

## Apparent photosynthesis of terrestrial mosses: An indicator of population functional health

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Apparent photosynthesis of terrestrial mosses: An indicator of population functional health. – Acta Mus. Siles. Sci. Natur., 68: 45-52, 2019.

**Abstract:** Terrestrial mosses dominate the ground in many vegetation types and most are long-lived perennials with highly complex canopies. Long-term population health continues through numerous wetting and drying cycles; however, extreme drought or extended wet periods may create conditions that cause some parts of the population to die or remain inactive. I examined apparent photosynthesis of fully hydrated populations of four terrestrial species of mosses occurring in leaf-free mesohabitats in temperate deciduous forests of eastern North America in order to explore photosynthetic variability of both populations and species. There was high variability in rates of apparent photosynthesis among the populations of mosses for all four species examined in this study. Despite this variability within species, all four species achieved similar mean rates of photosynthesis. Two years after relocation to nearly bare ground habitats, populations of three of the four species achieved similar apparent photosynthetic rates as natural populations, and functioned in a similar manner.

**Key words:** Apparent photosynthesis, *Bryoandersonia illecebra*, deciduous forest, moss, *Thuidium delicatulum*

### Introduction

Bryophytes can form a dominant component of the terrestrial landscape in a number of vegetation types. For example, coniferous boreal forests have ground layers of a nearly continuous cover of feather mosses (Bonan & Shugart 1989; Esseen *et al.* 1997). Both minerogenous acidic (poor) fens and ombrogenous bogs have ground layers of 80-100% cover of *Sphagnum* mosses, while calcareous rich fens are dominated by a number of species of true mosses (Gorham & Janssens 1992; Vitt 2000; Wheeler & Proctor 2002). Higher elevation site-types in tropical areas can have ground layers with high cover (Richards 1984; Vitt 1991), as well as temperate rain forests at low elevations (DeLucia *et al.* 2014). Also, early successional stages of lava flows can have 100% cover of mosses in cool mesic climates such as those found in Iceland (Fig. 1) and higher elevations on the Hawaiian Islands. Temperate forests dominated by deciduous trees also have a rich flora of terrestrial bryophytes, but these are usually restricted in occurrence to areas where leaf litter is limited (Loeske 1901; Startsev *et al.* 2008, Fig. 2). In most of these situations, bryophytes can play a significant role in the moisture regime and carbon and nitrogen budgets of the ecosystem (Goulden & Crill 1997; DeLuca *et al.* 2002; Bond-Lamberty *et al.* 2004).

Like vascular plants, bryophytes have complex canopies with abundant leaves that provide the structure for photosynthesis. Also, like many vascular plants, many bryophytes are long-lived perennials with strong support mechanisms contained in the branches and stems. Unlike vascular plants, bryophytes are poikilohydric and have little ability to control water loss. The small size of bryophytes provides for high ratios of surface area to volume that means that they dry out quickly (Proctor *et al.* 2007) - as a result, metabolic activity, especially gas exchange is limited by water availability (reviewed by Vitt *et al.* 2014). As drying occurs, photosynthesis decreases and individual species each have different drying curve times. In most terrestrial

habitats mosses may spend a majority of their time dry and inactive and achieve maximum photosynthetic rates only when fully hydrated. Although overall long-term population health may continue with normal wetting and drying times, extreme drought or extended wet periods may create conditions that cause some parts of the population to die (Proctor *et al.* 2007). In these cases, populations may persist for some time, yet remain only partially healthy and active, with individual stems and/or leaves non-functional.



**Figs 1–2:** Photographs of terrestrial moss habitats. **1** – *Racomitrium lanuginosum* dominating old lava flows occurring near Nesjavellir Power Plant, southeastern Iceland. **2** – *Oxyrrhynchium hians* and *Haplocladium microphyllum* occurring in leaf-free areas of a temperate deciduous forest (Illinois, U.S.A.).

