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Review

Roles of Bryophytes in Forest Sustainability—Positive or Negative?

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Abstract: Bryophytes were traditionally ignored in most studies of forest ecosystem processes, or they were included with litter or soil. In the last few decades we have begun to understand their many roles that permit them to be ecosystem engineers. This review serves to pull together many scattered sources into a single source on the many contributions bryophytes can perform as ecosystem engineers and to support what several authors have already stressed: that bryophytes should not be treated as a single functional group. It puts bryophytes in perspective in terms of richness and biomass, then explores their roles as ecosystem engineers; that is, their roles in altering diversity, nutrient cycling, carbon sequestering, water retention, erosion depression, temperature modification, fire protection, fire and logging recovery, interactions with mycorrhizal fungi, effects on seed germination, and seedling survival. Interactions with other species are mentioned, but those regarding animals are largely omitted in favor of more detailed description of their relationships with trees throughout the world. Bryophytes provide both positive and negative interactions with forest trees, depending on the tree species, the ecosystem, and the bryophyte species. It is clear that different bryophytes have many different functional roles in sustaining the forest and making it suitable for germination, seedling success, and maintaining the mature forest. This review indicates those important roles and how they apply differently according to both tree and bryophyte species, and that different management practices are needed, depending on both bryophyte species and tree species, to sustain different forest types.



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Keywords: abundance; allelopathy; decomposition; ecosystem engineers; functional groups; nutrient cycling; productivity; richness; seedbeds; temperature modification; water retention

1. Introduction—Perceived Roles of Forest Bryophytes

“Ecosystems are more than the sum of their parts” [1]. It was always disappointing that forest studies rarely included bryophytes [2–6]. Bryophytes often were considered part of the soil. However, we are now understanding the important roles of bryophytes in sustaining forest communities. For example, mosses in old-growth Douglas fir forest added 20% to total biomass and 95% to photosynthetic tissue biomass [7] when compared to earlier studies [2,3].

Bryophytes are relatively sparse on the floors of deciduous forests, but in boreal forests the feather mosses *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt. form expansive cover [8,9]. Oechel and van Cleve [10] considered them to be interesting because they “may form a minor element of the community in terms of biomass, while simultaneously being a major element in terms of cover and primary productivity”. Bryophytes alter and even control ecosystem processes through their nutrient uptake and sequestration, and alteration of the thermal environment of soil, including depth of permafrost. These factors impact the trees in ways not accomplished by tracheophytes. (Tracheophytes are those plants traditionally referred to as vascular plants, but since we

now know that bryophytes often have vascular (but non-lignified) tissue, I shall use the term tracheophyte throughout to refer to non-bryophyte plants).

The bryosphere is a natural model system for the study of environmental change that results in changes in biodiversity and ecosystem function by uniquely integrating aboveground and belowground processes, indicating that it is an underutilized system with exceptional promise [11]. However, before we can use bryophytes to help us in sustaining forests, we must gain considerable understanding of their roles in forest ecosystems, not as a whole, but as functional groups and even species.

Although forest studies have traditionally focused on trees [12], this approach is changing as ecologists realize the roles bryophytes and other organisms play, especially in northern forests [13]. Bryophytes perform a number of ecosystem services, many of which are little known across multiple forest types [14,15]. Their ability to prevent erosion is widely known, but other roles are barely known beyond a few ecologists and bryologists [16], with managers and planners often not giving them any consideration (e.g., [6,17]). Understanding moss traits that regulate the performance of boreal forest ecosystems (ecosystem N supply, C sequestration, permafrost stability, and fire severity) is critical to understanding the resilience of the boreal forest region in Alaska, particularly in view of changing climate and disturbance regimes [18]. It is likely that they have unique roles in forests worldwide [19]. Such roles include: water trapping and retention; nutrient trapping; facilitation of N fixation, retention, and release; CO₂ trapping; productivity; seedbeds; rebuilding damaged environments; soil temperature modification; overwintering sites for amphibians; mating call sites for amphibians; homes for invertebrates; and providing suitable habitat for soil fungi and bacteria. In addition, long-term roles include altering the depth of permafrost formation and thaw, peat accumulation, and development of microtopography [20].

As our climate changes and northern habitats become warmer, bryophytes could play a significant role in determining which tree species remain and which are replaced. Turetsky and coworkers [20] considered that in northern ecosystems an extreme perturbation would be required before mosses would be eliminated. Would trees moving farther north be able to germinate on a moss-covered forest floor? Would others disappear if mosses disappeared or species changed? Dying mosses decompose slowly to return sequestered nutrients but would decompose more quickly at warmer temperatures. Two models [20] indicated that loss of mosses would reduce soil C accumulation by increasing decomposition rates and altering soil N availability. N availability would improve in the absence of mosses that sequester N and prevent it from supporting roots, but loss of N would occur due to reduced N fixation by Cyanobacteria among feather mosses, some liverworts, and probably other as yet unknown bryophyte hosts.

In the forests of Finland, the most important factor in the distribution of bryophytes and tracheophytes was site moisture, with soil acidity, intensity of water flow, stoniness, land use history, and exposure also contributing [21]. Bryophytes were more sensitive to N, Ca, and soil moisture than were tracheophytes. Tracheophytes were more sensitive to earlier land use, altitude, and Mg. Hence, bryophytes filled niches and functions where tracheophytes were unable to thrive. Such niche differences are likely to occur worldwide.

Turetsky and coworkers [20] have provided a good review of the role of bryophytes in boreal forests, but there is no recent comprehensive review on the roles and interactions of bryophytes in global forests; this has created a void in the management of forests, particularly in view of climate change, fire, and logging. This review is intended to fill that void and will emphasize the ability of bryophytes to alter the forest ecosystem in both beneficial and detrimental ways, as these differ among both tree species and bryophyte species. It emphasizes the importance of avoiding considering bryophytes as a single functional group and demonstrates how their roles differ among forest types. Because of the large number of relevant studies on bryophytes' roles in forests published in the past 40 years, the interesting and important topics of interactions with animals and effects on diversity will not be addressed, but rather I will emphasize the interactions with trees.

Bryophytes are often a major photosynthetic component in the forest, and through their activities in moisture retention, nutrient sequestering, and temperature modification they make it possible to sustain (or deprive) mature forests and to promote or exclude seed germination and seedling development. Optimal management of the forests will be incomplete without understanding these roles as bryophytes interact with the forest species to sustain or change the forest. This review pulls together our current state of knowledge, discusses the functional roles of different bryophyte species, and indicates the areas of need for further research to optimize management for forest sustainability. This review will answer the question of what are the positive and negative roles of forest bryophytes, as we currently understand them, in providing richness and biomass, altering the physical environment, providing rapid recolonization following disturbance, contributing to nutrient cycling and carbon sequestration, and making live or die conditions for tree seedlings. It emphasizes the problems in treating bryophytes as a single functional group.

2. Review Methods

This review used three primary sources: Google Scholar searches, searches on my extensive personal bibliography accumulated over more than 60 years, and literature cited in papers I found. The search words included such combinations as bryophytes and forest sustainability, forest bryophyte productivity, forest bryophyte richness or diversity, forest bryophyte abundance, forest bryophyte roles, bryophyte forest ecology, bryophytes as forest seed beds, forest bryophytes and fungi, forest bryophytes and bacteria, bryophyte decomposition, bryophytes and nutrient cycling. Topics raised in the resulting references, especially those on roles and on nutrient cycling, suggested additional search words that helped determine the topics covered in this review. I stopped sifting through the results when I found one or more results pages with no new references containing useful information. The important area of animal interactions was omitted due to space limitations. The review begins with an overview of the richness and abundance of forest bryophytes, to provide a sense of their availability in various forest types. There are surely more papers related to sustainability, but those included should provide the most important aspects of the roles—both positive and negative—of bryophytes in forest sustainability. I have attempted to synthesize and evaluate the various roles for the major forest types.

3. Bryophyte Presence

Bryophyte presence increases species richness, their abundance provides substrate cover, and their biomass contributes to productivity, all depending on the ecosystem and types of forest trees.

3.1. Richness

The richness (number of species) of forest bryophytes varies widely, but in many of these ecosystems they contribute considerable diversity, rivaling that of tracheophytes in many forest types [22]. Furthermore, as substrate diversity increases, so does bryophyte diversity [23]. Whereas bryophytic epiphytes are relatively few on most **conifers**, they can reach considerable numbers on trees in the tropics. **Deciduous forests** can have high bryophyte diversity because of emergent substrates and the variety of exposed branch and bark substrates. Forests affected by fire disturbance tend to harbor more bryophyte species than those unaffected by fire disturbance; the amount of dead wood present is an important contributor to that diversity [24]. Table 1 represents but a small fraction of forest types to show examples of bryophyte richness, but caution should be exercised because of greatly differing sample sizes and included substrata. Nevertheless, they point to a bryophyte species richness that cannot be ignored.

Table 1. Bryophyte species richness (number) of various forest types and locations around the world.

Forest Type	Location	Substrate Layer	Species Number	Ref.
Mixed temperate	Acadia, ME, USA	Epiphytes	62	[25]
<i>Picea-Abies</i>	S Appalachian Mtns, USA	Ground	97	[26]
<i>Picea glauca-Abies</i>	N. Amer. taiga	All	133	[8]
<i>Picea abies virgin</i>	SW Sweden	All?	88	[27]
<i>Picea abies managed</i>	SW Sweden	All?	56–72	[27]
Boreal old-growth swamp	Sweden	All	195	[24]
Sub-boreal spruce	B C, Canada	Ground, epiphyte	46, 1	[28]
<i>Populus tremuloides</i>	SW QC, Canada	Epiphytes	41	[29]
Forest patches	central Norway	All	285	[30]
Evergreen laurel	Madeira Island, Portugal	Epiphytes	110	[31]
Submontane rainforest	Bolivia	Epiphytes	80	[32]
<i>Quercus copeyensis</i> , cloud forest	Costa Rica	Tree trunks	44	[33]
Mountain rainforests	Ecuador	Epiphytes	65	[34]
Neotropical lowland	Guianas	Epiphytes	154	[35]
Upper montane oak	Costa Rica	All	206	[36]
Cloud forest	Monteverde, Costa Rica	All	190	[37]
European	Terceira Island, Azores	All	106	[38]
Mediterranean	Tuscany, Italy	Ground, epiphytes	128	[39]
Tropical rainforest	Chiapas, Mexico	Major habitats	136	[40]
Atlantic Forest	SE Brazil	All (only liverworts)	238	[41]
Swamp and upland evergreen	Atewa Forest, Ghana	Altitudinal gradient	164	[42]

Old-growth forests tend to have more bryophyte species than do early successional stages [43]. In western Massachusetts, USA, for example, old-growth forests had nearly twice the number of epiphytic bryophyte species found in second-growth forests. Even when comparing trees of the same diameter and species, **sugar maple (*Acer saccharum* Marshall)**, in old-growth forests compared to those in second-growth forests, these richness differences were present.

3.2. Abundance and Biomass

Both abundance and biomass (Table 2) of bryophytes vary with forest type. Coniferous forests tend to have more bryophyte ground cover than most other types, but most conifer species have poor epiphytic bryophyte communities.

