surface.



Figure 66. *Drummondia prorepens* on wood, a species in which one cm^2 of substrate has $\sim 15 \text{ cm}^2$ of photosynthetic moss surface. Photo by Dale Vitt, with permission.

The **leaf area index (LAI)** has been used to express the relationship of the leaf-to-light interception (Smith 1990). It is the ratio of the leaf area to ground area, using the same units. Thus, a low LAI indicates wasted sunlight. A value of 1 indicates full usage, and a value of greater than 1 permits maximum usage at more angles of the sun. Since bryophyte leaves generally are not perpendicular to the sun, a higher LAI is required to obtain the same amount of light.

Simon (1987) estimated LAI measurements on *Syntrichia ruralis* (Figure 40), with 2030 leaves cm^{-2} , and *Ceratodon purpureus* (Figure 8), with 27,966 leaves cm^{-2} . These had leaf area indices (LAI) of 44 and 129 respectively. We can state the LAI for *Drummondia prorepens* (Figure 66), based on Vitt's (1990) data, as 15, discounting the portion of the leaf that is non-photosynthetic. Vitt (1990) reported a mean leaf area of $1960 \text{ mm}^2 \text{ cm}^{-2}$ (LAI = 19.6) for mosses in the boreal biome.

Energy Content

One distinction among plants is the amount of their tissue used for storage vs that used for photosynthesis. In this regard, the bryophyte uses nearly all of its tissue for photosynthesis, although I question whether it is as high as the 95% shown in

Table 2. Using the category of cryptogams includes the lichens, club mosses, horsetails, and ferns, complicating the interpretation of the number.

Fungal Partners

Although most bryophytes are self-reliant, photosynthetic organisms, some do benefit from fungal partners. The achlorophyllous thallose liverwort *Cryptothallus mirabilis* (Figure 67) relies totally on an endophytic fungus for its carbon input (Ligrone *et al.* 1993). The fungus is associated with the bases of the rhizoids and does not penetrate the thallus. There is no evidence that a third partner is involved; associated trees have a different fungal partner. Rather, it most likely gains its carbon from the organic nutrients in the soil and litter. Its dependency on this fungal carbon source is supported by its failure to develop beyond a few cells in sterile culture.



Figure 67. *Cryptothallus mirabilis*, an achlorophyllous thallose liverwort. Photo by Michael Lüth, with permission.

In *Aneura pinguis* (Figure 68; Ligrone *et al.* 1993), *Conocephalum conicum* (Figure 69) (Ligrone & Lopes 1989), and *Phaeoceros laevis* (Figure 70) (Ligrone 1988),

it appears that it is the fungus that benefits, not the liverwort.

Table 2. Comparison of biomass devoted to photosynthesis vs storage and respiration for plants from major biomes. From Larcher 1983 and compiled from many sources.

Plant	Green mass (photo- synthetically active organs) shoots	Purely respiratory organs	
		Woody stems above ground	Roots and subterranean
Evergreen trees of tropical and subtropical forests	ca. 2%	80-90%	10-20%
Deciduous trees of the temperate zone	1-2%	ca. 80%	ca. 20%
Evergreen conifers of the taiga and in mountain forests	4-5%	ca. 75%	ca. 20%
Alpine scrubwood	ca. 25%	ca. 30%	ca. 45%
Young conifers	50-60%	40-50%	ca. 10%
Ericaceous dwarf shrubs	10-20%	ca. 20%	60-70%
Grasses	30-50%		50-70%
Steppe plants			
Wet years	ca. 30%		ca. 70%
Dry years	ca. 10%		ca. 90%
Desert plants	10-20%		80-90%
Arctic tundra			
Tracheophytes	15-20%		
Cryptogams (including bryophytes)	>95%		
Plants of the high mountains	10-20%		80-90%



Figure 68. *Aneura pinguis*, a thallose liverwort. Photo by Michael Lüth, with permission.



Figure 70. *Phaeoceros laevis*, a species that can suffer photosynthate loss due to a fungus. Photo by Bob Klips, with permission.



Figure 69. *Conocephalum conicum*, a species that can suffer photosynthate loss due to a fungus. Photo by Janice Glime.

Recent History Effects

Previous conditions have a strong influence on the photosynthetic performance of plants, at least among some Alaskan mosses (Alpert & Oechel 1987). Assemblages of mosses having recent experience with low water availability achieved maximum net photosynthesis at lower water contents than did those that had remained hydrated. Likewise, those mosses that occurred in sites with low light availability achieved higher net photosynthesis at lower light intensities than mosses that had recent history in high light intensities. And a close relationship exists between the lower temperature limit for 85% photosynthesis and the mean maximum tissue temperature for the previous five-day period (Oechel 1976).

Recent history of weather conditions most likely accounts for the considerably lower productivity in spring, compared to summer, in *Atrichum undulatum* (Figure 71), *Plagiomnium affine* (Figure 72), and *Polytrichum formosum* (Figure 62) (Baló 1967). One reason for this is the much higher chlorophyll *a* content in summer, compared to spring. Such previous histories can account for much of the variation we see between measurements of the same species and even the same individuals.



Figure 71. *Atrichum undulatum* fresh growth, a species with lower productivity in spring, compared to summer. Photo by Michael Lüth, with permission.



Figure 72. *Plagiomnium affine*, a species with lower productivity in spring, compared to summer. Photo by Janice Glime.

Mitotic Activity

It appears that mitotic activity, the initial step in new growth, has its own clock. In a study on *Pellia borealis*, a thallose liverwort, the greatest activity occurs between 11:00 and 14:00 hours (Szewczyk 1978). However, further studies are needed to determine if this is an endogenous rhythm or is tied to a daily ecological event in its habitat.

Respiration

Nearly every photosynthetic study includes respiration measurements. However, these may not be reported separately. **Net photosynthesis** is that incorporated carbon that remains after carbon is lost as CO₂ in respiration.

Bryophytes, as C₃ plants, exhibit both dark respiration and photorespiration. **Photorespiration** (respiration in the light) is difficult to measure because of the ability of a plant to put that same lost CO₂ immediately back into carbohydrate through the photosynthetic pathway. Photorespiration in C₃ plants is generally up to three times greater than dark respiration and accounts for the loss of energy at high temperatures. But even dark respiration increases in summer, as noted in *Plagiomnium acutum* (Figure 73) and *P. maximoviczii* (Figure 74) in China (Liu *et al.* 2001).



Figure 73. *Plagiomnium acutum*, a species in which dark respiration increases in summer. Photo by Show Ryu, through Creative Commons.



Figure 74. *Plagiomnium maximoviczii*, a species in which dark respiration increases in summer. Photo by Hiroshima University Digital Museum of Natural History, with permission.

Priddle (1980b) found that dark respiration of two Antarctic species of aquatic mosses [*Warnstorfia sarmentosa* (Figure 75) and *Drepanocladus s.l.* sp. (Figure 76) differed little from that of algal communities in the same lake. At normal lake temperatures (up to 5°C), the mosses respired approximately 0.3 g mg⁻¹ ash-free dry mass h⁻¹.



Figure 75. *Warnstorfia sarmentosa*, a species with respiration rates similar to those of algae in the same Antarctic lake. Photo by David Holyoak, with permission.



Figure 76. *Warnstorfia fluitans*, a genus with respiration rates similar to those of algae in the same Antarctic lake. Photo by Michael Lüth, with permission.

In the high Arctic Svalbard, *Sanionia uncinata* (Figure 77) exhibits a high Q_{10} (ratio of reaction rates for a 10°C rise) of 3 for respiration in the range of $7\text{--}23^{\circ}\text{C}$ (Uchida *et al.* 2002). In the same range, photosynthesis exhibits very little difference, resulting in low temperature optima.



Figure 77. *Sanionia uncinata*, a species that experiences a rapid rise in respiration with temperature in the Arctic Svalbard. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Habitat and Geographic Comparisons

Because of the length of the growing season, temperatures during the growing season, day length, available water, and other geographic and climatic factors, productivity in various biomes differs. Table 3 compares the various biomes to provide a framework for the discussion of habitat differences among bryophytes. Table 4 and Table 5 compare rates on biomass and area bases, respectively.

Although **water** may be a good indicator of productivity of a habitat, the general water availability of the habitat is not a good indicator of the productivity at the time that water is available. In fact, the relationship seems to be inverse. As can be seen in Table 3, the highest productivity seems to be from the driest habitats and from the plants adapted to those habitats. On the other hand, Suba *et al.* (1982) found that hygrophytic and mesophytic mosses of a beechwood community had more photosynthetic intensity than more xerophytic rock-inhabiting mosses. History is probably important here.

In the boreal forest, it appears that the **light use efficiency** of *Pleurozium schreberi* (Figure 3) ($102 \text{ mM CO}_2 \text{ M}^{-1}$) is well above that of most of the plants there ($70\text{--}80 \text{ mM CO}_2 \text{ M}^{-1}$), but its productivity is still lower ($1.9 \mu\text{M m}^{-2} \text{ s}^{-1}$ (Whitehead & Gower 2001). Other understory shrubs and herbaceous plants had productivity mostly between 9 and $11 \mu\text{M m}^{-2} \text{ s}^{-1}$.