Carbon fixation is determined by the maximum rate of photosynthesis when the bryophyte canopy is fully hydrated and the rate of photosynthesis that is associated with the individual species drying curves. Previous studies have in general, demonstrated in the laboratory that rates of photosynthesis of bryophytes are similar to those of vascular plants when based on chlorophyll contents (Martin & Adamson 2001). Other studies, (e.g., Wang *et al.* 2017) have extracted individual plants or the green portions of individual plants from bryophyte populations and measured photosynthesis under fully hydrated conditions in the laboratory and report data on a mass basis. However, studies that examine rates of photosynthesis of natural populations are rare. Under natural conditions, undisturbed bryophyte populations consist of three dimensional canopies of overlapping leaves containing chlorophyll, along with structural components of stems, branches, and rhizoids without chlorophyll. From an ecosystem perspective, it is important to know the extent that natural populations are healthy and actively sequestering carbon and how this activity varies across a number of populations of the same species occurring in a similar habitat. In this study, I examined rates of photosynthesis achieved in microcosms populated by natural, fully hydrated populations in order to provide an indicator of population health and how it compares across a number of mono-specific populations. I asked two questions: 1) Do different species of mosses have similar apparent photosynthetic rates when fully hydrated and 2) How do the carbon flux rates of these populations vary when fully hydrated?

Many mosses, including many terrestrial species, interact and receive moisture mostly (or only) from the atmosphere, rather than from the substrate (Busby *et al.* 1978; Vitt & Glime 1984). These mosses have complex canopies and structural features that enable hydration and water retention with little interaction with the underlying substrate. However as far as I am aware it is not known if when removed from the the substrate and relocated to a nearby locality with similar substrate if 3) these populations continue to have similar carbon flux rates and 4) if the relocated populations function similar to the original ones?