3.2.1. Coniferous Forests

Bryophyte biomass in the ground layer of coniferous forests can be quite significant compared to that of most other forest types. In the **dark coniferous forest** on the north slope of Changbai Mountain, China, it varied with altitude; the lowest biomass (54,300 mg m⁻²) occurred at 1100 m asl and the greatest (509,700 mg m⁻²) at 1250 m [44]. In the northwestern Himalayas, which are dominated by dense coniferous forests with some temperate broad-leaved species, total bryophyte biomass was significantly higher (25,580 mg m⁻²) in canopy gap areas compared to non-gap areas (20,440 mg m⁻²) [45].

Table 2. Bryophyte biomass of various forest locations and habitats around the world.

Forest Type	Location	Habitat	mg m ⁻²	Ref.
Dark coniferous	Changbai Mountain, China	1100 m asl	54,300	[44]
		1250 m asl	509,700	[44]
Dense coniferous	Himalayas, India	Gaps	25,580	[45]
		Non-gaps	20,440	[45]
<i>Pseudotsuga menziesii</i>	Cascade Mtns, OR, USA	Ground layer	1075	[46]
		epiphytes	2.6 kg/tree	[46]
<i>Pseudotsuga menziesii</i>	California, USA	Bryo epiphytes	4.7 kg/1 tree	[47]
Redwood	California, USA	<i>Picea sitchensis</i> epiphytes	36.2 kg/tree	[48]
<i>Picea mariana</i>	Interior Alaska, USA	Lowland	5,460,000	[49]
		Upland	4,550,000	[49]
<i>Picea abies</i>	Northern Finland	Forest floor feather mosses	180,000	[50]
Boreal	N of Lake Superior, Canada	Understory	13,000	[51]
Boreal	Manitoba, Canada	Well-drained soil	47,000–230,000	[52]
		Poorly drained	102,000–228,000	[52]
Deciduous	Near Eger, Hungary	Epiphytes	4140	[53]
Deciduous to alpine	Mt. Washington, NH, USA	Ground layer	2000–238,000	[54]
Tropical	Southern Thailand	Lowland epiphytes	1150	[55]
		Lower montane epiphytes	199,000	[55]
		Low elevation epiphytes	240	[55]
		High elevation epiphytes	6200	[55]
Wet tropical	Mauna Kea, Hawaii	<i>Sphagnum</i>	~300,000	[56]
Other tropical		Non- <i>Sphagnum</i>	5,000,000	[56]
Mixed tropical karst	Central Guizhou, China	Rocks, soil, wood	7800	[57]
Tropical montane	General	Canopy epiphytes	3,960,000	[58]
Subtropical montane	Gongga Mtn, China	Terrestrial	700,300	[59]
Tropical montane cloud	Chilan Mountain, Taiwan	Epiphytes	26,950	[60]
Tropical montane cloud	Peru	Epiphytic bryo	4,500,000	[61]
Montane cloud	Costa Rica	Oak stems	13,000–68,000	[33]
<i>Quercus costaricensis</i> cloud	Costa Rica	Mostly epiphytes	169,700	[62]
Montane rainforest	Andes	Bryo on trunk	80,000	[34]
		Bryo on branches	1,873,000	[34]
		Bryo on twigs	1,230,000	[34]
Tropical cloud	High altitude	Mostly epiphytes	1,000,000	[63]
Tropical lowland cloud	Northern South America	Mostly epiphytic bryo and lichens	59,000	[64]
Tropical lowland rainforest	Northern South America	Mostly epiphytic bryo and lichens	35,000	[64]

In the west central Cascade Mountains, Oregon, USA, on **Douglas fir** (*Pseudotsuga menziesii* (Mirb.) Franco), *Eurhynchium oreganum* (Sull.) A. Jaeger contributed 92% cover and *Hylocomium splendens* 7% [7]. In addition to forest-floor bryophytes, Douglas fir epiphytic bryophytes can contribute significantly (Table 2), unlike most coniferous trees [46].

3.2.2. Boreal Forests

The role of bryophytes in the **boreal forest** is perhaps the best understood of all forest types. Boreal forests are characterized by feather mosses, especially *Hylocomium splendens* and *Pleurozium schreberi* [27,65]. *Sphagnum* L. species occupy wetter areas. Both groups can provide extensive ground cover that affects various tree species differently. Spruce species dominate in many boreal forests [49,50,66]. In the **Black spruce** (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) forest of the Alaskan interior, the 20–30 cm moss-organic layer comprises 80–90% of aboveground biomass, especially in cold, wet stands. Drier stands typically reach only 0–10 cm in thickness. The fine needles of conifers permit mosses to grow through litter and obtain sunlight.

In the central **boreal forest** of Canada, production was $8 \text{ g m}^{-2} \text{ y}^{-1}$ and turnover was $67.6\% \text{ y}^{-1}$ [51]. Woody and herbaceous biomass, production, and turnover rates were higher in deciduous broadleaf forests, whereas those for bryophytes were higher in conifer forests. Dry weights of boreal bryophytes are typically higher in poorly drained stands than they are in well-drained stands dominated by feather mosses, as seen near Thompson, Manitoba, Canada (Table 2) [52].

3.2.3. Deciduous

Deciduous forests typically have greater species diversity but less biomass of ground-layer bryophytes than do conifer forests due to competition with tracheophytes and leaf litter. In hardwood forests “virtually no moss occurs” on the forest floor [66]. On the other hand, tree trunks, rocks, and other elevated surfaces can support substantial quantities [53,54]. In the nine ecosystems on Mount Washington, New Hampshire, USA, standing crop increased from **oak woods** to **northern hardwoods** to **coniferous** to **high alpine** to **alpine** [54]. Coverage alone was a poor indicator because of variability in size of bryophytes; biomass and calories are better measures.

By contrast, on slopes with roots and boulders and little litter in moist **sessile oakwood** (*Quercus petraea* (Matt.) Liebl.) forest in northwest Wales, bryophytes formed 90% of the standing crop of ground vegetation with epiphytic bryophytes forming only 4% of bryophyte biomass [67].

3.2.4. Tropical

The biomass of epiphytic bryophytes in equatorial latitudes increases from the tropical lowlands to the treeline [68]. In southern tropical forests of Thailand, dry weight of epiphytic bryophytes increased from the lowland to the maximum in lower montane forests, with estimated dry weight increasing upward in elevation (Table 2) [55]. In a Hawaiian wet forest on Mauna Kea, thick *Sphagnum* patches provided 14% of the ground layer and had low biomass, but at four other sites the biomass was 10–16 times as great, at 26–85% cover [56]. Bryophytes are only minor biomass components in karst evergreen and deciduous broad-leaved mixed forests in central Guizhou, China [57].

3.2.5. Tropical Montane and Cloud Forests

In some **tropical montane forests**, bryophytes provided more photosynthetically active biomass (Table 2) than all other plant groups combined, comprising 90% of the canopy epiphytes [58]. On the subtropical Gongga Mountain of China, the terrestrial bryophyte biomass at 3758 m asl [59] contributed to a maximum thickness of 8 cm. In the **tropical montane cloud forests** of Chilan Mountain in northeastern Taiwan, bryophytic epiphytes similarly contributed significant biomass [60].

In *Quercus costaricensis* Liebm.-dominated **cloud forest** of Cerro de La Muerte, Costa Rica, cryptogam biomass occurred predominantly as epiphytes in lower branches [62]. By contrast, in the **tropical lowland cloud forest** of northern South America the mean total epiphytic biomass was much lower, but was still greater than in **lowland rainforest**, where fog was lacking (Table 2); likewise, mean cover was greater in **lowland cloud forest** (70%) than in **lowland rainforest** (15%) [64].

3.2.6. Epiphytes

Conifers typically have fewer bryophytic epiphytes than do deciduous trees. On **Sitka spruce** (*Picea sitchensis* (Bong.) Carrière) in the **redwood forest** in Humboldt County, California, USA, only 17 epiphytic bryophyte species were found [48]. Tree trunks supported 83% of the biomass—11.3 times that on branchlets. The moss *Isotheceum myosuroides* Brid. and leafy liverwort *Frullania nisquallensis* Sull. were among the five most abundant bryophyte species. In conifer forests, bryophytes exhibit much greater biomass on axes than on branchlets and dominate the sheltered portion of the branch gradient [48,69,70]. These researchers concluded that extensive bryophyte mats promoted biological diversity on **Sitka spruce** in the **redwood forest** by storing water and providing habitat for desiccation-sensitive organisms.

In the **redwood** (*Sequoia sempervirens* (D. Don) Endl.) forest of northwestern California, an environmental gradient from exposed to sheltered habitats contributed most to the structure of epiphytic communities, including bryophytes [71]. One old-growth 400-year-old **Douglas fir** (*Pseudotsuga menziesii*) illustrates the available surface area differences: trunk—223 m² cover; axes (>4 cm)—81 m²; living twigs (<4 cm)—373 m²; dead twigs—104 m²; needles—2860 m² [47].

In the **cloud forests** of Costa Rica, as in conifer forests, bryophytes mostly occupy the inner crowns of mature forests, whereas lichens occupy drier isolated crowns with more sunlight [70]. Epiphytic bryophytes in cloud forests are mostly mats and pendants; forms that most likely optimize water capture, with pendants directing the water to the growing tips. In **tropical cloud forests**, epiphytes prepare the habitat that permits canopy-dwelling plants to become established; epiphytes comprise the greatest volume and number of **montane rainforest** species [72]. In the Andes **montane rainforests**, most of the biomass is on the branches, with the least on the trunks (Table 2) [34]. In a rare tropical experiment on a **flood plain forest** in the Luquillo Experimental Forest in Puerto Rico, wooden stakes accumulated 21–140 g m⁻² ash-free biomass of bryophytes in 10 years; this is a range similar to that in fine litter [73]. High altitude **tropical cloud forests** generally have a high standing crop of more than 1 million mg m⁻² of bryophytes, which is mostly contributed by epiphytes [63]. But where more moisture is available in a **cloud immersion zone of tropical montane forest** of Peru, epiphytic bryophytes comprise up to 4.5 million mg m⁻² [61].

4. Alteration of Physical Parameters

Bryophytes can contribute extensively to the microclimate and structure of a forest by modifying water economy, altering soil temperature, and preventing erosion pathways [74,75]. Furthermore, they create microhabitats by altering microtopography and boundary layers.

4.1. Water Retention

In recent studies, forest ecologists have recognized that bryophytes can perform important functions in water cycling in forests [13]. Mosses are often described as behaving like sponges. Water retention by moss mats can be beneficial in reducing water loss from the soil, but they can also impede the penetration of light rain into root systems beneath the soil surface.

Bryophytes can use external, internal, or both pathways to move water about the plants [76], creating differences in their ecosystem functions. Some mosses, such as *Polypodium commune* Hedw., with an internal conduction system, lose water through their spread leaves and changes in the water potential deficit of shoots. As these mosses dry, their leaf bases lose water and no longer project leaves away from stems. Other mosses are ectohydric (having external transport) and have little internal conduction and little control over water loss, although some have limited control by repositioning their leaves. Growth forms contribute greatly to differences in water storage and loss.