For aquatic bryophytes, **depth** affects light intensity. Growth rates of deepwater mosses can be quite slow (10 mm per year in Canadian High Arctic lakes), and vary little between years (Sand-Jensen *et al.* 1999). Martínez Abaigar *et al.* (1994) found that *Scapania undulata* (Figure 78) had a leaf specific area of $317 \text{ cm}^2 \text{ g}^{-1} \text{ DM}$ (dry mass) at 5 cm depth, but at 45 cm depth, the **LSA** (whole-plant leaf surface area) increased to $399 \text{ cm}^2 \text{ g}^{-1} \text{ DM}$. Concomitantly, the leaf specific weight (mass) was reduced from 3.16 mg cm^{-2} to 2.50 mg cm^{-2} . These differences can be interpreted as a response to the lower light availability at 45 cm. Canopy leaf fall, on the other hand, caused an increase in accessory pigments relative to chlorophyll *a*.



Figure 78. *Scapania undulata*, a species in which whole-plant leaf surface area increases with water depth. 1 Michael Lüth, with permission.

Furness and Grime (1982) found that species of disturbed habitats (**ruderal species**) such as *Funaria hygrometrica* (Figure 79) had high relative growth rates, as did perennial pleurocarpous species such as

Brachythecium rutabulum (Figure 28) from fertile habitats. Most species grew best at temperatures of 15-25°C, whereas temperatures above 30°C eventually killed moist mosses.



Figure 79. *Funaria hygrometrica*, a ruderal species with a high growth rate. Photo by Michael Lüth, with permission.

Rates of Productivity

Productivity varies with habitat (Table 3). Mosses, typically living in shaded habitats, are low in productivity compared to other plant groups (Table 6). In the Antarctic, Davey and Rothery (1996) found greater seasonal variation in bryophytes from hydric habitats than from the less hydric sites.

Probably the highest productivity ever measured for a bryophyte is that of *Sphagnum* (Figure 43-Figure 48), with a productivity of 12 tons per hectare per year (Schofield 1985). C₄ plants average a CO₂ uptake of up to 80 mg dm⁻² hr⁻¹, whereas C₃ plants seem to have a max of about 45 (Larcher 1983). Mosses, on the other hand, have a max of only 3! For some reason, perhaps the thick cuticle and other adaptations that reduce the light, CAM plants have a maximum of only 20. However, since measurement time may not coincide with the period of photosynthesis, we may need to interpret these numbers somewhat differently.

Table 3. Comparison of net primary production, biomass, chlorophyll, and leaf surface area in major biomes. From Whittaker *et al.* 1974; Larcher 1983.

Ecosystem Type	Area 10 ⁶ km ²	Net Primary Production			Leaf Surf Area Biomass (dry matter)			Chlorophyll		LAI	
		Normal range g m ⁻² yr ⁻¹	Mean g m ⁻² yr ⁻¹	Total 10 ⁹ t yr ⁻¹	Normal range kg m ⁻²	Mean kg m ⁻²	Total 10 ⁹ t	Mean g m ⁻²	Total 10 ⁶ t	Mean m ² m ⁻²	Total 10 ⁶ km ²
Tropical rain forest	17.0	1000-3500	2200	37.4	6-80	45	765	3.0	51.0	8	136
Tropical seasonal forest	7.5	1000-2500	1600	12.0	6-60	35	260	2.5	18.8	5	38
Temperate forest:											
Evergreen	5.0	600-2500	1300	6.5	6-200	35	175	3.5	17.5	12	60
Deciduous	7.0	600-2500	1200	8.4	6-60	30	210	2.0	14.0	5	35
Boreal forest	12.0	400-2000	800	9.6	6-40	20	240	3.0	36.0	12	144
Woodland and shrubland	8.5	250-1200	700	6.0	2-20	6	50	1.6	13.6	4	34
Savanna	15.0	200-2000	900	13.5	0.2-15	4	60	1.5	22.5	4	60
Temperate grassland	9.0	200-1500	600	5.4	0.2-5	1.6	14	1.3	11.7	3.6	32
Tundra and alpine	8.0	10-400	140	1.1	0.1-3	0.6	5	0.5	4.0	2	16
Desert and semidesert scrub	18.0	10-250	90	1.6	0.1-4	0.7	13	0.5	9.0	1	18
Extreme desert-rock, sand, ice	24.0	0-10	3	0.07	0-0.2	0.02	0.5	0.02	0.5	0.05	1.2
Cultivated land	14.0	100-4000	650	9.1	0.4-12	1	14	1.5	21.0	4	56
Swamp and marsh	2.0	800-6000	3000	6.0	3-50	15	30	3.0	6.0	7	14
Lake and stream	2.0	100-1500	400	0.8	0-0.1	0.02	0.05	0.2	0.5		
Total continental:	149	782	117.5	12.2	1837	1.5	226	4.3	644		
Open ocean	332.0	2-400	125	41.5	0-0.005	0.003	1.0	0.03	10.0		
Upwelling zones	0.4	400-1000	500	0.2	0.005-0.1	0.02	0.008	0.3	0.1		
Continental shelf	26.6	200-600	360	9.6	0.001-0.04	0.001	0.27	0.2	5.3		
Algal beds and reefs	0.6	500-4000	2500	1.6	0.04-4	2	1.2	2.0	1.2		
Estuaries (excluding marsh)	1.4	200-4000	1500	2.1	0.01-4	1	1.4	1.0	1.4		
Total marine	361	-	155	55.0	-	0.01	3.9	0.05	18.0		
Full total	510	336	172.5	3.6	1841	0.48	243				

Table 4. Productivity rates for bryophytes based on bryophyte mass, ordered from most productive to least. Values refer to CO₂ incorporated; dm refers to dry mass – if dm is not indicated, dry or wet mass is not known for certain.