## Study Areas

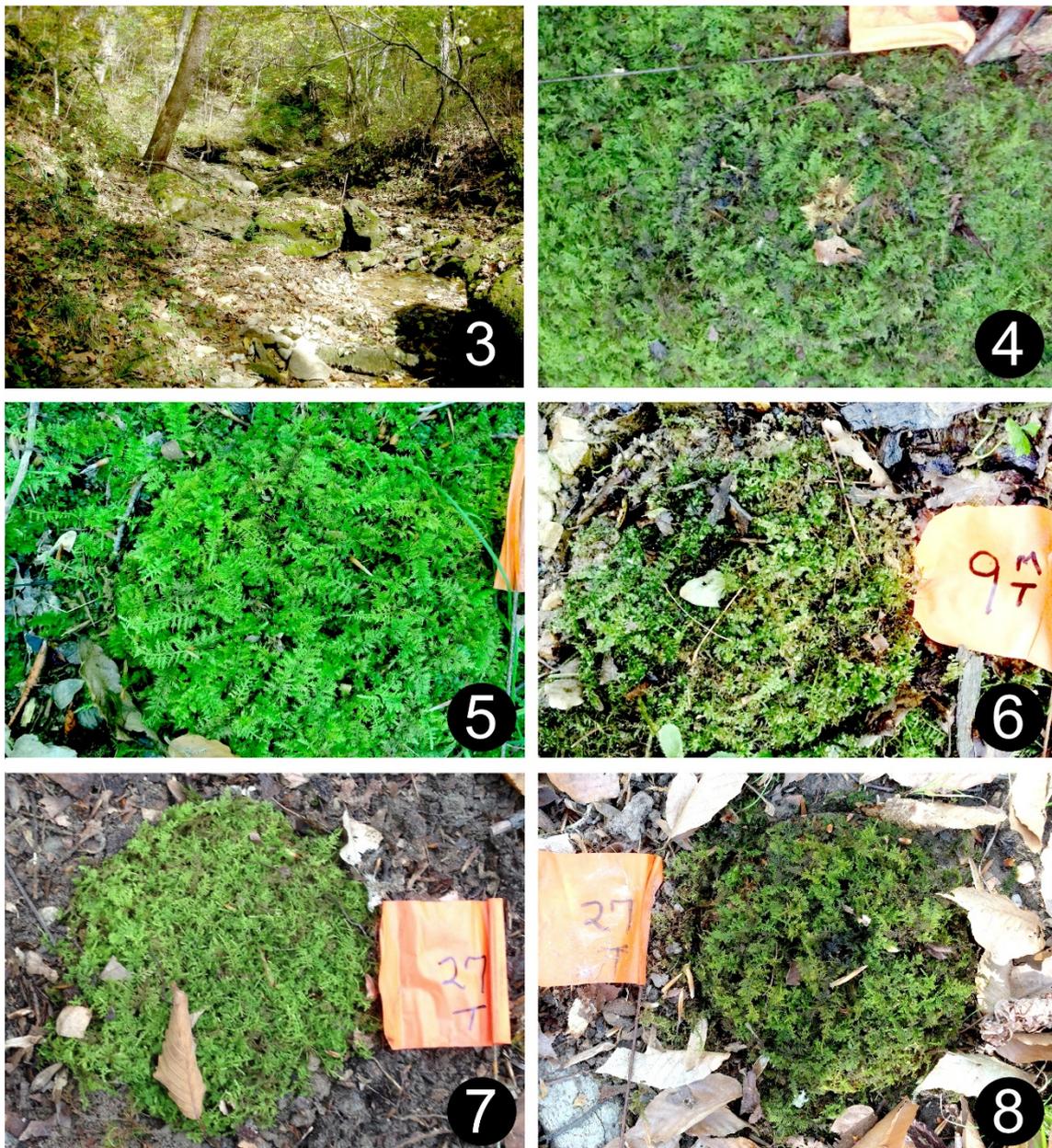
Forested watersheds along two headwater streams, one in Fairfax County, Virginia (38°40'22"N; 77°12'07"W) and one in McDonough County, Illinois (40°25'55"N; 90°53'35"W), were sampled for moss populations occurring on terrestrial, exposed micro-sites, especially frequent along the banks of small streams (Fig. 3). Both study areas are located in largely undisturbed, mature, eastern deciduous, temperate forests. In Virginia, the dominant tree species is *Fagus grandifolia*, along with *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Fraxinus* spp., *Carya alba*, *Acer saccharum*, and *Quercus prinus*, with a sparse understory of *Ilex opaca*. In Illinois the dominant tree species are *Quercus alba*, *Q. rubra*, *Q. velutina*, *Tilia americana*, *Carya* spp., and *Platanus occidentalis*. Bryophytes occur on exposed micro-sites where leaf litter is reduced due to slightly higher elevations and proximity to streams with less canopy cover (Vitt *et al.* 2018). At the Virginia site, *Thuidium delicatulum* and *Bryoandersonia illecebra* are abundant, while at the Illinois site, *Plagiomnium cuspidatum* and *Oxyrrhynchium hians* are the most abundant species. Site characteristics and a list of bryophytes found in the research plots are in Vitt *et al.* (2018). Climate of the two study areas is similar, with long-term annual precipitation and mean annual temperature varying from 97 cm and 14.5°C (Illinois) to 101 cm and 9.9°C (Virginia), respectively.

## Methods

At each study area, 28 patches of bryophytes on stream banks were selected, with each site about 30-50 m apart. At each site and within well-established natural moss populations, a 158 cm<sup>2</sup> circular plot was established and permanently marked by a sharpened circular plastic sleeve (Figs. 4-5). In October of 2015, a second 158 cm<sup>2</sup> circular plug was removed from the natural population and relocated to nearby bare soil (Figs. 6-8). Over the course of two years (October 2015-October 2017) plots were monitored and their fate recorded each spring and fall. During this time period, some of the natural populations and relocated samples were lost to erosion or stochastic events (e.g., limb and tree fall) as well as leaf litter cover for the relocated populations. For the purposes of this study and when feasible, during the first year these lost plots were replaced with plots from nearby natural populations or extracted and placed in the same location as the earlier relocated sample. After two years and in

October 2017, 42 samples from the Virginia study area and 29 samples from Illinois study area were gently lifted from the underlying mineral soil and transported to the laboratory.