A large bryophytic surface area not only traps water, but also releases it. For example, during just one month, an evaporative loss of 24 mm from mosses under a leafless canopy of **larch** (*Larix gmelinii* (Rupr.) Kuzen.) occurred, representing 23% of water flux into

the larch forest; evaporative water loss in May from the moss understory comprised 22% of total evaporative loss above the canopy from April to October of 1 year [77]. Table 3 provides a sampling of the little we know about water losses from mosses in the field, based on boreal forest species.

Table 3. Bryophyte water loss in various boreal forest locations around the world.

Forest Type	Location	Habitat	Loss	Ref.	
<i>Larix gmelinii</i>	Siberia, Russia	Moss understory	24 mm mo ⁻¹	[77]	
Subalpine forests	Japan	<i>Pleurozium schreberi</i>	0.37 mm d ⁻¹	[78]	
		<i>Sphagnum riparium</i>	1.43 mm d ⁻¹	[78]	
<i>Picea mariana</i>	Central Alaska, USA	Total forest	2 mm d ⁻¹	[79]	
		Dense with <i>Hylocomium splendens</i>	Ground	0.3 mm d ⁻¹	[79]
		Open with <i>H. splendens</i>	Ground	0.9 mm d ⁻¹	[79]
Bog		Ground	1.5 mm d ⁻¹	[79]	

Thick layers of insulating mosses make it difficult to track soil dynamics [80]. The high water-retention capacity of bryophytes permits them to retain moisture quickly and release it slowly, creating humid forest microclimates, regulating water flow, and preventing flash floods, erosion, and even landslides [58]. This role of mosses in the hydrological cycle in boreal forests was inaccurate in most hydrologic models [81]. When bryophyte effects were added to the model, total evaporation from the canopy and soil surface increased by 61%. The ability of mosses to keep deep layers of soil frozen reduces water vapor, and in summer, sponge-like behavior permits mosses to soak up a lot of water [80]. About one-third of the total water that evaporates from a boreal ecosystem in summer is derived from the moss layer within only a few days after rain. Mean bryophyte storage capacity is 2.7 mm. Without them, the figure used in models was 0.4 mm. Thus, bryophytic contributions have significant influence on the global hydrologic cycle. These roles in regulating ecosystem hydrology have been termed **effect traits** [82].

Water cycling is one of the strong influences that bryophytes have in northern ecosystems [20]. Even within forests, peat mosses (*Sphagnum* spp.) can create hummocks and hollows. Compared to hollow species, hummock species must be more efficient at moving or using water to avoid desiccation [83–85]. Differences in moisture and temperature also result in differences in decomposition rates between hummocks and hollows; this affects peat properties and water movement over time, again causing moisture differences among these microhabitats [86,87]. These microhabitats are suitable for different types of seedlings and other plants. The microtopography of hummocks and hollows also increases resistance to fire; this is an event that greatly alters water retention in the ecosystem, in part because of moisture differences [87,88]. The ability of hummock mosses to retain water inhibits both initiation of fire and its downward movement [89].

The water-holding capacity of bryophytes (Table 4) far exceeds that of the aboveground parts of most tracheophytes. For example, bryophytes from temperate rainforests in New Zealand held an average of 1375% water when fully saturated and 250% when air-dried [90]. Water-holding capacity ranges widely among bryophytes; *Polytrichum commune* has an absolute water content of 646% and *Sphagnum subnitens* Russow & Warnst. has an absolute water content of 5584% [91,92]. Water loss follows an exponential decay curve. The researchers concluded that bryophytes will act as key components during climate change [92], making their ecosystems more resilient, due to their own tolerance of a wide range of conditions [20].

Table 4. Bryophyte water-holding capacity in various forest types around the world. Capacity represents the interception capacity as a percent of dry weight. Those in mm represent mm of rainfall required to saturate. However, some started with dry weight and others with field weight.

Forest Type	Location	Habitat	Capacity	Ref.
Boreal			2.7 mm	[80]
<i>Pseudotsuga menziesii</i>	Pacific Northwest, N. A.	Epiphytes	>30 mm	[93]
Temperate rainforest	New Zealand	Fully saturated	1375%	[90]
		Air-dried	250%	[90]
Temperate mixed	Azores, Portugal	<i>Polytrichum commune</i>	646%	[92]
		<i>Sphagnum subnitens</i>	5584%	[92]
		Overall bryophytes	60%	[92]
Tropical cloud	High altitude	Branch microepiphytes	471%	[63]
		Trunk microepiphytes	395%	[63]
		Ground bryophytes	393%	[63]
Pine barrens	NJ, USA	Dry moss	15.7 mm	[94]
		<i>Dicranum</i>	13.2 mm	[94]
		<i>Ceratodon purpureus</i>	17.2 mm	[94]
		<i>Leucobryum glaucum</i>	17.2 mm	[94]
Tropical rainforest	Near Nairobi, Kenya	Bryophytes in mist	196 mm y ⁻¹	[95]
Rainforest	Uluguru Mtns, Africa	Epiphytes	~200 mm y ⁻¹	[96]
		Ground bryophytes	3000 L ha ¹ y ⁻¹	[96]
Old-growth cloud forest			36–418%	[97]
		Second growth	0.36 mm	[97]
		Old growth	4.95 mm	[97]
Tropical montane cloud	Réunion Island	Dom epiphytic liverworts	3.46 mm	[98]
Tropical montane	Peru	Epiphytic bryophytes	20 mm	[61]

In the Pacific Northwest of North America, epiphytes on old-growth **Douglas fir** (*Pseudotsuga menziesii*) required more than 6 mm of precipitation before they became saturated [93,99]. The maximum water fraction (maximum mass of internal and external water stored by epiphyte divided by its tissue dry mass) of bryophytes was the greatest (10.0 ± 0.5); while that of fruticose lichens was the lowest (2.2 ± 0.4). Canopy water storage by epiphytes averaged 3.1–5.0 mm and impeded drainage of water from branches. The researchers concluded that epiphytes (mostly bryophytes) increase canopy water storage in old-growth **Douglas fir** forest by more than 1.3 mm, but reduce water reaching the ground.

In an altitudinal transect in Japan, the highest water storage capacity of bryophytes occurred in **subalpine forests** [100]. The feather moss *Pleurozium schreberi* in a 77-year-old dry stand has a loose weft growth form and a low water retention of 0.37 mm d⁻¹, whereas *Sphagnum riparium* Ångström in a 43-year-old bog has a high retention of 1.43 mm d⁻¹ [78]. *Hylocomium splendens* and *Sphagnum capillifolium* (Ehrh.) Hedw. contribute considerable evaporation to boreal **black spruce** (*Picea mariana*) forests [79]. The amount of water held varies with the openness of the canopy and the frequency of precipitation. Similarly, in an **Alaskan boreal spruce forest**, evaporation is much higher when the surface layer, including mosses, is wet [101]. However, mosses also inhibit evaporation from the soil, maintaining moist soil in a dry atmosphere, even covering pools of standing water. In the **pine barrens** of New Jersey, USA, moss mats (Table 4) covering 90% of the surface in the field could retain as much as 50% of throughfall. Lichens there retain about half that amount.

Nevertheless, even at maximum interception, the bryophyte layer in these pine barrens was not as important as the litter layer in areas not experiencing prescribed burning.

4.1.1. Tropical Forests

Many researchers have noted the role of epiphytic bryophytes in the interception of rainfall, decreasing the amount reaching the forest floor and reducing runoff on the ground, thus decreasing erosion [102–104]. In the Colombian Andes **upper montane rainforest** and **tropical montane forests** of Panama, epiphytes (mostly bryophytes and decaying matter) captured water from rainfall efficiently [103,104]. Excess water drained very gradually and evaporation was slow. Although the lowest epiphyte biomass occurred in **ravine forest**, the highest water storage capacity occurred there [105]. Fine-scale topography played a role in the differences in water-holding capacity. In the Uluguru Mountains of Tanzania, **mossy elfin forest** with $\sim 1,400,000 \text{ mg m}^{-2}$ epiphytic biomass intercepted $50,000 \text{ L ha}^{-1}$ in a single rainfall [106]. In **submontane rainforest** bryophyte biomass was estimated to be only 213 g m^{-2} but it intercepted $15,000 \text{ L ha}^{-1}$. Aerial humus in **elfin forests** is a major contributor to interception. In Ecuadorian **montane rainforest**, a tree 27 m in height averages 65.4 kg dw of epiphytic bryophytes that store 669 L of water [34].

4.1.2. Cloud Forests

In cloud forests, fog deposition on epiphytic bryophytes is accomplished because of their fine, wirelike, i.e., mist-trapping, structure [95]. Pendent bryophytes, including mosses *Pilotrichella flexilis* (Hedw.) Ångström, *Phyllogonium viscosum* (P. Beauv.) Spruce, *Zelometeorium* Manuel sp., *Squamidium leucotrichum* (Taylor) Broth., liverworts *Frullania convoluta* Lindenb. & Hampe, *Frullania Raddi* spp., and *Usnea* lichens, were instrumental in the interception of water in **tropical montane forests** in Costa Rica, especially from fog and mist [107]. Bryophytes in Mt. Marsabit forest, a **tropical rain forest** north of Nairobi, Kenya, had a water retention capacity six times their dry weight [95]. Mist water trapped by bryophytes was 8 L m^{-2} per mist day. Although canopy epiphytes intercept water, reducing that available to plants and animals, it is nevertheless “the compensation factor that supports the forest ecosystem.” It provides important cooling effects. In the **subtropical montane** Yuanyang Lake forest ecosystem in northeastern Taiwan, fog water deposition averaged $0.63 \text{ g water g}^{-1} \text{ dw h}^{-1}$, equivalent to 0.17 mm h^{-1} [108]. In February, more than 50% of ecosystem ion input arrived through fog depositions. In the **rainforests** of the Uluguru Mountains of eastern Africa, 8% of annual precipitation was absorbed by epiphytic bryophytes [96].

In the **tropical lowland cloud forest** of French Guiana, high humidity and morning fog promote rich cover of epiphytic bryophytes, supporting significantly more epiphytic cover and biomass (59 g m^{-2}) when compared to **lowland rainforest** (35 g m^{-2}) [64]. Relative air humidity is higher in this **lowland cloud forest** in both wet and dry seasons and maintains humidity significantly longer into the day.

Data on canopy water storage in regeneration forests are largely lacking [97]. In the **montane cloud forest** stands in Costa Rica, old-growth **cloud forest** had a mean of 1621.5 g m^{-2} epiphyte biomass, whereas in 30-year-old second-growth forest it was only 130.5 g m^{-2} . Epiphytic bryophytes lost a maximum of 251% of their dry weight, whereas canopy humus lost only 117% through evaporation. However, it is unlikely that bryophytes, particularly in old-growth **cloud forest**, were completely dry, thus losing a lower percentage than these estimates.