Species	Productivity Value	Conditions/Location	Reference
<i>Sphagnum auriculatum</i>	232 mg g ⁻¹ h ⁻¹	submersed at light comp point	Wetzel <i>et al.</i> 1985
<i>Platyhypnidium riparioides</i>	20.24 mg g ⁻¹ h ⁻¹	max; converted from mM O ₂ g ⁻¹ h ⁻¹	Allen & Spence 1981
<i>Fontinalis antipyretica</i>	15.4 mg g ⁻¹ h ⁻¹	max; converted from mM O ₂ g ⁻¹ h ⁻¹	Allen & Spence 1981
<i>Plagiomnium acutum</i>	19.9 mg g ⁻¹ h ⁻¹	summer; converted from μM kg ⁻¹ s ⁻¹	Liu <i>et al.</i> 2001
<i>Plagiomnium maximoviczii</i>	15.0 mg g ⁻¹ h ⁻¹	summer; converted from μM kg ⁻¹ s ⁻¹	Liu <i>et al.</i> 2001
<i>Plagiomnium maximoviczii</i>	9.86 mg g ⁻¹ h ⁻¹	winter; converted from μM kg ⁻¹ s ⁻¹	Liu <i>et al.</i> 2001
<i>Plagiomnium acutum</i>	9.20 mg g ⁻¹ h ⁻¹	winter; converted from μM kg ⁻¹ s ⁻¹	Liu <i>et al.</i> 2001
<i>Hygrohypnum</i> spp.	2.3-8.7 mg g ⁻¹ dm h ⁻¹	Alaska stream	Arscott <i>et al.</i> 2000
<i>Polytrichum formosum</i>	8 mg g ⁻¹ dm h ⁻¹	Hungary, summer, light saturation	Baló 1967
<i>Plagiomnium affine</i>	6 mg g ⁻¹ dm h ⁻¹	Hungary, summer, light saturation	Baló 1967
<i>Atrichum undulatum</i>	5 mg g ⁻¹ dm h ⁻¹	Hungary, summer, light saturation	Baló 1967
<i>Calliergon sarmentosum</i>	4.4 mg g ⁻¹ dm h ⁻¹	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
<i>Polytrichastrum alpinum</i>	4.4 mg g ⁻¹ dm h ⁻¹	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
<i>Rhytidiadelphus squarrosus</i>	3.5 mg g ⁻¹ dm h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Ptilium crista-castrensis</i>	3.4 mg g ⁻¹ dm h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Hylocomium splendens</i>	3.2 mg g ⁻¹ dm h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Sphagnum girgensohnii</i>	3.0 mg g ⁻¹ dm h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Polytrichum commune</i>	2.79 mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Sphagnum balticum</i>	2.7 mg g ⁻¹ dm h ⁻¹	subarctic mire	Johansson & Linder 1980
<i>Polytrichum commune</i>	2.65 mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Hylocomium splendens</i>	2.5 mg g ⁻¹ h ⁻¹	max, subarctic Finland	Kallio & Kärenlampi 1975
<i>Rhytidiadelphus triquetrus</i>	2.5 mg g ⁻¹ h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Sphagnum magellanicum</i>	2.2 mg g ⁻¹ dm h ⁻¹		Petersen 1984
<i>Pleurozium schreberi</i>	2.0 mg g ⁻¹ dm h ⁻¹	max, South Sweden	Stålfelt 1937
<i>Pohlia drummondii</i>	2.0 mg g ⁻¹ h ⁻¹	max, subarctic Finland	Kallio & Kärenlampi 1975
<i>Sphagnum papillosum</i>	1.95 mg g ⁻¹ dm h ⁻¹	max, Aug	Gaberscik & Martincic 1987
<i>Sphagnum fuscum</i>	1.7 mg g ⁻¹ dm h ⁻¹	subarctic mire	Johansson & Linder 1980
<i>Polytrichum juniperinum</i>	1.6 mg g ⁻¹ h ⁻¹	max, subarctic Finland	Kallio & Kärenlampi 1975
<i>Schistidium agassizii</i>	0.59-1.6 mg g ⁻¹ dm h ⁻¹	AK stream, converted O ₂ to CO ₂	Arscott <i>et al.</i> 2000
<i>Dicranum fuscescens</i>	0.1-2 mg g ⁻¹ dm h ⁻¹	Arctic, 10 Oct & 7 July, respectively	Hicklenton & Oechel 1976
<i>Dicranum fuscescens</i>	1.5 mg g ⁻¹ dm h ⁻¹	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
<i>Pterobryum arbuscula</i>	1.5 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Thuidium kanedae</i>	1.4 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Leucobryum neilgherrense</i>	1.4 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Hylocomium splendens</i>	1.39 mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK; moist?	Skré & Oechel 1981
<i>Dicranum elongatum</i>	1.3 mg g ⁻¹ dm h ⁻¹	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
<i>Macromitrium gymnostomum</i>	1.3 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Sphagnum nemoreum</i>	1.2 mg g ⁻¹ dm h ⁻¹	lake, New York, USA	Titus <i>et al.</i> 1983
<i>Ulotia crispula</i>	1.2 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Pleurozium schreberi</i>	1.20 mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
	1.1 mg g ⁻¹ h ⁻¹	max, south Finland	Kallio & Kärenlampi 1975
<i>Hylocomium splendens</i>	1.08 mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Dicranum bonjeanii</i>	1.0 mg g ⁻¹ dm h ⁻¹	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
subsp <i>angustum</i>			
<i>Neckera konoii</i>	1.0 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Calliergon austrostramineum</i>	1.0 mg g ⁻¹ h ⁻¹	max, Antarctica	Rastorfer 1972
<i>Sphagnum rubellum</i>	0.9 mg g ⁻¹ dm h ⁻¹	max, moorland	Grace 1970
<i>Anomodon giraldii</i>	0.9 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Macrosporiella scabriseta</i>	0.9 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Boulaya mittenii</i>	0.9 mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Pohlia nutans</i>	0.9 mg g ⁻¹ h ⁻¹	max, Antarctica	Rastorfer 1972
<i>Dicranum elongatum</i>	0.9 mg g ⁻¹ h ⁻¹	max, subarctic Finland	Kallio & Kärenlampi 1975
<i>Sanionia uncinata</i>	0.9 mg g ⁻¹ h ⁻¹	max, Antarctica	Rastorfer 1972
	0.9 mg g ⁻¹ h ⁻¹	max, subarctic Finland	Kallio & Kärenlampi 1975
<i>Neckera pennata</i>	0.8 mg g ⁻¹ dm h ⁻¹	May, Adirondack Mt. Forest on tree	Tobiessen <i>et al.</i> 1977
<i>Racomitrium lanuginosum</i>	0.8 mg g ⁻¹ h ⁻¹	max, Antarctica	Kallio & Kärenlampi 1975
<i>Polytrichum strictum</i>	0.7 mg g ⁻¹ h ⁻¹	max, Antarctica	Rastorfer 1972
<i>Racomitrium lanuginosum</i>	0.6 mg g ⁻¹ dm h ⁻¹	Fennoscandia tundra	Kallio & Heinonen 1975

<i>Thuidium cymbifolium</i>	0.6	mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Hylocomium brevirostre</i> var. <i>cavifolium</i>	0.6	mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Homaliiodendron flabellatum</i>	0.6	mg g ⁻¹ h ⁻¹	max, epiphyte, Japan	Hosokawa <i>et al.</i> 1964
<i>Sphagnum subsecundum</i>	0.57	mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Pleurozium schreberi</i>	0.46	mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Sphagnum nemoreum</i>	0.25	mg g ⁻¹ h ⁻¹	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
<i>Mnium cuspidatum</i>	0.16	mg g ⁻¹ dm h ⁻¹	July, Adirondack Mt. Forest on tree	Tobiessen <i>et al.</i> 1977
<i>Anomodon rugelii</i>	0.00	mg g ⁻¹ dm h ⁻¹	July, Adirondack Mt. Forest on tree	Tobiessen <i>et al.</i> 1977
<i>Neckera pennata</i>	no PS		July, Adirondack Mt. Forest on tree	Tobiessen <i>et al.</i> 1977
<i>Ulota crispa</i>	no PS		July, Adirondack Mt. Forest on tree	Tobiessen <i>et al.</i> 1977
<i>Calliergon sarmentosum</i> & <i>Drepanocladus</i> spp.	6	mg g ⁻¹ dm d ⁻¹	max, Antarctica lake bottoms	Priddle 1980a
<i>Calliergon giganteum</i>	48.8	mg g ⁻¹ dm d ⁻¹	0.03% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
	293.0	mg g ⁻¹ dm d ⁻¹	1% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
<i>Lophozia quinqueidentata</i>	25.4	mg g ⁻¹ dm d ⁻¹	0.03% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
	155.2	mg g ⁻¹ dm d ⁻¹	1% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
<i>Polytrichum juniperinum</i>	14.5	mg g ⁻¹ dm d ⁻¹	dry, 0.03% CO ₂ , Arct mineral sedge marsh	D'Yachenko 1976
	87.2	mg g ⁻¹ dm d ⁻¹	dry, 1% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
<i>Sphagnum squarrosum</i>	13.0	mg g ⁻¹ dm d ⁻¹	0.03% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
	77.8	mg g ⁻¹ dm d ⁻¹	1% CO ₂ , Arctic mineral sedge marsh	D'Yachenko 1976
<i>Dicranum fuscescens</i>	7	mg g ⁻¹ dm d ⁻¹	max, subarctic	Hicklenton & Oechel 1977

Table 5. Productivity rates for bryophytes on an area basis. Values refer to CO₂ incorporated.

Species	Productivity Value	Conditions/Location	Reference
<i>Sphagnum</i> spp.	14 $\mu\text{M m}^{-2} \text{s}^{-1}$	max, summer	Williams & Flanagan 1998
<i>Sphagnum</i> spp.	6 $\mu\text{M m}^{-2} \text{s}^{-1}$	max, autumn	Williams & Flanagan 1998
<i>Sphagnum</i> spp.	5 $\mu\text{M m}^{-2} \text{s}^{-1}$	max, spring	Williams & Flanagan 1998
<i>Pleurozium schreberi</i>	1.9 $\mu\text{M m}^{-2} \text{s}^{-1}$	Canadian boreal forest	Whitehead & Gower 2001
<i>Ceratodon purpureus</i> & <i>Bryum pseudotriquetrum</i>	4 $\mu\text{M m}^{-2} \text{s}^{-1}$	max, Langhovde, E Antarc, 9-17 Jan	Ino 1990
<i>Hypnum cupressiforme</i>	0.045 $\text{g m}^{-2} \text{s}^{-1}$	Southern Finland, 5°C	Kallio & Kärenlampi 1975
<i>Pleurozium schreberi</i>	0.045 $\text{g m}^{-2} \text{s}^{-1}$	Southern Finland, 15°C (optimum)	Kallio & Kärenlampi 1975
<i>Hydrogonium consanguinium</i>	0.88 $\text{g m}^{-2} \text{d}^{-1}$	July, India	Munshi 1974
<i>Hydrogonium consanguinium</i>	1.05 $\text{g m}^{-2} \text{d}^{-1}$	August, India	Munshi 1974
<i>Hydrogonium consanguinium</i>	1.05 $\text{g m}^{-2} \text{d}^{-1}$	September, India	Munshi 1974
<i>Physcomitrium</i> spp.	0.17 $\text{g m}^{-2} \text{d}^{-1}$	December	Munshi 1974
<i>Physcomitrium</i> spp.	0.08 $\text{g m}^{-2} \text{d}^{-1}$	January	Munshi 1974
<i>Physcomitrium</i> spp.	0.07 $\text{g m}^{-2} \text{d}^{-1}$	February	Munshi 1974
<i>Hydrogonium consanguinium</i>	31.53 $\text{g m}^{-2} \text{mo}^{-1}$	August, India	Munshi 1974
<i>Hydrogonium consanguinium</i>	26.60 $\text{g m}^{-2} \text{mo}^{-1}$	July, India	Munshi 1974
<i>Hydrogonium consanguinium</i>	14.80 $\text{g m}^{-2} \text{mo}^{-1}$	September, India	Munshi 1974
<i>Physcomitrium</i> spp.	5.13 $\text{g m}^{-2} \text{mo}^{-1}$	December	Munshi 1974
<i>Physcomitrium</i> spp.	2.44 $\text{g m}^{-2} \text{mo}^{-1}$	January	Munshi 1974
<i>Physcomitrium</i> spp.	2.10 $\text{g m}^{-2} \text{mo}^{-1}$	February	Munshi 1974
bryophyte cover	754 $\text{g m}^{-2} \text{yr}^{-1}$	Marion Island (45°54'S) drainage line	Russell 1985
<i>Hypnum cupressiforme</i>	188 $\text{g m}^{-2} \text{yr}^{-1}$	Austria	Zechmeister 1998
<i>Pleurozium schreberi</i>	161 $\text{g m}^{-2} \text{yr}^{-1}$	Austria	Zechmeister 1998
<i>Abietinella abietina</i>	144 $\text{g m}^{-2} \text{yr}^{-1}$	Austria	Zechmeister 1998
<i>Hylocomium splendens</i>	129.8 $\text{g m}^{-2} \text{yr}^{-1}$	Norway, Sweden	Tamm 1953
<i>Hylocomium splendens</i>	127 $\text{g m}^{-2} \text{yr}^{-1}$	Austria	Zechmeister 1998
<i>Sphagnum papillosum</i>	101.0 $\text{g m}^{-2} \text{yr}^{-1}$	moor	Newbould 1960
<i>Hydrogonium consanguinium</i>	72.93 $\text{g m}^{-2} \text{yr}^{-1}$	net production, India	Munshi 1974
<i>Calliergon sarmentosum</i> & <i>Drepanocladus (sensu lato)</i> spp.	40 $\text{g m}^{-2} \text{yr}^{-1}$	max, Antarctica lake bottoms	Priddle 1980a
<i>Sanionia uncinata</i>	30 $\text{g m}^{-2} \text{yr}^{-1}$	max, High Arctic, Svalbard (79°N)	Uchida <i>et al.</i> 2002
bryophyte cover	21 $\text{g m}^{-2} \text{yr}^{-1}$	Marion Island (45°54'S) fellfield	Russell 1985
bryophyte cover	12.8 $\text{g m}^{-2} \text{yr}^{-1}$	max, East Ongul Island, Antarctica	Ino 1983
<i>Physcomitrium</i> spp.	11.30 $\text{g m}^{-2} \text{yr}^{-1}$	Annual net production	Munshi 1974
<i>Polytrichum strictum</i>	2-5 mm yr^{-1}	Antarctic	Longton 1974?
<i>Polytrichum strictum</i>	15-55 mm yr^{-1}	Pinawa, Manitoba	Longton 1979?