In the field, the individual moss samples were collected in 81 cm<sup>2</sup> petri dishes, closed with tape, and transported to the laboratory, sprayed until saturated with deionized water and left for 30 minutes for surface water to evaporate, and placed in a chamber (158 cm<sup>2</sup> area with a volume of 1,100 mL). These microcosms were maintained at 20°C and provided with 1,000 mmol m<sup>-2</sup> sec<sup>-1</sup> light covering the photosynthetic spectrum (CI 301 LA light source). CO<sub>2</sub> flux was measured using a PP Systems Model EGM-4 IRGA. Microcosms were left for 15 min to equilibrate before flux measurements and CO<sub>2</sub> flux recorded after an additional 5 min. Rates are here reported as apparent photosynthesis - defined as the rate of photosynthesis less the rate of photorespiration (Wohlfahrt & Gu 2015).



**Figs 3–8:** Photographs of one study area and various plot types. **3** – Typical forest along stream in Illinois. Photo taken October 2017. **4** – Natural population of *Thuidium delicatulum* (Virginia) with a few shoots dry (center) among the remaining wet population. Photo taken May 2017. **5** – Natural population of *Plagiomnium cuspidatum* (Illinois). Photo taken May 2017. **6** – Transplant population of *Plagiomnium cuspidatum* (Illinois). Photo taken May 2017. **7** – Recent transplant at plot 27 (October 2015) of *Thuidium delicatulum* (Virginia). Photo taken October 2015. **8** – Transplant population at plot 27 of *Thuidium delicatulum* (Virginia). Note bark in both Fig. 7 and 8 in lower left of photos. Photo taken October 2017.