Seemingly similar bryophyte species can have greatly different impacts in the same habitat, as seen by two abundant epiphytic liverwort species in one **tropical montane cloud forest** [98]. *Bazzania decrescens* (Lehm. et Lindenb.) Trevis. stores double the mean and maximum volume of water per hectare compared to that of *Mastigophora diclados* (Brid. ex F.Weber) Nees. Nevertheless, *M. diclados* has greater ability to intercept that moisture. Together, they store an estimated $34,569 \text{ L ha}^{-1}$ of water.

In the **tropical montane** forests of Peru, the water-holding capacity of epiphytic bryophytes in **cloud immersion zones** was equivalent to a 20 mm precipitation event [61]. We lack studies on midday dew formation on corticolous epiphytes in **wet tropical rain forest** [109]. Lichens benefitted from diurnal dew formation of 0.29–0.69 mm d⁻¹ on bark surfaces and lichens. If lichens are growing among bryophytes, we should expect even greater effects.

4.1.3. Paludification

Ground layer mosses can alter the hydrology of a forest sufficiently to change the type of ecosystem by impeding drainage [110–112]. This process of paludification results from ground-layer bryophytes that kill very fine feeder roots. This process is particularly evident when *Sphagnum* encroaches, increasing tree root depth and reducing diversity while facilitating a transition from forest to bog.

4.1.4. Fire Protection

Because of their high water retention, bryophytes can play an important role in fire protection. They can be especially important for underground structures by insulating them from heat. They can also create islands of moisture that protect emergent plants during fires. In a **black spruce forest** in Alaska, *Sphagnum* is especially important in minimizing soil moisture fluctuations and protecting vegetation associated with it; only 20% of soil organic matter was destroyed by fire in *Sphagnum* sites, whereas 45% was destroyed in feather moss or lichen sites [113]. The ability of bryophytes, particularly *Sphagnum*, to reduce fire damage is an important aspect of mosses as ecosystem engineers [18].

4.2. Temperature Modification

With water evaporation comes temperature modification. Bryophytes insulate the forest floor [80,114–116], playing important roles in forest temperatures, particularly in the root zone. One such role is in keeping the soil frozen longer in boreal regions, resulting in moving permafrost closer to the surface. When the effects of mosses were added to the BOREAS model, the model made much better soil temperature predictions [80].

The **black spruce (*Picea mariana*)** forest floor displays a thick layer of mosses and organic matter; this layer provides thermal insulation and maintains permafrost [117]. Previous studies overestimated the thermal conductivity of this moss layer but later measurements showed that it ranged 0.03–0.09 W m⁻¹ K⁻¹ over a growing season (water has a thermal conductivity of 0.6 W m⁻¹ K⁻¹ at 20 °C, air of 0.024 W m⁻¹ K⁻¹).

Heat flux of moss surfaces comprises 22% of net all-wave radiations under **larch (*Larix gmelinii*)** canopy in the **taiga** of eastern Siberia [76]. Evapotranspiration by ground-layer mosses provides a significant contribution to the energy budget in these forests. The thickness of the moss mat influences the amount of heat that reaches the soil surface [114, 115]. Herbivores can reduce this thickness by trampling and consumption. For example, exclusion of both barnacle geese and reindeer for 7 years on Spitsbergen resulted in an increase in the moss layer and a subsequent reduction of 0.9 °C in soil temperature [114]. Lower temperatures under mosses caused a 50% reduction in tracheophyte forest floor species such as *Poa arctica* R. Br. and *Cardamine nymanii* Gand. On the other hand, the moss *Polytrichum commune* can reduce frost heaving that is detrimental to tree seedlings [118,119].

Mosses keep soil temperatures near the surface cooler in summer; this is most likely due to their ability to accelerate soil water evaporation [120]. It is likely that this behavior will alleviate the effects of some of the extreme temperatures predicted to result from climate change. When air temperatures exceed 30 °C, evaporation from mosses increases drastically, keeping the maximum soil temperature at ~30 °C [120], a phenomenon similar to that of mossy green roofs [121].

4.3. Alteration of Permafrost Level

Mosses in boreal **black spruce** (*Picea mariana*) can keep the root zone frozen longer in spring and keep deeper layers as permafrost [80]; this is a role that extends over centuries [20]. Temperatures in boreholes in the permafrost region of Russia have risen 0.5–2 °C over the last 20–30 years at the level that was the permafrost level, suggesting the effect of deeper moss mats [122,123]. Similarly, in the **black spruce** (*Picea mariana*) forests of interior Alaska, *Sphagnum* insulates soil, causing a rise in the permafrost level, sometimes to only 38 cm in depth [124]. Burning surface moss layers increases soil temperatures.

In northern Siberian, **Gmelin larch** (*Larix gmelinii*) forests are limited by the thawing depth of permafrost [125]. Data indicate that the depth of thaw increases with the reduction in thickness of moss-lichen and duff layers. Surface fires are used to burn off moss-lichen layers to increase timber production.

4.4. Creating Microtopography

Bryophytes can contribute to forest diversity through the creation of greater microtopography [20,126,127]. Due to their growth forms, even non-*Sphagnum* bryophytes can create hummocks and hollows that add microniches to the landscape. Bryophyte diversity also increases with increasing varieties of microhabitats [23]. Bryophytes had the highest specificity for particular microlandforms in *Cryptomeria japonica* (Thunb. ex L. f.) D. Don and *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. plantations, followed by pteridophytes and flowering plants [23].

4.5. Erosion Prevention

Forest floors are less susceptible to erosion than open soil because of the canopy (including epiphytic bryophytes) and leaf litter that soften the impact of falling rain and slow down flow. However, on slopes the litter is unable to accumulate, responding instead to gravity. Here, bryophytes are of importance in forming mats that both absorb water and anchor soil [128]. They capture the first drops of rain or gushing snowmelt runoff, permitting water to enter the soil slowly [129]. Since most forest bryophytes are perennials that survive above ground, they are there to absorb that spring runoff, in some cases preventing flooding [58,102]. Moss cover was important in distributing precipitation under forest canopy following a typhoon in Japan [130]. Rock surfaces, emerging above leaf litter, become sponges instead of impervious surfaces. In addition, in the tropics and other humid forests, epiphytes can absorb considerable rainfall and slow its descent to the soil, greatly retarding erosion [63,106]. In a **Chinese red pine** (*Pinus massoniana* D. Don) forest in Yichang, HuBei Province, China, the combination of litter and moss had a greater effect on runoff velocity than forest litter alone (Figure 1) [131].

In an early successional Chinese subtropical forest, when the forest floor mats (mostly mosses) had a cover of less than 10%, mean sediment delivery was 302 g m⁻² and mean runoff volume was 39 L m⁻² [129]. However, when moss (biocrust) cover was greater than 50%, there was mean sediment delivery of only 74 g m⁻² and mean runoff volume of only 29 L m⁻².

Bryophytes, including bryophyte protonemata, appeared immediately after disturbance in **temperate forests** [132]. As bryophytes developed, they persisted until overtaken by tracheophytes and leaf litter. *Oxyrrhynchium hians* Hedw. Loeske and *Brachythecium rutabulum* Hedw. Schimp. were the most important and persistent of these species. Sediment discharge from disturbed soil was 22 times that of undisturbed soil, implying that established bryophytes and tracheophytes were significantly preventing erosion. Hence, the roles of bryophyte-dominated mats in forests have been underestimated.

Following spruce budworm and drought in a dry conifer forest in the central Blue Mountains of eastern Oregon, USA, over half the recent disturbance treatment areas—areas with reduced overstory and understory vegetation, litter, and coarse woody debris as well as disturbed soil—had been colonized by short, pioneering mosses by year 3 [128]. Treatments of logging and burning caused changes in species composition, but not in

species richness. New cover in treated areas was primarily comprised of the mosses *Funaria hygrometrica* Hedw., *Ceratodon purpureus*, and especially *Bryum caespiticium* Hedw., replacing former larger pleurocarpous mosses such as *Brachythecium* Schimp. and *Rhytidiadelphus* (Limpr.) Warnst. and resulting in a change in species compositions, but not in species richness. Bryophytes provided important ecosystem services by colonizing rapidly, then stabilizing the soil, protecting it from wind and water erosion.

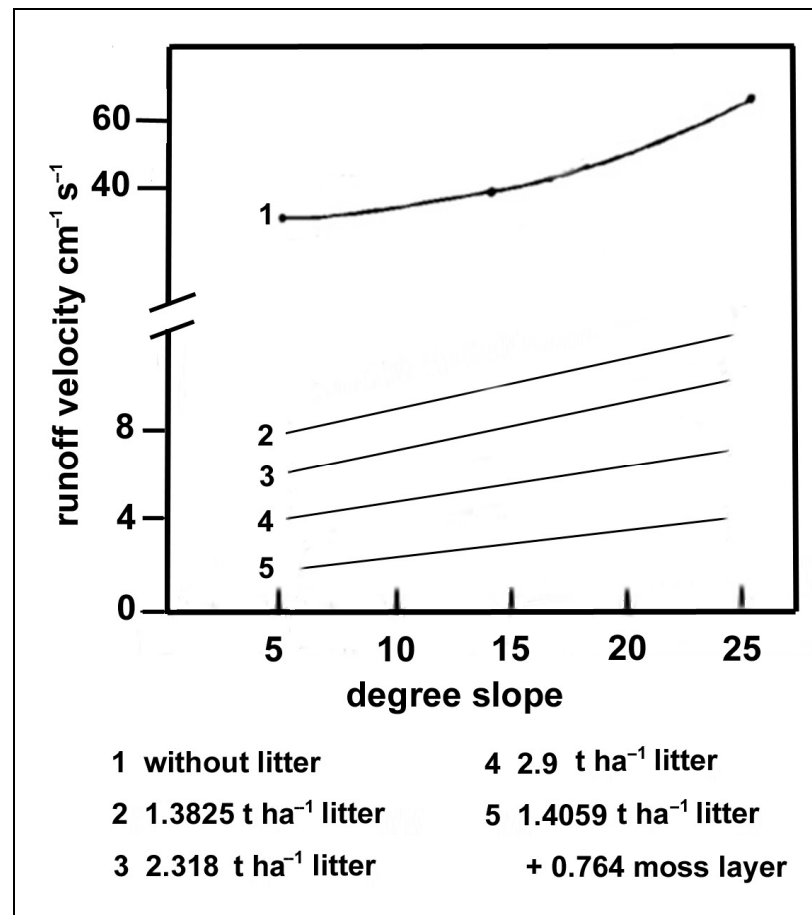


Figure 1. Comparison of runoff velocity with five levels of soil cover, including litter of *Pinus massoniana*, at various slopes. Based on [131].

As they colonize, bryophytes form netted and webbed protonemata and gametophores, covering exposed soil surfaces [133]. They then are able to spread by frequent branching, providing early protection against erosion, as seen in a **mixed oak-conifer forest**. The mosses *Atrichum* P. Beauv., *Pogonatum* P. Beauv., *Pohlia* Hedw., and *Trematodon* Michx., and leafy liverwort *Nardia* Gray, among others, are good inhibitors of soil erosion because they are trample-resistant and have good regenerative capacity.

In the fire-adapted **eucalypt plantations** of central Portugal, moss crusts developed quickly following fire [134]. In areas with moss cover above 67%, mosses significantly reduced sediment losses by 65% (0.40 metric ton ha⁻¹) and organic matter losses by 34% (0.15 metric ton ha⁻¹), leading researchers to conclude that mosses should be considered in ecosystem restoration and management.