Table 6. Mean maximum values for photosynthesis (CO_2 uptake) and biomass (DM) increase at natural CO_2 levels, saturating light intensity, optimal temperature, and adequate water availability. From Larcher 1983.

Plant group	CO ₂ uptake	
	mg dm ⁻² h ⁻¹	mg gDM ⁻¹ h ⁻¹
Land Plants		
Phanerogams		
Herbaceous plants		
C ₄ plants	30-80 (108)	60-140
C ₃ plants		
Crop plants	20-45 (60)	30-60
Plants of sunny habitats (heliophytes)	20-40 (94)	30-60
Shade plants (sciophytes)	4-20	10-30
Plants of dry habitats (xerophytes)	20-45	15-33
Grain and fodder grasses	15-35 (40)	
Wild grasses and sedges	8-20 (25)	8-35
CAM plants		
In the light	3-20	0.3-2
In the dark	10-15	1-1.5
Woody plants		
Tropical and subtropical trees		
Fruit trees	18-22	10-25
Forest canopy trees	12-24	
Understory trees	5-10	
Broad-leaved evergreens of the		
Subtropics and warm-temperate regions		
Sun leaves	10-18	
Shade leaves	3-6	
Seasonally deciduous trees		
Sun leaves	15-25 (35)	
Shade leaves	5-10	
Conifers		
Winter-deciduous		10-40
Evergreen	5-18	4-18
Mangrove trees	6-12 (20)	
Sclerophylls of periodically dry regions	5-15	3-10
Bamboos	5-10	
Palms	6-10	(12)
Desert shrubs	(4) 6-20 (30)	(2) 5-15 (35)
Dwarf shrubs of heath and tundra		
Winter- deciduous	10-25	15-30
Evergreen	5-10(15)	2-10
Cryptogams		
Ferns	3-5	
Mosses	up to 3	0.6-3.5
Lichens	0.5-2 (6)	0.3-2.5 (4)
Aquatic Plants		
Swamp plants, emersed hydrophytes	20-40 (50)	
Submersed cormophytes	2-6	5-25
Seaweeds	3-10	1-20 (30)
Planktonic algae		2-3

Although the biomass of bryophytes is small, their carbon sequestration is not inconsequential. Cryptogamic covers sequester ~ 3.9 Pg of carbon per year (Elbert *et al.* 2012). This equals about 7% of the net primary production in the terrestrial ecosystem. The uptake of N is ~ 49 Tg per year, accounting for nearly half of the biological N fixation on land.

Latitude Differences

It is difficult to determine if responses of populations in different parts of the world are the result of genetic differences or differences in acclimation history (Sveinbjörnsson & Oechel 1983). *Polytrichum commune* (Figure 13) from five diverse regions from Alaska (71°N) to Florida (29°N) were grown under common garden conditions in constant temperature conditions of 5 and 20°C. In this common set of conditions, plants from lower latitudes had higher photosynthetic rates except for the temperate St. Hilaire population. There was a sevenfold difference between the extreme values. Populations from the lower latitudes had more maximum photosynthetic response to the two temperatures than did populations from higher latitudes. On the other hand, bryophytes from higher latitudes had higher energy contents than those from lower latitudes (Russell 1990; Figure 80).

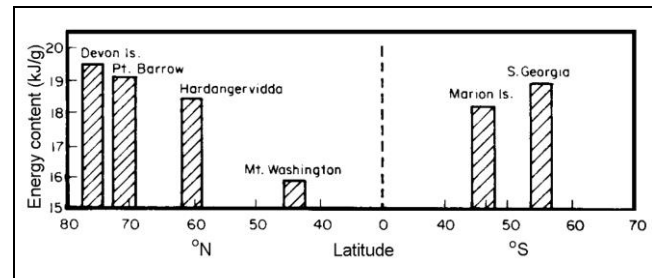


Figure 80. Comparison of mean energy content of bryophytes related to latitude in several tundra sites in Devon Island and Point Barrow, Alaska; Hardangervidda, Denmark; Mt. Washington, New Hampshire; and Marion Island and South Georgia, Antarctica. Reprinted from Russell 1990.

Antarctic

Temperatures in the Antarctic (Figure 81) have rather large daily fluctuations during the growing season. Therefore, it is not surprising to find that bryophytes growing there show little response to changes in temperature and little acclimation to any temperature (Davey & Rothery 1996). Nevertheless, the species exhibit summer maxima in productivity; no seasonal variation seems to exist for optimum temperature of gross or net photosynthesis.



Figure 81. Antarctic ice on Green Island. Photo by Matt Amesbury, through Creative Commons.

But temperature is not the only limiting factor in the Antarctic climate (Bramley-Alves *et al.* 2014). In addition to temperature, water availability likewise limits productivity. More recently, the ozone hole is limiting productivity, in part due to the increased UV-B radiation, but also because of the associated increase in wind in the ozone hole.

Frigid Antarctic

The **frigid Antarctic**, with mean air temperatures generally below 0°C and very dry air, is entirely vegetated by cryptogams: **Cyanobacteria**, algae, lichens, and mosses. The most conspicuous vegetation is small turf and cushion-forming mosses including **Bryum** (Figure 23) and **Grimmia** (probably **Schistidium**; Figure 82) species (Longton 1979). Standing biomass is similar to the annual production of the tundra, reaching 1000 g m⁻², but more typically 5-200 g m⁻² (Longton 1974, Kappen 1985). Annual production seems to be less than 5 g m⁻² yr⁻¹ (Longton 1974, Ino 1983).



Figure 82. *Schistidium antarctici*, a species with very limited annual production in Antarctica. Photo courtesy of Rod Seppelt.

The **cold Antarctic**, with summer mean air temperatures of 0-2°C, has a production of 200-900 g m⁻² in the larger moss turfs and carpets (Longton 1970, Davis 1981), comparable to temperate grassland (Longton 1992)! In this area, the biomass is more commonly 300-1000 g m⁻² for green shoots, and reaches 20,000 - 30,000 g m⁻² for total biomass, including older brown parts (Longton 1992). It is interesting that the production here is generally higher than in the Arctic tundra (Longton 1988, Russell 1990), exceeding 1000 g m⁻² yr⁻¹ (Russell 1990), perhaps due to greater precipitation and enhanced soil N and P from the marine environment (Longton 1992).

Arctic

Even in the cold Arctic (Figure 83), water is a major controlling factor in photosynthesis. *Sanionia uncinata* (Figure 77) has high photosynthetic activity only when water content is high during or following rainfall (Uchida *et al.* 2002). Temperature has little effect on net photosynthetic rates in this species, with photosynthetic rate being constant in the range of 7-23°C.