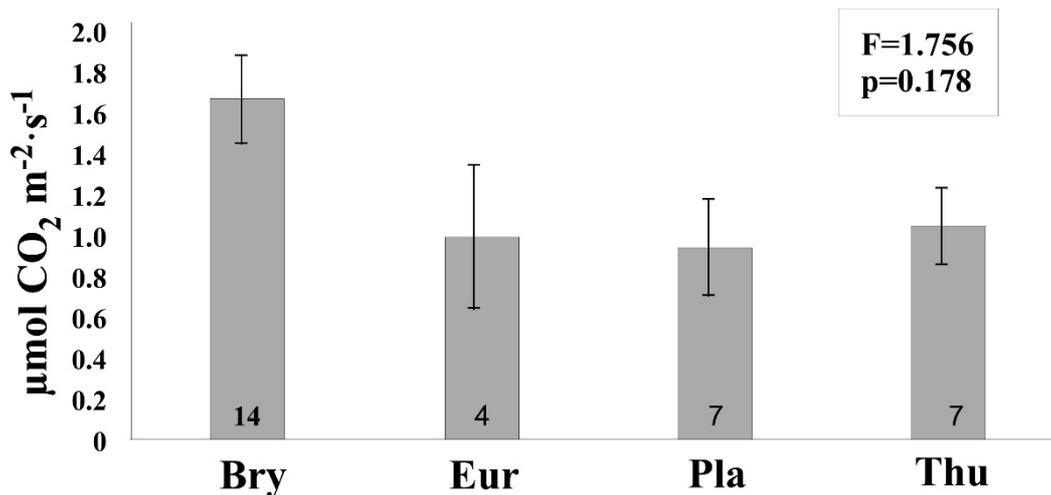
## Results

**Site comparisons.** In total, we collected and analyzed 42 natural moss populations (23 from Virginia and 19 from Illinois) and 29 relocated populations (16 from Virginia and 13 from Illinois). Apparent photosynthesis was not different between the two sites for either the natural populations (t-test:  $p=0.574$ ) or the relocated populations (t-test:  $p=0.192$ , Table 1) despite the two study sites having very different moss floras. Thirteen moss species occurred in the plots with a total of 38 occurrences at the Virginia study site, with *Thuidium delicatulum* occurring as the dominant species in 46% of the plots, and *Bryoandersonia illecebra* occurred as a dominant in 25%. In comparison, at the Illinois site, 16 moss species occurred in the plots, and in total these occurred 64 times, with *Plagiomnium cuspidatum* dominant in 36% of the plots. *Oxyrrhynchium (Eurhynchium) hians* was found in 10 of the plots (Vitt *et al.* 2018).

**Tab 1:** Comparison of mean (S.E.M.) CO<sub>2</sub> flux ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for microcosms with populations from the two study areas in Fairfax Co., Virginia and McDonough Co., Illinois. Non-significant differences tested with t-test with alpha <0.05.

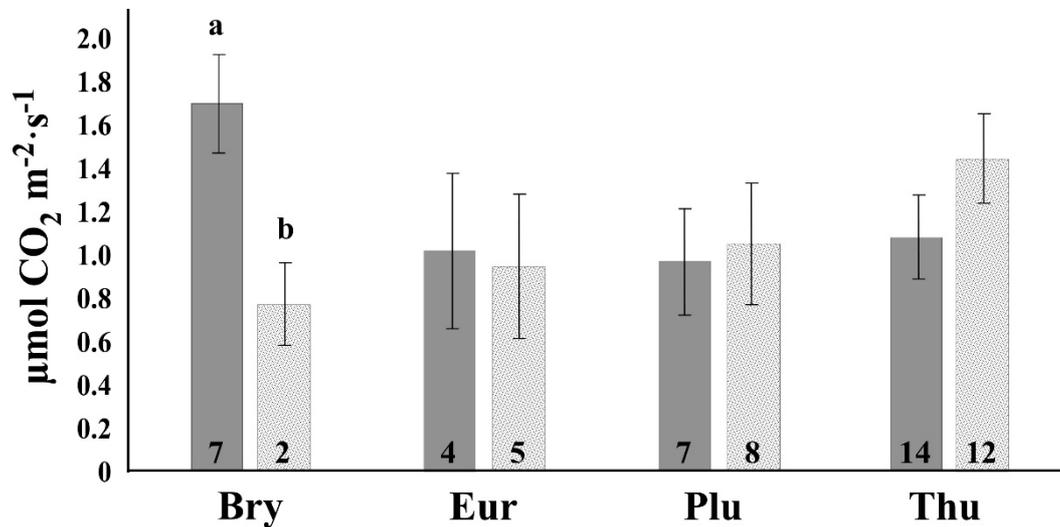
	Virginia	Illinois		
<b>Natural populations</b>	1.29 [n=23] (0.15)	0.96 [n=19] (0.14)	t=1.61	p=0.574
<b>Relocated populations</b>	1.25 [n=16] (0.17)	1.02 [n=13] (0.19)	t=0.88	p=0.192

**Species comparisons.** We examined fully hydrated apparent photosynthesis for the four most abundant species, *Thuidium delicatulum* and *Bryoandersonia illecebra* from the Virginia site and *Plagiomnium cuspidatum* and *Oxyrrhynchium hians* from Illinois. Mean apparent photosynthesis ranged from  $1.67 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *B. illecebra* to  $0.95 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *Plagiomnium cuspidatum*; however, apparent photosynthesis for the four species did not differ significantly ( $f=1.756$ ,  $p=0.178$ , Fig. 9). Overall, considerable variation was present in the microcosms ranging from 0.57 to  $3.03 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .



**Fig 9:** Comparison of CO<sub>2</sub> flux within microcosms from natural populations of four moss species (mean  $\pm$ S.E.M. with one-way ANOVA). Numbers in bars are number of samples. Bry = *Bryoandersonia illecebra*, Oxy = *Oxyrrhynchium hians*, Pla = *Plagiomnium cuspidatum*, Thu = *Thuidium delicatulum*.

**Relocation comparisons.** Microcosms with relocated populations did not differ from those from natural populations for *Thuidium delicatulum* (t-test:  $p=0.107$ ), *Oxyrrhynchium hians* (t-test:  $p=0.444$ ), and *Plagiomnium cuspidatum* (t-test:  $p=0.406$ ) with  $\text{CO}_2$  flux varying from  $1.42 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$  to  $0.93 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Apparent photosynthesis for relocated populations was different for *Bryoandersonia illecebra* (t-test:  $p=0.019$ ), with relocated populations about 45% less than natural populations (Fig. 10).



**Fig 10:** Comparison of  $\text{CO}_2$  flux from microcosms from natural and relocated populations of four moss species (mean  $\pm$  S.E.M.). Different letters indicate significant differences at  $\alpha < 0.05$  (one-way ANOVA for each species calculated separately). Numbers in bars are number of samples. Bry = *Bryoandersonia illecebra*, Oxy = *Oxyrrhynchium hians*, Pla = *Plagiomnium cuspidatum*, Thu = *Thuidium delicatulum*.

## Discussion

Fully hydrated rates of photosynthesis at saturating irradiance for the four moss species were within the ranges usually reported for bryophytes on an area basis (Rice *et al.* 2008, Waite & Sack 2010; Wagner *et al.* 2014; Wang *et al.* 2014; Liu *et al.* 2015). Wang *et al.* 2017 reported a mean of  $1.45 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  with a range of  $0.41$  to  $7.01 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , values that encompass those reported here. Likewise, Delucia *et al.* (2014), who utilized microcosms similar to those used here, reported somewhat similar values of (gross) photosynthesis and also reported considerable variation in rates of photosynthesis.

Although the mean photosynthetic rate of *Bryoandersonia illecebra* is considerably higher than the other three species, there are no significant differences between the four species (two from each site) due to the high levels of variation within microcosms for each species. There are several possible reasons for this high variation – 1) our methodology for wetting the microcosms did not provide consistent hydration for the moss canopy, 2) natural populations have inherent variability in functioning photosynthetic units, and/or 3) portions of natural populations are variably non-functional (see Fig. 4). It could be that our rehydration procedures (similar to those many others have used, (see DeLucia *et al.* 2017; Wang *et al.* 2017) may have led to some small, yet unknown, portion of the variability. It is also possible that there is significant natural variability among moss populations, both in terms of canopy density, amount of living vs. dead stems and leaves, and per cent of functional tissue that are contributing to photosynthesis at any one time. However, despite variable photosynthetic rates, it is remarkable that the four species have similar mean photosynthetic rates and have similar functional contributions to the ecosystem carbon flux.

The microcosms containing the relocated populations achieved similar photosynthetic rates as the microcosms with natural populations for three of the four species, again with similar variation. The one exception, microcosms with relocated *Bryoandersonia illecebra*, had significantly lower photosynthetic rates. This species is a relatively large species with loose canopy structure that is easily damaged during the establishment period or to inability to re-establish a cohesive canopy after relocation.

In conclusion, there is high variability in rates of photosynthesis among the populations of mosses that were examined in this study, indicating that overall health of individual populations may also be variable and may be related to recent periods of drying, with severe desiccation periodically damaging the functioning of moss populations (Abel 1956). Despite this variability within species, all four species achieved similar mean rates of photosynthesis. Relocating populations of mosses that are highly dependent on atmospheric inputs suggests that in three of the four species interactions with the underlying mineral soil have little influence on photosynthetic rates.

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