Little difference between lost soil in moss-covered vs. leaf-covered stream banks occurred on headwater stream banks in Virginia and Illinois, USA [135]. However, microsites with mosses accumulated only 12–14% leaf litter cover at the two sites, whereas those with no mosses accumulated 57% leaf litter cover. This indicates that mosses are associated with

more exposed, and probably steeper, sites. Bryophytes were limited on the forest side by leaf litter and on the stream side by erosion.

4.6. Alteration of Light Quality and Intensity

Bryophytes require light, but are able to subsist and grow in low light levels compared to that required by lichens and most tracheophytes [136]. Bryophytes come in a variety of colors, with canopy bryophytes often developing dark pigments that protect them from the high light levels there [137–139]. Nevertheless, we know little about their responses to light quality or how they alter the quality of light travelling through the canopy.

Bryophytes may lower the red/far red ratio, as well as the light intensity on the soil beneath them [140]. This affects germination signals to seeds below them, differing from that on open soil. Bryophytes can lower the R:FR ratio by 30–60%. Although this was reported for chalk grassland, it could affect some kinds of forest seeds that germinate in spring or autumn, when leaves are off the trees in the forest. Experiments are needed.

5. Rapid Recolonization

With a greater number of fires, droughts, floods, and other destructive weather events occurring more frequently [141], recolonization will be important in restoring forest ecosystems. In particular, ecosystem services will be threatened, but bryophyte diversity is likely to increase [142]. Bryophytes are typically rapid colonizers following forest disturbance.

Bryophytes reproduce by both spores and vegetative means. Spores are typically small, enabling them to travel long distances and to spread quickly, whereas their great variety of vegetative means permits bryophytes to colonize quickly; mostly they colonize nearby, but sometimes this occurs over great distances when they travel with animal carriers [143]. The bryophytes have more types of regeneration methods than do tracheophytes and most spores are smaller than the smallest seeds [142]. This means that following forest destruction (fire, deforestation, deglaciation, volcanic eruption) they are among the first species to invade, spreading quickly by both vegetative means and as spores, enabling them to stabilize soil, trap nutrients to enrich soil, reduce erosion, and reduce water evaporation.

Mosses tend to colonize different substrata from that of tracheophytes. In **old-growth boreal forest** in northwestern Sweden, mosses were more numerous on disturbed forest patches of mineral soil with the most severe disturbance, whereas tracheophytes had the greatest species numbers on disturbed patches of humus [142]. Furthermore, bryophytes recovered more quickly and species richness exceeded that of undisturbed adjacent patches within 2–3 years.

In **upland forests** in the Northwest Territories, Canada, recovery after fire was by vegetative reproduction and propagule invasion for both tracheophytes and bryophytes [144]. Buried viable seeds seemed to have little role in recovery. Poorly competitive, rapidly growing, short-lived species establish first but are later replaced by longer-lived, slower-growing species. Feather mosses, so prominent in **boreal forests**, have the greatest abundance in sites with closed canopies and greater soil nutrients. In a fire-damaged forest in southeastern Spain, the frequency of pioneer bryophytes had diminished to less than half their year 1 frequency by year 10 [145].

Bonfires create more ash deposit and higher-intensity heat than do rapid fires [146]. Bonfire sites in England inhibited both flowering plant and bryophyte growth. The moss *Funaria hygrometrica* predominated. Rapid-fire sites were colonized primarily by pre-burn species, perhaps because these fires had little effect on surface soil and nutrients.

Bryophyte species richness changes little in response to disturbances such as clear cutting [147]. Nevertheless, species differences remain 30–50 years following clear cutting. Raised surfaces are important in their recovery, and loss of these, especially in fires, exacerbates losses. Narrow buffer strips (10 m on each side) can reduce or eliminate loss of these bryophyte species, especially streamside.

A major source of propagules in some situations is diaspore banks [148–150]. In the lab, 40 species of mosses and liverworts emerged from spores and other propagules from

soil samples from a **Norway spruce** (*Picea abies* (L.) H. Karst.) forest [151]. *Pohlia nutans* (Hedw.) Lindb., *Sphagnum* spp., and *Polytrichum commune*/*Polytrichastrum longisetum* (Sw. ex Brid.) G.L.Sm. were the most abundant. Bryophyte richness averaged 9.9 species from each mineral soil sample, which was higher than the 6.6 that developed from humus. Nevertheless, some of the most abundant species from the forest floor did not appear from these samples. In old-growth **spruce** forests in Norway, *Polytrichum* spp. were among the most frequent mosses in propagule banks [148].

Unfortunately, diaspore banks in the tropics are poorly known. On various substrates from the **Atlantic rainforest** in Brazil, the most species emerged from bark (68) and decaying wood (55), compared to soil (22) [150]. These diaspores were important in the rapid re-establishment of bryophytes after disturbance in **tropical rainforests**. Monoicous (i.e., both sexes on the same plant) moss species dominated over dioicous (i.e., separate sex) species and liverworts. Spores were important in monoicous mosses and asexual reproduction in dioicous mosses.

6. Stability in Response to Change

Bryophytes can respond to different conditions compared to those favorable for tracheophytes. For example, bryophytes in a **temperate broad-leaved forest** in France increased in richness and humus increased from mull to moder [152]. Tracheophytes had the opposite response, likely due to differences in nutrient capture strategies. As Turetsky et al. [20] noted, bryophytes are more stable in response to change and disturbance. Understanding bryophyte roles requires understanding their nutrient relationships in various forest types.

7. Nutrient Relationships

In some forest biomes, bryophytes are major functional units of the ecosystem [5]. Among bryophytes, *Sphagnum* is an extreme ecosystem engineer. Not only does it control the hydrologic cycle, it sequesters nutrients through cation exchange, removing them from availability to other plants [153]. This causes plants living there to depend on atmospheric nutrients, giving *Sphagnum* a competitive edge even against trees.

We know that nutrients can be transported both internally and externally in bryophytes. The feather moss *Hylocomium splendens* can transport N acropetally (i.e., toward the tips) [154]. *Hylocomium. splendens* is able to transfer Mg, but not Ca, from the brown, decaying segment to growing tissue, a routine it can use on an autumn day [155]. In winter and spring, it appears to take its Ca and Mg primarily from aerial sources. When the moss was transplanted from a lime-contaminated site to an uncontaminated site, it maintained the Ca and Mg levels in green segments, probably transferring it from old to new tissue. There was no evidence of loss of these two nutrients by leaching.

7.1. Nutrient Capture

The ability to trap and hold nutrients may be one of the most important functions of bryophytes in forest ecosystems. Mosses rely mostly on interception of dust and atmospheric water for nutrients [156]. Bryophytes offer tremendous surface area per unit stem. Small spaces provided by bryophyte leaves serve as traps for both airborne and waterborne dust and nutrients, making the bryophytes efficient filters [10,157]. In canopy, tree trunk, and soil surface positions, bryophytes capture nutrients before they can reach the soil and roots of tracheophytes. However, tracheophytes must obtain their nutrients after they have travelled through the bryophytes; in most cases this is dependent on the slow decay of bryophytes to release nutrients to the soil.

The efficiency of bryophytes in grabbing various nutrients is demonstrated by Cs tracers in a **tulip tree** (*Liriodendron tulipifera* L.) forest [158]. Some cryptogams had more accumulated Cs than did tree foliage. However, terrestrial bryophytes receive most of their Cs and other nutrients directly from throughfall from the tree canopy; trunk epiphytes

receive it from stemflow. Terrestrial bryophyte mats had 92% efficiency in Cs uptake. Tree base mosses + bark substrate absorbed 90%.

Chemical weathering by lichens and bryophytes provides another source of P and N, particularly in early succession leading to forests [159]. Predictions based on organism requirements indicated that $3.5\text{--}34 \text{ Tg yr}^{-1}$ N and $0.46\text{--}4.6 \text{ Tg yr}^{-1}$ P are required, leading to estimates of chemical weathering of $0.058\text{--}1.1 \text{ km}^3 \text{ yr}^{-1}$ of rock, supporting the hypothesis that lichens and bryophytes can play important roles in biogeochemical cycles through their contributions to weathering.

7.1.1. Boreal Forests

In addition to internal storage, small external spaces of bryophytes can hold water and nutrients among leaves long after bare soil is dry. Particularly in **boreal forests**, bryophytes can have major effects on nutrient cycling [10]. Bryophytes tend to have rapid nutrient acquisition, and slow decomposition and nutrient loss. Decomposition in bryophytes occurs at about 10% of the rate found for tracheophyte tissue. Hence, bryophytes can be effective competitors for nutrients against tracheophytes on the forest floor, particularly in conifer forests. This competition can result in a decrease in forest tree productivity in older conifer stands, as recorded in central Alaska [160]. As moss abundance increases in these forests, soil nutrient levels decrease. In central Alaska tree productivity was inversely correlated with moss production and biomass, with mosses exhibiting nearly four times as great a productivity when compared to annual **black spruce** (*Picea mariana*) foliage production [161]. Mosses are major components of cover and primary productivity in forests of Alaskan taiga [10]. Mosses may actually control ecosystem function through their rapid uptake of nutrients, as well as their effects on thermal environments.

Fine roots of trees became concentrated at the base of the moss layer in a **black spruce** (*Picea mariana*) forest in Quebec, Canada, suggesting that decomposing mosses were important in providing mineral nutrition to trees by creating a collection point for elements, especially N, that had been intercepted and absorbed by mosses from throughfall [162].

In the Canadian **boreal forest** of **black spruce**, **trembling aspen** (*Populus tremuloides* Michx.), and **Jack pine** (*Pinus banksiana* Lamb.), tracheophyte biomass was generally associated with higher **aspen** presence and linked to greater nutrient availability [163]. On the other hand, bryophyte biomass was positively associated with **conifer** abundance, especially in wet sites. Nutrient content of *Pleurozium schreberi* increased as light intensity decreased [164]. Nutrient uptake of these forest floor mosses was 23–53% of that estimated for trees. N from the canopy and rainfall was sufficient for moss requirements and mosses became a major source of N for trees. In old-growth forests, mosses such as *Hylocomium splendens* can effectively capture > 90% of dissolved N [165]. Eventually, these nutrients can be available to enhance growth of tracheophytes, but after 28 months the feather moss layer in a **black spruce** forest still retained more than 90% of labelled N.

At about the same time as these studies, we were beginning to recognize the role of N fixation in forest moss communities (see Nitrogen Fixation below). Bryophyte associates generally fix C and N from atmospheric pools, reduce N availability for tracheophytes and microbes, release dissolved compounds that are immobilized by soil microbes or lost in runoff, and transform C and N into recalcitrant organic matter [166]. In the tropics, liverworts often exceed mosses in species richness and in biomass, but our understanding of the role of liverworts is meager compared to what we know about mosses. We know that bryophytes cannot be treated as a single functional group.