Figure 83. Arctic Lapland. Photo by Michael Lüth, with permission.

In Arctic habitats, bryophytes are often poorly represented in models on climate change and carbon balance (Street *et al.* 2012). Nevertheless, they are important components of the vegetation, and their seasonal dynamics are poorly understood. In a system dominated by *Polytrichum piliferum* (Figure 84) and *Sphagnum fuscum* (Figure 45). Street and coworkers found that seasonal changes in bryophyte photosynthetic capacity are important in determining gross primary productivity for both species and in contributing to the Arctic carbon balance. Gross primary productivity of *Polytrichum piliferum* was ~360 g C m⁻² for one year, for *S. fuscum* 112 g C m⁻², figures that represent 90% and 30% respectively of the productivity of tracheophytes in the same area. Furthermore, the bryophytes are not significantly affected by the turf water content during the growing season.



Figure 84. *Polytrichum piliferum*, a species with differences in photosynthetic capacity in different seasons in the Arctic. Photo by Jessica, through Creative Commons.

Wetlands

In the Arctic wetlands (Figure 85), mosses account for 91% of the above ground biomass (Oechel & Sveinbjörnsson 1978). Grasses and sedges usually arise from a bed of mosses, including the turf-forming *Meesia* (Figure 86) and *Cinclidium* (Figure 87) and carpet-forming *Calliergon* (Figure 88) and *Drepanocladus s.l.* (Figure 76)

species (Longton 1992). The annual production of 100-300 g m⁻² can be 20-45% bryophyte (Longton 1992) and the biomass is up to 150 g m⁻² (Oechel & Sveinbjörnsson 1978).



Figure 85. Arctic wetlands. NOAA, through public domain.



Figure 86. *Mesia longiseta* in Lapland, a genus that forms Arctic turfs where grasses and sedges grow. Photo by Michael Lüth, with permission.



Figure 87. *Cinclidium arcticum*, a genus that forms Arctic turfs where grasses and sedges grow. Photo by Michael Lüth, with permission.



Figure 88. *Calliergon sarmentosum*, an Arctic carpet-forming genus. Photo by Michael Lüth, with permission.

Tundra

In the tundra (Figure 89), mosses exhibit about 10% of the productivity of higher plants, despite occupying 50% of the above ground biomass. Whereas *Polytrichum strictum* (Figure 65) can have an annual production of 450-500 g m⁻² in the cool Antarctic grassland (Figure 90), it reaches only 100-150 g m⁻² in the Arctic spruce woodland (Figure 91) (Longton 1979). However, in some areas, the production reaches 50-90% of higher plant production and values up to 1000 g dry wt m⁻² yr⁻¹ can be measured (Clarke *et al.* 1971, Kallio & Kärenlampi 1975, Oechel & Sveinbjörnsson 1978, Russell 1990). More typical values are 1-50 g dry wt m⁻² yr⁻¹. Ratios of biomass to production can be exceedingly high, up to 70:1, illustrating the slow growth and the extreme longevity of the plants (Longton 1992). In heath communities in the tundra of northern Sweden, biomass reaches 156 g m⁻² (Jonasson 1982). However, in below ground biomass, the phanerogams far exceed the bryophytes, with underground parts contributing more than 50% of the total production of all plants (Longton 1984).



Figure 89. Tundra at Svalbard. Photo by Michael Lüth, with permission.



Figure 90. Tussock grass with Antarctic Fur Seal pups. Photo by Liam Quinn, through Creative Commons.



Figure 91. *Picea* in Alaska. Photo by Vita Plasek, with permission.

Coxson and Mackey (1990) found that the subalpine *Pohlia wahlenbergii* (Figure 1) exhibited strong diel periodicity in midsummer conditions, declining from $8 \text{ mg CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$ to $\sim 5 \text{ mg CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$.

Boreal Forest

In the boreal forest (Figure 92), the dominant mosses are feather mosses, especially *Hylocomium splendens* (Figure 12) and *Pleurozium schreberi* (Figure 93) (Longton 1992). Biomass can reach $170\text{--}290 \text{ g m}^{-2}$ under spruce in Alaska (Figure 92), but only $4\text{--}6 \text{ g m}^{-2}$ under *Betula* (Figure 94) and *Populus* species. Likewise, production was hardly measurable in the *Betula* and *Populus* forests, but reached $70\text{--}150 \text{ g m}^{-2}$ under spruce, often exceeding the productivity of the spruce itself (Longton 1992)! Similar rates to those under spruce are found for feather mosses in other coniferous forests (Tamm 1953; Weetman 1968; Pakarinen 1978). *Pleurozium schreberi* in black spruce forests in New Brunswick, Canada, had an annual productivity of $44\text{--}66 \text{ g m}^{-2}$ (Timmer 1970). Tamm (1953) reported $45\text{--}60 \text{ g m}^{-2}$ for *Hylocomium splendens* in a Swedish spruce forest and Damman reported 50 g m^{-2} for it in Newfoundland black spruce forests. Van Cleve and coworkers (1983), for black spruce forests near Fairbanks, Alaska, reported an even higher value of 100 g m^{-2} .



Figure 92. *Picea mariana* boreal forest with *Pleurozium schreberi* on the forest floor. Photo by Richtid, through Creative Commons.



Figure 93. *Pleurozium schreberi*. Photo by Jan-Peter Frahm, with permission.



Figure 94. *Betula papyrifera* forest. Photo by Nicholas A. Tonelli, through Creative Commons.

In addition to feather mosses, *Sphagnum* (Figure 43–Figure 48) is a prominent member of many boreal communities. In a black spruce forest, Swanson and Flanagan (2001) found that *Sphagnum* had higher maximum rates of gross photosynthesis than did the feather mosses and exhibited distinct seasonal changes in its photosynthetic capacity.

Several species of *Dicranum* occur in boreal forests, and Kellomäki *et al.* (1978) found that they differ physiologically in their ability to tolerate desiccation and photosynthesize. Even within the same species, two varieties can differ substantially. For example, the photosynthetic rate of *D. fuscescens* var. *congestum* (see Figure 42) increases more rapidly at 12.5°C than at 17.5°C with increasing light than does that of *D. fuscescens* var. *flexicaule* (see Figure 42), in which the rates at the two temperatures are essentially identical. In *D. fuscescens* var. *congestum*, the rate at 12.5°C is nearly double that at 17.5°C. However, water deficit has a strong effect on the photosynthetic rate. The best photosynthesis seems to occur in the morning when the plants are able to use morning dew while the temperature is still relatively cool.

Temperate Forest

Ground cover of bryophytes in temperate forests (Figure 95) varies widely. In oak forests (Figure 96) in Hungary, production is only 4.3 g m⁻² (Smith 1982). Oceanic European oak forests may reach 35.5 g m⁻² (Pócs 1982). Forman (1969) reported a scant 2-3 g m⁻² in deciduous forests in New Hampshire (Figure 97), USA, whereas Rieley and coworkers (1979) reported 1600-2900 g m⁻² in a Welsh *Quercus petraea* (Figure 98) woods. In these oakwoods, the production was 170-210 g m⁻² for the mosses, whereas the herbs had a production of only 120 g m⁻². Many of the oakwoods in England are on rocky hillsides where litter accumulation is small, whereas many North American temperate forests bury the mosses in litter (Figure 99) just as the fall growth season for mosses begins (Pitkin 1975). However, Rieley and coworkers (1979) offer another explanation. Sheep eat the grasses selectively and leave the mosses behind. On tree trunks and logs (Figure 100), above the litter, temperate forest bryophytes can be significant.



Figure 95. Temperate deciduous forest. Photo by Paul Bolstad, through Creative Commons.



Figure 96. *Quercus* forest understory habitat of *Ilacme plenipes*. Photo by P. Marek, W. Shear, and J. Bond, through Creative Commons.



Figure 97. Deciduous forest, NH. Photo by Ben Kimball, through public domain.



Figure 98. *Quercus petraea*. Photo by Rosser, through Creative Commons.



Figure 99. Deciduous forest floor in spring Chestnut Ridge Metro Park, Ohio. Photo by Janice Glime.



Figure 102. Douglas fir and Ponderosa pine forest, southern Oregon. Photo by Jsayre64, through Creative Commons.



Figure 100. Epiphytes on trees in California. Photo by Michael Lüth, with permission.

In the temperate rainforest (Figure 101) of Washington, USA, biomass can be as great as 800 g m^{-2} of tree surface, translating to 500 g m^{-2} of forest floor. In the Douglas fir forests (Figure 102) of Oregon, USA, bryophyte biomass can be as high as 8.9 kg on a single 65 m tall tree (Pike *et al.* 1972). On Mt. Baker (Figure 103) in Washington, bryophyte biomass averages ca 180 g m^{-2} (Edwards *et al.* 1960). However, in pine forests (Figure 104) in France, the moss *Pseudoscleropodium purum* (Figure 33) has a relatively low annual production of only 39 g m^{-2} (Kilbertus 1968).



Figure 101. Hoh National Rainforest, a temperate rainforest in Washington, USA. Photo by Molonecr7, through Creative Commons.