Further evidence of functional group differences among bryophytes was revealed by experiments with N and P additions in **high Arctic heath** vegetation [167]. N increases caused increases in the proportion of physiologically active bryophyte shoots and decreased their nitrate assimilation capacity; but the effects of P addition was even greater, contributing to the alteration of species composition. In fact, individual species exhibited contrasting responses to nutrient additions. There are significant relationships between bulk N deposition and N content in *Pleurozium schreberi* and *Pseudoscleropodium purum*

(Hedw.) M. Fleisch [168]. Increasing N deposition caused decline in biomass, reflecting reduction in stem density, especially in *P. schreberi*. *Pleurozium schreberi* typically harbors N-fixing Cyanobacteria, and that N fixation is inhibited by high N levels.

P is often the limiting nutrient in forest ecosystems [169]. In **Alaskan black spruce (*Picea mariana*)** forest, mosses, equalling 49% of plant productivity, accumulate 75% of aboveground annual P accumulation by plants, despite constituting only 6% of total plant biomass [170].

Sphagnum subsecundum Nees and feather mosses (*Hylocomium splendens*, *Pleurozium schreberi*) have greater capacity to absorb P (mostly through leaves) than do fine roots of **black spruce** beneath them [170]. Mosses can compartmentalize P somewhat, with the greatest phosphate absorption occurring in older green tissue and decreasing with the age of brown tissue. When mycorrhizal activity was suppressed, mosses increased their phosphate retention, and phosphate loss from experimental plots was reduced. This is evidence that mycorrhizae are instrumental in transferring P from moss carpets to roots of black spruce, permitting these trees to compete with overlying mosses. In experiments, the endohydric *Polytrichum commune* obtained most of its phosphate not through leaves, but through stems that reached mineral soil [170]. (See Section 7.6 below on Fungal Interactions).

In N and P pulse treatments in situ, *Actinohydium hookeri* Mitt. Broth. and *Hylocomium splendens* in a **subalpine fir forest** in the eastern Tibetan Plateau both readily took up both nutrients from pulse additions [171]. New growth segments reflected these increased concentrations, indicating that pulse nutrients had been relocated, following source-sink transport, as new segments grew.

Bryophytes are able to conduct nutrients to their ramets (vegetatively produced plants in a single colony), as seen in *Hylocomium splendens* [172]. Current segments of both endohydric *Polytrichum commune* and ectohydric *Hylocomium splendens* are strong sinks for N. One-year-old segments of *H. splendens* increased their N pool, while older green segments lost 50%.

Bryophytes can even contribute through animal mediation. Various predators can carry salmon into the forest [173]. When these are abandoned, mosses can absorb nutrients from decomposing fish, tying them up for extended periods due to slow decomposition.

7.1.2. Other Coniferous Forests

In a **Douglas fir (*Pseudotsuga menziesii*)** forest in the Cascade Mountains of Oregon, USA, mosses accounted for 5% of Ca and K uptake and 10% of N and P uptake above ground [7], yet they comprised only 0.13% of aboveground biomass. This suggests that their role in modifying the nutrient budget of the forest is far more important than has been considered.

Polytrichum was able to accumulate $1.01 \text{ g N m}^{-2} \text{ y}^{-1}$ in an early successional stage of recovering **hemlock (*Tsuga canadensis* Carrière)-sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britton) forest** in New Hampshire, USA [174]. Labelled N, in simulated rainfall, revealed that soil and belowground live moss retained most of the N. Soils with high organic matter content retained more (47%) compared to soils with low organic content (27%). When mosses were removed, a short-term retention of N ensued in the soil, followed soon after by losses that exceeded inputs.

Work in the **coniferous forest** of the Changbai Mountains, China, demonstrates the worldwide similarity in bryophyte–tree nutrient relationships [175]. Researchers measured 5.437 g N m^{-2} in bryophytes, representing 12.22% of total N content of tree, shrub, and herb layers. Measured bryophyte K content was 1.2 g m^{-2} and P 3.17 g m^{-2} , holding 5.63% and a huge 70.57%, respectively, of the total. Not only was bryophyte P content greater than that of trees, but it was 792 times that in the shrub layer. This translated into a lower soil P content under bryophytes ($0.346 \pm 0.017 \text{ g kg}^{-1}$) compared to soil with no bryophytes ($0.419 \pm 0.023 \text{ g kg}^{-1}$).

7.1.3. Broadleaf Forests

Mosses alone in a **mixed oak-conifer forest** accounted for about 75% of annual P accumulation [133]. Mosses in rich fens are able to drive redox conditions, thus influencing P cycling [176]. Removal of mosses increased tissue P of forbs and microbes, whereas anion exchange membrane resin P was lower where mosses remained intact. Thus, it appears that there is both higher availability and greater demand for P in moss-covered soils. Mosses permitted greater microbial activity, more root vigor, and greater P demand, as well as greater P supply. Could this same advantage occur in forests, particularly in wet, low-lying areas?

In the tropics, bryophyte communities in a **flood plain forest** in the Luquillo Experimental Forest in Puerto Rico serve as biotic filters that retain nutrients [73]. In **upper montane forest** of the Rwenzori Mountains, Uganda, the upper canopy was dominated by lichens, whereas the lower canopy was dominated by cushion-forming liverworts, including species of *Chandonanthus* Mitt., *Herbertus* Gray, and *Plagiochila* (Dumort.) Dumort [177]. Bryophytes contained about 8% of aboveground nutrients, likewise serving as nutrient filters.

Bryophyte species do not have a uniform response to nutrients. Mineral inputs from substrata seem especially important in rapidly growing forest species such as *Brachythecium rutabulum*, a species that is able to gain its nutrients from seasonal tracheophyte litter [178]. Slower-growing mosses such as *Pseudoscleropodium purum* seem to depend mostly on atmospheric water sources for their minerals; although phosphate might be obtained mostly from the substrate. Cation exchange, which is greater than that of tracheophyte roots, may be important in their ability to obtain essential cations such as Mg.

Hypnum cupressiforme Hedw. in an evergreen **holly oak** (*Quercus ilex* L.) forest modified its nutrient uptake based on drought conditions [179]. Drought caused greater enrichment of P, K, Ca, Mg, S, and Mo, suggesting that during drought a greater proportion of these elements in mosses was derived from the atmosphere, particularly for elements linked to drought resistance (C and K). Elements such as Mo and Fe that were important for plant productivity decreased under drought conditions. This could change both moss–herbivore relationships and decomposition rates.

7.1.4. Seasonal Fluctuations

Since mosses tend to be dormant in summer and active in spring and autumn, we should expect seasonal differences in sequestering and release of nutrients. In soils under mosses in a **Scots pine** (*Pinus sylvestris* L.) forest in Hungary, pH decreased from spring to autumn [180]. Furthermore, pH values decrease from xerophytic species to mesophytic ones. CaCO₃ has the opposite behavior, with values in humus increasing from spring to autumn and being lowest with xerophytic mosses. Potassium content is very low and fluctuates only in soils under xerophytic mosses. Levels of ammonium-N are low under mosses, increasing in concentration from xerophytic species to mesophytic species. The minimum nitrite-N occurs with xerophytic mosses, increasing there in autumn. This provides further evidence that mosses cannot simply be grouped as mosses, but that there are functional groups that could be identified.

7.1.5. Epiphytes

Bryophytes that live on tree trunks and branches (epiphytes) may, in some forests, have more roles than ground-level species, and they carry out many of the same functions [181–183]. They are more difficult to sustain because they receive more airborne pollutants [184,185]. In addition, when they are torn from trees, particularly for moss harvesting for horticultural uses, it is more difficult for them to recolonize [67]; many vegetative diaspores that can help a colony expand on the ground have difficulty becoming anchored on tree trunks. Even propagules that lodge on bark may be washed away by the next rainfall.

A major role for bryophytic epiphytes is in their ability to trap airborne dust that contains nutrients and can also contain pollutants [156]. When summer is dry, dust is

more prevalent, and bryophytes on trunks and branches of trees accumulate it among their leaves. Then, when rain arrives, if it is sufficient for stemflow on trees, nutrients wash from the trunk bryophytes and reach the bases of trees; additionally, they can come from the throughfall from bryophytes among branches.

Epiphytic biomass varies widely with variations in climate. A comparison of canopy epiphytic biomass in **lowland** vs. **montane forests** in Ecuador revealed a pattern of higher biomass in the montane region (6.0 kg m⁻² on central branches in Los Cedros, 1.8 kg m⁻² in Otonga) vs. lowland forests (1.3 kg m⁻² in Yasuni, 1.8 kg m⁻² in Tiputini) [186]. In Taiwan, epiphytic biomass and associated detrital matter was 336 g m⁻² [187]. Although this was less than 2% of the aboveground biomass of this **moist subtropical forest**, epiphytes comprised ~21–43% of nutrient capital in this ecosystem. In g m⁻², epiphyte nutrient capital was N = 4.24, P = 0.19, Mg = 0.55, Na = 0.13, Ca = 1.45, and K = 2.89. These nutrients, along with leaf nutrients, are more readily available to other organisms than those stored in wooden components, placing epiphytes among the major nutrient functional groups in these forests.

Low bryophyte abundance in **lowland rainforests**, compared to that in higher altitudes, can be caused by low light and rapid drying during the day, coupled with moist, warm nights [188]. This causes high respiration rates that are not balanced by sufficient photosynthesis. Differences in altitude explained most variations in data on epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes [189]. The mosses, liverworts, and lichens differed in alpha and beta diversity patterns, with liverworts achieving greatest species richness in a transition zone at mid-altitude (2550–3190 m asl). A general increase with altitude in bryophyte biomass in the canopy coincided with a rise in humidity.

In a **subtropical moist forest** of the *Lithocarpus* Blume–*Castanopsis* (D. Don) Spach association in Ailao Mountains of Yunnan, China, stemflow and throughfall were modified compared to nutrient concentrations in rainfall [190]. In this forest, epiphytic bole bryophytes altered the chemical composition of stemflow through their selective uptake or release of nutrient elements. On trees with bryophytes, total N, NH₄⁺-N, Mg, Na, and SO₄²⁻-S were enhanced in stemflow, whereas NO₃⁻-N, K, P, and Ca were depleted.

In a **tropical montane forest** in Monteverde, Costa Rica, approximately 85% of nitrate N (0.02 g m⁻²) from atmospheric deposition to the canopy was retained [191]. Epiphytic bryophytes accumulated N at 1.8–3.0 g m⁻² yr⁻¹ [192]. About 30% of initial N was released rapidly from both epiphytic and ground-layer bryophytes. Green bryophyte shoots on the forest floor had greater N loss, with about 47% of initial N lost within the first three months of measurement in enclosures. There was no evidence for net N immobilization by either litter or green shoots, but N that remained in litter was apparently recalcitrant. Epiphytic bryophytes accumulated an estimated 37–64 g C m⁻² yr⁻¹ and 0.8–1.3 g N m⁻² yr⁻¹. These epiphytic bryophytes transform highly mobile inorganic N (~50% of atmospheric deposition as NO₃⁻) to less mobile NH₄⁺ and recalcitrant forms within the bryophytes, and their litter and humus [193]. This research predicted that epiphytes retained ~0.34 g m⁻² yr⁻¹ N. This was derived by their interception and retention of 33–67% of inorganic N deposited there in cloud water and precipitation.

In a Colombian **upper montane rainforest**, there was an estimated 4400 g m⁻² of epiphyte biomass and suspended soil [194]. A single individual of **Mariquita tree** (*Weinmannia mariquitae* Szyszyl.) and its associated epiphytic load contained 2360 g N, 215 g P, 1350 g K, and 99 g Ca, of which 51, 58, 80, and 72%, respectively, were present in the tree itself. Accumulation of dead vegetation and living bryophytes was most likely promoted by low temperatures, continuously high humidity, low air turbulence, and forest structure. This canopy “vegetation” therefore plays a major role in overall nutrient economy and productivity.

Tropical montane cloud forest epiphytes are important in the interception of water and nutrients [195]. These interceptions provide a means of trapping nutrients that would otherwise be unavailable to forest floor vegetation. The range of both biomass and water

storage of epiphytes varies considerably among sites. The largest and richest bryophyte communities in a **montane cloud forest** of the Venezuelan Andes occurred on understory boles and inner canopy communities [196]. Canopy communities stored and released nutrients used by understory communities that in turn were important in regulating humidity in the forest.

Nutrients typically are released from bryophytes in pulses because of changes in wet vs. dry leakage [197]. Loss by leaching upon rewetting of dry bryophytes from **cloud forest** canopy was greatest for those ions held inside cells. This amounted to solute efflux from stem segments of canopy bryophytes of $8.01 \text{ g m}^{-2} \text{ yr}^{-1}$ for K, $0.14 \text{ g m}^{-2} \text{ yr}^{-1}$ for P, and $1.18 \text{ g m}^{-2} \text{ yr}^{-1}$ for N during experimental rewetting. Under natural field rewetting episodes, these numbers were smaller ($2.87 \text{ g m}^{-2} \text{ yr}^{-1}$ for K and $0.02 \text{ g m}^{-2} \text{ yr}^{-1}$ for P). Reduction in numbers in the field may reflect internal recycling within bryophyte mats. Nevertheless, bryophyte loss to throughflow during these rewetting episodes is a significant portion of nutrients held within those canopy mats. Nutrient release upon rewetting provides access to nutrient pools that would otherwise be inaccessible to the forest floor. This source can further enhance recycling transformation of nutrients in epiphylls and stimulate decomposer communities through this pulse enrichment.

In addition to mineral nutrients, bryophytes release sugars and polyols, including fructose, mannitol, glucose, erythritol, glycerol, and sucrose [198,199]. Wetting and drying cycles induce accumulation of these substances, amounting to more than 95 g m^{-2} in **cloud forest** canopy in Guadeloupe. These were almost three times as great in the upper canopy leafy liverwort *Frullania atrata* (Sw.) Nees ex Mont. (17% of dry weight) compared to the lower canopy moss *Phyllogonium fulgens* (Hedw.) Brid. (<6% dry weight). However, release was reversed, with 0.9 g m^{-2} released during rewetting episodes in lower canopy bryophyte mats compared to only 0.3 g m^{-2} from the upper canopy. These sugars and polyols are released in pulses during rewetting and contribute to the success of microbial decomposition and asymbiotic N fixation.

Recently, the discovery of **lowland cloud forests** has provided us with opportunities to compare epiphytes of similar moisture regimes in lowland vs. montane sites [200]. Like **montane cloud forests**, **tropical lowland cloud forests** are characterized by increased epiphytic species diversity of bryophytes in comparison to that of **lowland rainforest**. The two types of forest in French Guiana differ in functional composition of canopy epiphytes, especially in the mid and outer canopy. The **lowland cloud forest** has both higher biomass and cover of bryophytes with a richer array of life forms than other **lowland forests**. Almost absent in the **rainforest**, tail, weft, and pendants are frequent in **lowland cloud forests**. We need a comparison of the roles of these bryophyte types.

In **temperate forests**, biomass of epiphytes is usually considerably less than that in **tropical forests**. However, in a **sessile oakwood** (*Quercus petraea*) of northwestern Wales, bryophytes formed ca. 90% of the standing crop of ground vegetation, primarily comprising *Dicranum majus* Turner, *Rhytidiadelphus loreus* (Hedw.) Warnst., *Plagiothecium undulatum* (Hedw.) Schimp., *Polytrichastrum formosum* (Hedw.) G.L. Sm., and *Thuidium tamariscinum* (Hedw.) Schimp. [67]. Epiphytic bryophytes comprised only ca. 4% of the total bryophyte standing crop. Among ground-layer bryophytes, the ectohydric *Plagiothecium undulatum* had a higher concentration of Ca, Mg, K, and Na than other species, with the endohydric *Polytrichum formosum* having the lowest. In fact, the ground-dwelling *Polytrichum* presented no significant change of Ca, Mg, K, or Na from that in throughfall. The non-*Polytrichum* moss layer altered the chemical composition of the precipitation, with K being leached from canopy leaves and absorbed by the soil bryophyte layer. Bryophytes from the moss layer also removed Ca and N from precipitation; however, Mg ions were lost from the moss layer, making them available to the soil layer. *Rhytidiadelphus loreus* removed significant amounts of NO_3^- and *Polytrichastrum formosum* removed significant amounts of NH_4^+ , again demonstrating that bryophytes cannot be considered a single functional group.

Few early studies of bryophytes explored the nutrient content for temperate epiphytes (see *Hypnum cupressiforme* [181]). In **broadleaf forests**, bryophytes on soil are scarce except

for on slopes and other raised areas due to burial by leaf litter. However, as epiphytes, they can accrue considerable photosynthetic biomass. For example, in the **bigleaf maple** (*Acer macrophyllum* Pursh) community on the Olympic Peninsula of Washington, USA, epiphyte biomass (35.5 kg per maple tree, mostly bryophytes) is only 2% of aboveground biomass, but it has nearly four times as much biomass as do leaves of these maples [201]. Element contents in 35.5 kg standing crop of bryophytes include 370 g N, 44 g K, 145 g Ca, 50 g Mg, and 9 g Na. The most common epiphytes on **bigleaf maple** are the mosses *Eurhynchium oreganum*, *Isothecium myosuroides* Brid., *Rhytidiadelphus loreus*, liverworts *Porella navicularis* (Lehm. et Lindenb.) Pfeiff., *Radula bolanderi* Gottsche, and fern *Polypodium vulgare* L.

In old-growth **sub-boreal spruce forests** in central British Columbia, 47 species of bryophytes are known [28]. Only *Orthotrichum* Hedw. sp. among mosses is epiphytic. On the other hand, the soil layer community is almost entirely bryophytes. This finding of few bryophytes on conifer trees is not unusual and may relate to bark pH. In northern California, **coniferous trees** likewise had bark with lower pH and lower bryophyte cover, but drier conditions may contribute also [104]. Furthermore, bryophytes benefitted from thicker bark with greater water-holding capacity on broadleaf **Pacific madrone** (*Arbutus menziesii* Pursh). Tree species and bark pH were the most important characters determining the richness of epiphytic bryophytes and lichens in **boreo-nemoral forests** in Latvia [202]. Tree species were among the most important drivers of species composition for these bryophytes and lichens in managed **coniferous-deciduous mixed forests** of Hungary [136].

7.1.6. Epiphylls

In higher-latitude forests, epiphylls rarely exist. However, in the tropics they can be important nutrient filters. These communities consist of algae, lichens, bacteria, and bryophytes on leaves, with bryophytes usually being most conspicuous. In **Amazonian forests**, they filter nutrients much like ground bryophyte flora in northern forests [203]. Some form associations with Cyanobacteria that convert atmospheric N into forms usable by plants [204]. Most, perhaps all, scavenge nutrients in rainfall and dustfall, storing them both internally and externally, and causing nutrient concentrations in throughfall to be lower than that in rainfall [205]. (See also radioisotope scavenging [206] and canopy filtration functions [207]).

However, these epiphylls can have more direct effects that have rarely been considered [204]. Fixed N from these epiphyllous communities can be transferred directly to host leaves, as shown for **Amargo palm** (*Welfia regia* T. Moore & Mast.); 10–25% of leaf N came from these epiphyllous communities.

In **tropical ecosystems**, epiphylls can play important roles in providing habitat for invertebrates, storing and releasing nutrients, providing sites for N fixation, and modifying water flow through the canopy. These tiny plants obtain nutrients from both throughfall and free-living N₂-fixing organisms, as well as using leachates from host leaves [208]. Upon rewetting following drying events, these bryophytes lose significant quantities of nutrients through leaching across leaky membranes (see also [205]). These nutrients can then be taken up by host leaves. However, these relationships vary widely, with epiphyllous bryophytes getting 1–57% of their N needs from host leaf leachates. Both epiphylls and host leaves take up labelled N, but leachates from epiphylls provided less than 2.5% of host leaf N after 14 days. Timing can be important. In short, gentle storms these nutrients might remain with epiphylls, but in heavy storms the beginning burst of water can wash external nutrients out of epiphyll colonies and into throughfall [67,197]. Observations for 180 days revealed that this nutrient release is highly dynamic, with epiphyllous bryophytes serving as an intermittent sink [208].

Epiphylls can steal water from host leaves as epiphylls dry. The osmotic potential for the epiphyllous liverwort *Radula flaccida* was −30 to −35 bars, a value much lower than that of host leaves (−10 to −12 bars) [209,210]. This would draw water from the host leaf to the liverwort. Surprisingly, the interception of light by epiphylls was less than 2%, causing

no measurable difference in chlorophyll contents of the host leaf. There was no movement of photosynthate from the epiphylls to host leaf or *vice versa*.

Perhaps the most important contribution of epiphylls is their ability to house N-fixing Cyanobacteria. Cyanobacteria benefit by glucose and mineral nutrients leached from the host leaf, suitable light intensity, and desiccation protection afforded by epiphylls [205]. A large portion of fixed N is transferred to the host leaf, often accounting for 10–25% of total leaf N. Epiphylls cause the leaf habitat to dry more slowly by maintaining water in capillary spaces and by drawing water from the host leaf [209]. Furthermore, the epiphyll-covered portion of the leaf will become wet faster because of these capillary spaces. Free-living N-fixing organisms require 200 g of glucose for every g of N fixed [211]. Nevertheless, much of the N is trapped by epiphylls and host leaves; water running off host leaves actually has less N than that in rainfall in the open.

Few epiphylls occur outside the tropics, but some temperate forests do present the right conditions. Four species of *Orthotrichum* and one species of liverwort were growing on the leaves of **western red cedar** (*Thuja plicata* Donn ex D. Don) in western British Columbia, Canada [212]. None of these taxa is exclusive to leaves. Their roles in that ecosystem remain to be discovered.

7.2. Decomposition and Nutrient Cycling

Rates of bryophyte decomposition have not been studied extensively in many ecosystems [213]. Yet the decomposition process is a key part of nutrient cycling of bryophytes in forest communities. Bryophytes contribute to humus formation and have effective nutrient uptake and slow nutrient release, hence sequestering forest nutrients and having significant impact on the forest root zone [13]. Bryophyte decomposition is slow compared to that of most tracheophytes [214–218].