Figure 103. Forest habitat on Mt. Baker. Photo from Wild Earth Guardians, through Creative Commons.



Figure 104. *Pinus halepensis*, Aleppo Pines grove, Pinet, Hérault, France. Photo by Christian Ferrer, through Creative Commons.

Epiphytes

Neckera pennata (Figure 105) demonstrates that colony growth in area is proportional to colony size, thus exhibiting exponential growth (Wiklund & Rydin 2004). Precipitation was an important parameter in determining colony growth. Presence of other species reduced growth. Wiklund and Rydin estimated that the colony needs to attain a size of 12-79 cm² before reproducing sexually, taking 19-29 years to attain that size.



Figure 105. *Neckera pennata*, an epiphytic moss. Photo by Michael Lüth, with permission.

Peatlands

Peatlands (Figure 106) are often 3-d habitats with hummocks and hollows (Figure 107). Grigal (1985) projected that the surface area is 35% greater in a Minnesota peatland due to this 3-d microtopography. In addition to the increase in surface area, three other factors seem to be important in carbon sequestration:

- differences in dominant plant functional type
- interactions between temperature and water table depth
- ecosystem succession (Flanagan 2014).

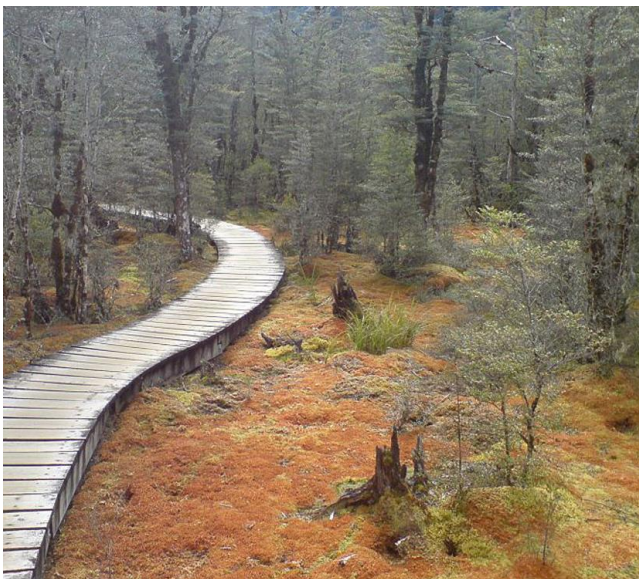


Figure 106. Bog with *Sphagnum* in Fiordland, NZ. Photo through Creative Commons.



Figure 107. Bohemia bog with *Sphagnum cuspidatum* and *S. denticulatum*, showing hummocks and hollows. Photo by Jonathan Sleath, with permission.

Moore (1989) found a slight tendency for production of *Sphagnum* (Figure 106) to decrease as temperatures decrease northward. Wider differences, however, occur within a single peatland. Hummocks (Figure 108) can have annual production of 100-150 g m⁻², lawns 500 g m⁻², and pools 600-800 g m⁻² (Clymo 1970, Clymo & Hayward 1982), suggesting that water availability is the limiting factor for production. Vitt (1990) reported that production varies from 70 to 400 g m⁻² per year, with fen mosses at the lower half of the range. The highest productivity measured in peatlands seems to be that of *Sphagnum* (868 g m⁻² yr⁻¹) in a recently burned *Eriophorum* (Figure 109) community in Great Britain (Heal *et al.* 1975). Grigal (1985) found a productivity of 320-380 g m⁻² yr⁻¹ in a forested Minnesota bog (Figure 110) and Elling & Knighton (1984) found slightly higher results (390 g m⁻² yr⁻¹) in an open Minnesota bog (Figure 111). These figures of production compare with a standing crop of 500 g m⁻² in west Norway (Laennergren & Oevstedal 1983). Somewhat lower values have been reported for Moor House, England, *Sphagnum*, where the productivity was 213 g m⁻² yr⁻¹ (Forrest & Smith 1975).



Figure 108. *Sphagnum papillosum* hummock. Photo by James K. Lindsey, with permission.



Figure 109. *Eriophorum scheuchzeri*. Photo by Meneerke Bloem through Creative Commons.



Figure 110. Spruce forest, Minnesota bog. Photo by Justin Melssen, through Creative Commons.



Figure 111. Minnesota open bog with early stages of tamarack. Photo by Katy Chayka, through online permission.

Surprisingly, rich fen production is lower. Vitt (1990) found that in Alberta, Canada, at higher elevations it was $47\text{--}93\text{ g m}^{-2}\text{ yr}^{-1}$, whereas in the lower boreal sites it was $125\text{--}131\text{ g m}^{-2}\text{ yr}^{-1}$. Vitt attributes the lack of increased

productivity in rich fens to the similarity of N and P concentrations in the poor, rich, and extreme-rich fens. Nevertheless, in poor fens, Bartsch and Moore (1985) found that productivity of *Sphagnum* (Figure 36-Figure 37) in Quebec was only $58\text{--}73\text{ g m}^{-2}\text{ yr}^{-1}$ in hummocks and $9\text{--}19\text{ g m}^{-2}\text{ yr}^{-1}$ in lawns. It is somewhat puzzling that bog hummocks have less production than carpets, but that poor fen hummocks have double the production of lawns (Vitt 1990).

In peatlands, bryophytes are major contributors to the primary productivity. At a peatland in West Virginia, bryophytes covered 68% of the ground and contributed 43% of the aboveground net primary productivity, with 20, 10, and 27% contributed by herbaceous species, trailing shrubs, and upright shrubs, respectively (Wieder *et al.* 1989). Bryophytes covered 68% of the ground. Precipitation plays a major role in the productivity. Moore (1989) found that growth at the lawn sites was higher than that of hummocks in an average rainfall year, but in a dry year, growth in two of the three lawn sites was less than that in the hummocks.

Species can differ widely in their photosynthetic activity. Dry matter accumulated $141\text{--}206\text{ g m}^{-2}$ in *Sphagnum tenellum* (Figure 37), $32\text{--}190\text{ g m}^{-2}$ in *S. papillosum* (Figure 36), and $187\text{--}219\text{ g m}^{-2}$ in *S. capillifolium* (*S. nemoreum*; Figure 35) at the Takadayachi Moor in Hakkoda Mountains, Japan (Fukushima *et al.* 1995).

Temperature influences the light compensation point of peatland mosses in Alaska (Harley *et al.*). The light compensation point increased from $37\text{ }\mu\text{M m}^{-2}\text{ s}^{-1}$ at 10°C to $127\text{ }\mu\text{M m}^{-2}\text{ s}^{-1}$ at 20°C , despite little increase in the maximum CO_2 uptake rate. Laboratory experiments indicated that responses could be quite different from that in the field, with considerably lower light compensation points and higher light saturation rates of assimilation.

Peatlands can serve as important carbon sinks. In restored peatlands, Waddington and Warner (2000) found that the peatlands resulted in considerable decrease in the atmospheric CO_2 ($\sim 70\%$ decrease due to gross productivity, 30% to decreased respiration). Unfortunately, restoration did not restore the peatlands to a net carbon sink, but it greatly improved the sequestration of carbon.

The peatland bryophytes, especially *Sphagnum* (Figure 36-Figure 37), are particularly sensitive to the direct sunlight of their habitat (Hájek (2014)). Due to the wetness of their habitat, they are unable to go dormant to escape its potential damage, and it can be difficult to obtain CO_2 due to diffusion resistance through water. Many *Sphagnum* species are desiccation avoiders, but are quite sensitive to drought when they actually do dry out. While hydrated, they are subject to photodamage. Slow growth rates are partly the result of allocation of resources to water-holding tissues.

Desert

In the Chihuahuan (Figure 112), Sonoran (Figure 113), and Mojave Deserts (Figure 114) in North America, the highest biomass of mosses (2.24 g m^{-2}) occurred on the north slope of the Mojave (Nash *et al.* 1977).



Figure 112. Chihuahuan Desert at Big Bend. Photo by Adbar, through Creative Commons.



Figure 113. Sonoran Desert at sunset. Photo by Bob Wick, through Creative Commons.



Figure 114. Mojave Desert on Hualapai American Indian Reservation. Photo by Richard Martin, through Creative Commons.

In a sandy semidesert, Juhász *et al.* (2002) found that *Syntrichia ruralis* (Figure 40) exhibited their highest daily carbon fixation rates in December and January, whereas in the summer it went dormant. A net carbon gain did not occur until October. This species is able to maintain its physiological integrity and net photosynthetic gain by changing the surface reflectance and exhibiting thermal dissipation of excess light energy (Hamerlynck *et al.* 2000).

Grimmia laevigata (Figure 115) from the inland chaparral of California, USA, is unable to survive in the most xeric sites because it is unable to maintain a positive carbon balance during repeated wet-dry cycles (Alpert & Oechel 1985).



Figure 115. *Grimmia laevigata*, a species that cannot maintain a positive carbon balance in the most xeric habitats. Photo by Michael Lüth, with permission.

In these dry habitats, cryptogamic crusts (Figure 116) are important producers and protectors of the soil (Coe *et al.* 2014). These are mixed communities of **Cyanobacteria** (Figure 117), algae, fungi, lichens, and bryophytes. Mosses comprise up to 30% of this crust cover. They are highly tolerant of desiccation and may remain dry for extended periods of time. They also are able to tolerate larger ranges of temperature, light, and cellular water content than mesic species.



Figure 116. Cryptogamic crust. Photo by Nihonjoe, through Creative Commons.

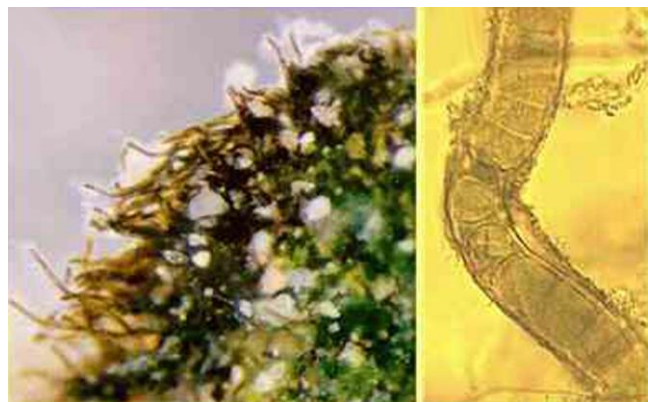


Figure 117. *Scytonema* (Cyanobacteria) in cryptogamic crusts. Photo from inactive website on Desert Ecology.

Elevated CO_2 stimulates the biocrust mosses, but it appears that they do not acclimate to long-term exposure by continued high rates of photosynthesis (Coe *et al.* 2014). Rather, the elevated levels might favor stress tolerance at the expense of growth, especially at high temperatures. Nitrogen appears to be an important limiting factor, but N deposition can be toxic, increase competition by tracheophytes, and interfere with nitrogen fixation by **Cyanobacteria** (Figure 117).

Dulai *et al.* (2014) used cryptogamic crusts containing **Cyanobacteria** (Figure 117) to test survival under Mars-like conditions. Those organisms that survived best were the ones from very salty and very dry habitats.

Savannah

In such dry habitats as the savannah (Figure 118), the life cycle can be shortened to accommodate the lack of water. Mosses such as *Archidium ohioense* (Figure 119), *Bryum coronatum* (Figure 120), *Fissidens minutifolius*, and *Trachycarpidium tisserantii* develop protonemata and gametophytes in March – April; by September and October the spores are being dispersed (Makinde & Odu 1994). All of these events occur within the rainy season, permitting maximum photosynthesis.



Figure 118. Savanna grassland with oryx in Samburu National Reserve, Kenya. Photo through Creative Commons.



Figure 119. *Archidium ohioense* with capsules, a savannah species. Photo by Li Zhang, with permission.



Figure 120. *Bryum coronatum*, a species that lives in dry savannahs. Photo by Michael Lüth, with permission.

Temperate Rainforest

Although the rainforest has its season of daily rain, it also has periods of continued dryness. Under these circumstances, respiration may exceed photosynthesis, causing negative photosynthetic gain (DeLucia *et al.* 2003). Forest floor bryophytes in a New Zealand rainforest (Figure 121) have an annual net carbon uptake of 103 g m^{-2} , compared to annual carbon efflux from the forest floor (bryophyte + soil respiration) of -1010 g m^{-2} . Bryophytes were unable to recover more than 10% of carbon lost from the forest floor. Water is the most likely limiting factor in their productivity.

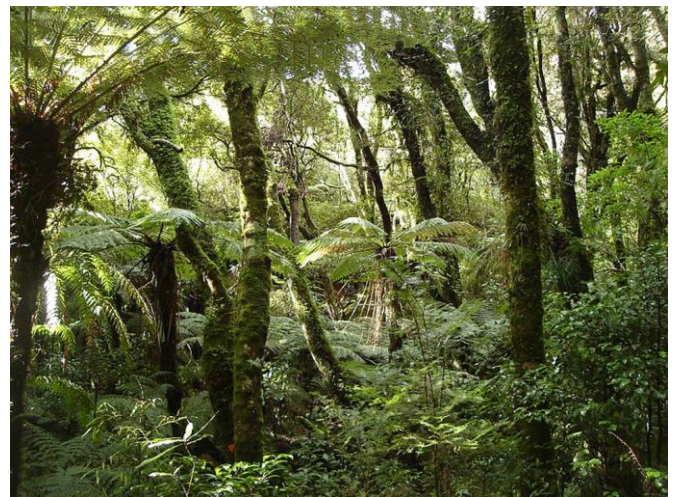


Figure 121. New Zealand rainforest. Photo by Stomac, through Creative Commons.

Tropical Rainforest

The biomass of bryophytes in the tropics rises sharply with elevation. Frahm (1990a) found standing biomass of bryophytes to be less than $10\text{--}12 \text{ g m}^{-2}$ of tree trunk at low elevations (up to 1000 m), up to 140 g m^{-2} in Peru (Figure 122), and $400\text{--}800 \text{ g m}^{-2}$ in Borneo (Figure 123). Exceptionally high biomass of bryophytes, up to 1030 g m^{-2} , can occur in high altitude epiphytes in Tanzania (Figure 124) (Pócs 1982). The astonishingly high figure of 1400 g m^{-2} productivity occurs among the epiphytic bryophytes of a Tanzanian cloud forest (Figure 125) (Pócs 1980).



Figure 122. Amazon rainforest. Photo through Creative Commons.



Figure 123. Bornean rainforest. Photo by Willo Eurlings, through Creative Commons.



Figure 124. Western Usambara Mountains and rainforest in Tasmania. Photo by David Ashby, through Creative Commons.

High temperatures and low light place severe limitations on tropical net productivity (Frahm 1990b). Temperatures above 25°C drastically decrease the net assimilation. Coupled with the low light, temperature causes productivity of bryophytes in tropical lowlands to be the lowest of any tropical altitude, with high rates of respiration often resulting in no net carbon gain.



Figure 125. Rain forest Tasmania. Photo by Owen Allen, through Creative Commons.

Tropical Altitudinal Relationships

Wagner *et al.* (2014) emphasized the importance of altitude (Figure 126) in affecting bryophyte diversity and productivity in the tropics, asserting that the bryophytes and lichens demonstrate a conspicuous increase with altitude in the tropics (Wagner *et al.* 2013). In the lowland rainforests (Figure 127), frequent fast drying events and low light greatly limit productivity, even for bryophytes (Wagner *et al.* 2014). These detriments are further enhanced by the warm, moist conditions at night, promoting high dark respiration. The optimum temperatures for net photosynthesis of the species at sea level, 500 m asl, and 1200 m asl in Panama were closely related to the mean temperatures in their habitats at each of those elevations (Wagner *et al.* 2013). However, the ratio of dark respiration to net photosynthesis did not decrease with altitude. Water, light, and CO₂ responses did not vary systematically with altitude. Lowland species often had near-zero carbon balances, most likely due to the rapid evaporation rate that restricts the time available for photosynthesis. This relationship seems to be consistent on a worldwide scale.



Figure 126. Gannett Peak alpine. Photo by Summitcheese, through Creative Commons.



Figure 127. Lowland Rainforest, Masoala National Park, Madagascar. Photo by Frank Vassen, through Creative Commons.

When comparing bryophytes across an elevation gradient on Mauna Loa (Figure 128), Hawaii, Waite and Sack (2011) found that nutrient concentrations in the bryophytes increased with soil nutrient availability. Nutrient concentrations on an area basis were related to irradiance, mediated by the bryophyte canopy mass per area. N and P behaved similarly to those nutrients in tracheophytes. Phosphorus increased and the N:P ratio decreased with elevation, a relationship that is consistent with increasing cold tolerance.



Figure 128. Mauna Loa. Photo by Joe Parks, through Creative Commons.

Problems in the Water

Productivity in aquatic systems is dependent on sufficient CO₂, suitable temperatures, and sufficient light (Glime 2014). Red light becomes negligible in deeper water, and even the CO₂ that is present is slowed by boundary layer resistance, all problems that are greater in water than in terrestrial habitats. Even pH is important in the availability of CO₂, with little or no dissolved CO₂ in alkaline water. Temperature becomes a problem when the bryophytes are wet and hot at the same time, a problem that can occur when the bryophytes are moist but not submersed (Figure 129). N and P are often limiting as well. The already limited light can be further reduced by sediments and algae on the plants (Figure 130-Figure 131).



Figure 129. *Platyhypnidium riparioides* experiencing hydrated conditions but not submersed. Photo by Michael Lüth, with permission.



Figure 130. *Fontinalis hypnoides* with sediments and detritus. Photo by Janice Glime.

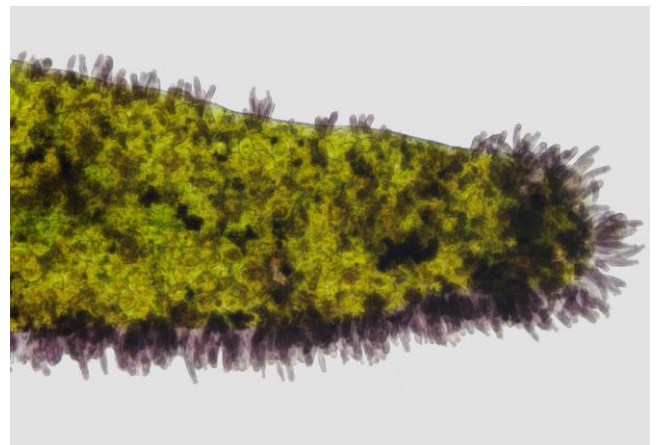


Figure 131. *Fissidens fontanus* with periphyton (algae) on its leaf. Photo by Dick Haaksma, with permission.

But there are some advantages not known in terrestrial systems (Glime 2014). The water serves as a UV filter. This can be enhanced in high light by production of protective pigments.

Rivers and Streams

Naiman (1983) considered mosses in 4th order or higher streams to be the most productive autotrophic members of the stream community in boreal forest

watersheds (Figure 132), producing $3.9 \times 10^{10} \text{ g yr}^{-1}$. This compares to periphyton productivity of only $2.1 \times 10^{10} \text{ g yr}^{-1}$ in the same watersheds. These higher order streams occupy 76.8% of the lotic surface area and are responsible for 86.3% of the gross productivity, demonstrating the importance of bryophytes in the stream ecosystem.



Figure 132. Boreal forest in Canada. Photo by Rich Bard, with permission.

But stream habitats can be rather unfavorable, especially for mosses. In one study in Oregon, *Fontinalis* (Figure 24) only had positive photosynthesis in the winter (Naiman & Sedell 1980). It was negative the rest of the year.

Despite their slow growth and low nutrient requirements, higher nutrients can favor enhanced growth in some bryophyte taxa. In Alaskan streams (Figure 134), *Hygrohypnum alpestre* (Figure 133) and *H. ochraceum* (Figure 135) increased in cover following phosphorus enrichment, whereas *Schistidium agassizii* (Figure 136-Figure 137) showed little response (Arscott *et al.* 2000). Although the *Hygrohypnum* species were intolerant of desiccation, they were more tolerant of high temperatures than *S. agassizii*, having the higher productivity ($1676\text{--}6342 \mu\text{g O}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$) compared to that of *S. agassizii* ($428\text{--}1163 \mu\text{g O}_2 \text{ g}^{-1} \text{ dry mass h}^{-1}$).



Figure 133. *Hygrohypnum alpestre* in Norway. Photo by Michael Lüth, with permission.



Figure 134. Alaska mountain and stream. Photo by Dhilung, through Creative Commons.



Figure 135. *Hygrohypnum ochraceum*. Photo by Michael Lüth, with permission.



Figure 136. *Schistidium agassizii* Norway 1 Michael Lüth, with permission.



Figure 137. *Schistidium agassizii*. Photo by Des Callaghan, with permission.

Lakes and Ponds

Bryophytes in lakes enjoy the presence of constant water, permitting photosynthesis at any time other factors are favorable. Instead of being at the mercy of water availability like most bryophytes, these bryophytes face the limits of low light intensity, rapidly attenuated red light, and limited CO₂ availability. In most lakes, temperature is not a problem, with bottom temperatures of deep lakes generally not going below 4°C, and summer temperatures often not exceeding 10°C. In more shallow lakes and ponds, summer temperatures may become a problem if they reach 20°C and sustain that temperature for extended periods. Under those conditions, hydrated bryophytes not only lose more energy to respiration than they gain by photosynthesis, but they must compete with aquatic tracheophytes and algae that benefit from the higher temperatures. Sediment CO₂ can often contribute to the productivity of bottom-dwelling bryophytes in lake systems.

The floating liverwort *Riccia fluitans* (Figure 138) increased its relative growth rate from 0.011 d⁻¹ at low light and CO₂ to 0.138 d⁻¹ at high light and CO₂ (Andersen & Pedersen 2002). There was strong acclimation to light and CO₂ conditions. Nevertheless, high light intensities resulted in decreased maximum net photosynthesis while increasing CO₂ continued to increase the maximum net photosynthesis. The CO₂ compensation point for photosynthesis was strongly depressed by high light and low CO₂ and increased in low light and high CO₂. High levels of CO₂ within the floating mat permits photosynthesis at greater depths where the light intensity attenuates.

Wagner *et al.* (2000) found that in Waldo Lake, Oregon, liverworts, comprising 98% of the bryophyte biomass, exhibited growth similar to that of upland plants (1.5-3 cm annually).

Problems with Bryophyte Measurement

The first problem one faces is measuring productivity in the field vs the lab. In the field, logistics are difficult and effects of CO₂ from the soil may be measured along with respiratory CO₂ from the bryophyte. Even putting the equipment in place can disrupt the bryophyte canopy morphology and change light, temperature, moisture, and CO₂ relationships within the canopy. On the other hand, if

we take the mosses into the laboratory, we have disrupted the canopy morphology, lost the normal variation of the field, altered light quality, and in other ways failed to mimic the conditions that occur in the field. And furthermore, laboratory experiments often use only a branch, losing all the effects of the bryophyte canopy and mechanisms of external transport. While these may be useful for physiological studies, they can be misleading when measuring productivity is the objective.



Figure 138. *Riccia fluitans*, a floating thallose liverwort. Photo by Michael Lüth, with permission.

Past history matters. Some bryophytes have inducible desiccation tolerance. Others provide it as a constitutive trait. Hence responses to various manipulations will behave differently depending on the recent environmental weather.

Summary

Productivity can be considered in many ways, including ability to invade, linear growth, biomass increase, CO₂ uptake, O₂ production, C¹⁴ incorporation, chlorophyll concentration, and surface expansion. Biomass gain may often be uncoupled from linear growth, with the former typically occurring first.

Likewise, annual growth of the plant can be measured in many different ways, including length of branch internodes; distance between splash cups on a stem; height above a cranked wire, tag, nylon net, plastic bubbles, or dye, growth out of a nylon bag; photographic record of expansion on a grid. Pleurocarpous mosses typically exhibit exponential growth, whereas unbranched acrocarpous mosses have linear growth, thus requiring different measures of growth.

Etiolation (excessive elongation and loss of chlorophyll due to insufficient light) may occur in low-light environments, giving a false measurement of length as an indication of productivity.

Productivity is generally highest when there is a good supply of water and ceases when the bryophyte is desiccated, causing seasonal differences. Once the moisture requirement is met, temperature and light are important in determining maximum productivity, with most bryophytes diminishing in productivity above 20-25°C and dying at prolonged exposure above 30°C if hydrated. The lower limit varies geographically and

with species, with some species having their compensation point as low as -10°C . In water, bryophytes are limited by low light and low concentrations of CO_2 , but those on the bottom can take advantage of CO_2 from the sediments.

Belowground productivity may be extensive in some bryophytes, such as those in the Polytrichaceae. Capsules, and even spores, can contribute to overall productivity, but at the same time, they typically reduce productivity of the leafy gametophyte.

Life span may be months to centuries, but unlike tracheophytes, generally only the upper portion of the stem supports active productivity. Mortality of the whole stem can be high, reaching 32% in Antarctic young populations of *Polytrichum strictum*. On the other hand, longevity may reach 17 years in the Arctic, compensating for the slow growth, and apparently is even higher in some cold lakes.

The **Leaf Area Index** (LAI) indicates that bryophytes are well adapted to take advantage of the many angles of the sun, reaching such levels as 44 and 129 for sun-adapted species, whereas a value of 1 indicates full usage; anything higher than 1 permits maximum usage at more angles of the sun. Mosses in the boreal biome have an LAI of about 20. Light use efficiency can be very high, but productivity still remains low, perhaps due to CO_2 limitation. Mosses have a maximum CO_2 uptake of about $3 \text{ mg dm}^{-2} \text{ hr}^{-1}$, whereas C_3 tracheophytes reach 45 and C_4 plants reach 80.

Some bryophytes, especially *Cryptothallus mirabilis*, rely on fungal partners for their carbon input. Other thallose liverworts can lose energy to fungi.

The **highest productivity**, when it occurs, seems to be from bryophytes in the driest habitats. On the other hand, yearly productivity seems to be highest in *Sphagnum*, reaching 12 tons per hectare.

Striking differences occur among **latitudes** and **habitats**. For example, Antarctic bryophytes have drastic daily temperature fluctuations and show little response temperature differences. Cool tundra populations of *Polytrichum strictum* may have only 1/4 – 1/3 the production they exhibit in the cool Antarctic grassland. The ultimate limit to productivity, hence to distribution, is achieving a positive carbon balance. Heat causes respiratory loss and frequent wet-dry cycles require excessive repair, both reducing the net carbon gain in some habitats to 0 and ultimate death.

Acknowledgments

Klaus Weddelling, Brian O'Shea, and Marshall Crosby helped me find the new name for *Hylocomium parietale*. It appears to have been *H. parietinum*, now *Pleurozium schreberi*. Several bryonettors helped me locate the current name of *Homaliodendron scalpellifolium*, which is now *H. flabellatum*.

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