Bryophytes store nutrients both internally and externally. External nutrients are easily washed off and lost through leaching. We need to distinguish between nutrient components stored in these two locations because they represent very different accessibilities [219].

Until recently, bryophytes were considered to be of low nutrient value. However, in six New Zealand forest moss species, the C:N ratio was high (53–188), as was the C/P ratio (206–815) [220]. Approximately 90% of acid-soluble N was derived from amino acids and proteinaceous compounds, indicating a high quality of N in litter unless these were complexed and recalcitrant. N mineralization studies indicated that N was released mostly as ammonium ions, facilitated by microbial activity. Leaching also produced high N levels.

Nevertheless, feather moss decomposition is slow compared to that of leaf litter [221], causing buildup of moss litter below live moss and above the humus layer [222,223]. This layer is able to retain moisture and actually accelerates decomposition of forest tracheophyte litter [221]. These senescent and dead moss layers increase buffering the soil against temperature changes [222–224] by increasing the depth of insulation and reducing penetration of sunlight [10,225]. However, this further complicates the role of bryophytes because it means lower temperatures in summer can decrease litter decomposition rates.

Soil nutrient concentrations are also important factors in forest soil decomposition [226]. For example, decomposition is much faster in extreme-rich fens than in bogs and poor fens. It is likely that similar relationships are typical in forests. Since bryophytes affect these nutrient levels, they can be important ecosystem engineers in the decomposition process [154,166]. They can accumulate recalcitrant polyphenols, exhibit control over soil hydrology, maintain low soil nutrients, lower pH, and lower summer temperatures, all of which affect decomposition rates of both bryophyte and tracheophyte litter. Their interactions with tracheophytes are both to facilitate and to compete.

7.2.1. Boreal Forests

Bryophytes typically provide the predominant cover in **northern forests** [10]. Because of their effects on soil temperature and raising permafrost depth, they slow the decomposition of everything in the ground layer [218]. They are generally the first organ-

isms to intercept nutrients from the atmosphere, whereas tracheophytes must wait for the slow decomposition of bryophytes, which is estimated to be ~10% that of tracheophytes. Bryophytes are important in maintaining soil C by influencing both decomposition rates and soil N availability [20].

Decomposing Bryales (acrocarpous mosses) take 5–12 years to decompose to an unrecognizable state in a Canadian **black spruce** (*Picea mariana*) stand [162]. Turnover can last 6–250 years in **boreal** soils, causing extensive and rapid accumulation of C in surface mosses and detrital layers following fire [227]. Uplands with thick cover of moss and **black spruce** trees require 36–250 years for turnover of thick moss layers.

Hylocomium splendens and *Pleurozium schreberi* play a vital role in forest floor N economy in **boreal forests** [228]. N is retained immobile in moss tissue, then released very slowly to lower organic layers. In *Hylocomium splendens* from a **subarctic birch** (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) woodland, segments of living, green portions had a relatively long life span, resulting in long residence time for N before it became part of decomposing brown tissue [154].

In *Picea mariana* forests in interior Alaska, most tracheophyte roots are located in the thick carpet of feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*) [228]. N is immobilized in moss layers and released very slowly to soil. Uptake by tracheophytes is minimal. Little labelled N reached below the bryophyte layer. Temperature seemed to be the controlling factor for N flow.

Type of bryophyte is the most influential factor to affect decomposition in the **black spruce forest** of the Clay Belt of Ontario and Quebec, consequently driving C and nutrient cycles [218]. Decomposition, as measured by loss of biomass, differed in a sequence of *Pleurozium schreberi* > *Sphagnum capillifolium* > wood sticks > *Sphagnum fuscum* (Schimp.) H. Klinggr. and differed with depth.

Litter of the **boreal forest** moss *Dicranum polysetum* Sw. lost 15% of its biomass in the first year; after 2 years it had only lost 25% of its original biomass [229]. After 4 years, field populations had still lost only 50%. Despite a sharp decrease in the first few months, probably due to leaching, N concentration as a percentage later increased. N increase resulted from N accumulation [230]. Decomposition rates differ among bryophyte species and harvesting strategies, with some decreasing faster and others slower than wood decomposition (Figure 2) [217].

We should look for the effects of bryophyte life form on rates of forest litter decomposition. In Alaskan **tundra**, effects on decomposition rate seemed to group by growth form (all mosses are considered one growth form) [231]. Graminoid litter had the fastest breakdown rate and deciduous shrubs and mosses the slowest. Decomposition rates were mostly related to the quality of C, rather than to N concentration. However, bryophyte life forms differ widely, and studies on decomposition typically have not compared life forms.

Decomposition of mosses could provide a large proportion of annual nutrient requirements in a Canadian **black spruce** forest [156]. However, there was no experimental evidence to support this [220]. Nutrients in mosses may be particularly important in winter when tracheophytes are not very active in nutrient uptake. Bryophytes could sequester winter nutrient input, whereas in their absence those nutrients could be lost to the ecosystem. Those stored nutrients would subsequently be available through leaching and decomposition [232].

Sphagnum, a common component of **boreal spruce** and **tamarack** forests, has its own mechanisms for delaying breakdown through creating acidic, anaerobic, antibiotic conditions [233]. Weight losses at: the surface, the water-table, and 75 cm in the peat surface were roughly in the ratio 13:9:2 [215]. The decay rate was faster in a lowland bog that had higher temperatures when compared with those in an upland bog. However, one cannot lump all *Sphagnum* together. *Sphagnum papillosum* Lindb. experienced weight losses that were only half those of *S. cuspidatum* Ehrh. ex Hoffm. and *S. capillifolium* (Ehrh.) Hedw. The level where *Sphagnum* survives as peat and the upper level where sulfide is detected indicates that decomposition is due to microbial activity.

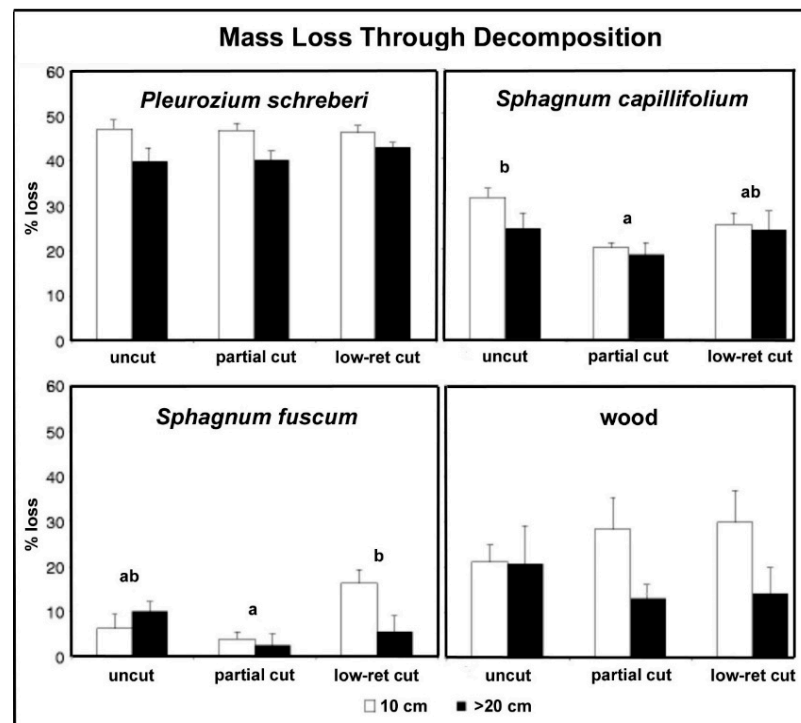


Figure 2. Percent mass loss through decomposition for different moss substrates compared to wood in three harvest treatments (uncut, partial cut, and low-retention cut) at two soil depths (10 cm and >20 cm). Different letters indicate statistically significant differences among harvest treatments tested individually for each species. Modified from [217].

Among several Antarctic mosses, decomposition potential from highest to lowest of inserted cotton strips was *Sanionia uncinata* (Hedw.) Loeske s.l. > *Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth. > *Sarmentypnum sarmentosum* (Wahlenb.) Tuom. & T.J. Kop. > *Polytrichum strictum* Menzies ex Brid. > *Cephaloziella varians* (Gottsche) Steph. [233]. The time period for 50% loss of weight to occur was 1–2 years for *S. uncinata* and *C. aciphyllum*, and 3–4 years for *P. strictum* and *C. varians*. While rates may differ in **northern boreal** climates, these Antarctic rates indicate potential differences among these mostly bipolar species. The causes of the low rates seemed to be low temperatures, short activity season, and low pH. However, when locations were compared, differences also related to nutrient status, water content, and anaerobic conditions.

In reciprocal transplants of *Sphagnum* species between hummocks and hollows, species differences in *Sphagnum cuspidatum* and *S. fuscum* had a much greater effect on decay rates than did microhabitat [234]. Decay rates for these two species were much slower during the later incubation interval (22 months) than they were during the first interval (19 months).

In contrast, in a Swedish **boreal forest**, over 4 years of study, litter from feather mosses and lichens provided the largest promotion of decomposition of litter type associated with them [221]. In general, it was slow-decomposing litters that had the greatest positive effects on decomposition of associated litters. However, in the second year, litter decomposed at the highest rate when associated with its own litter type.

Mosses decreased fungal activity in **Aleppo pine** (*Pinus halepensis* Mill.) litter in two pine forests in the eastern Iberian Peninsula [235]. *Hypnum cupressiforme* predominated at the first site; *Hylocomium splendens* (most abundant), *Dicranum scoparium* Hedw., *Rhytidiadelphus triquetrus*, and *Pseudoscleropodium purum* were the most abundant at the second site. Mosses caused a slight increase in decomposition rate of pine litter, possibly due to greater moisture and/or the high content of mineralizable N in the Oa horizon associated with mosses.

7.2.2. Scots Pine (*Pinus sylvestris*)

Decomposition rate of moss litter was “among the absolutely lowest” for **Scots pine (*Pinus sylvestris*)** forest in central Sweden; this was perhaps regulated by levels of chemical components not affecting needle litter loss as greatly [229]. Consequently, mosses constituted a large proportion of organic layers. Moss litter input contributed about twice as much to the organic layer as did needle litter.

It took 5 years for *Pseudoscleropodium purum* to decompose to humus in a **Scots pine forest** [236–239]. Fungi were present at decomposition depth, suggesting they played a role in decomposition. Furthermore, when decomposition accelerated, there was a concomitant increase in associated microflora. There was evidence of microbial attack on the moss, but no evidence of fungal penetration of tissues. Nevertheless, there was a significantly higher ratio of number of mycorrhizae to root dry weight under *Pseudoscleropodium purum* than under bare soil (mean 280.2 ± 14.5 compared to 202.2 ± 9.2), perhaps indicating a favorable microclimate [240].

In a **birch (*Betula*) carr** in The Netherlands, *Sphagnum recurvum* P. Beauv. release of nutrients N, P, and K was greater than that of organic matter [241]. One year after cells were dead, they were barely damaged and had poor colonization by microorganisms, accounting for slow breakdown. Moss litter decomposition had a rate constant of 0.22; this was the lowest of the decomposition groupings. Turnover time for mosses was 4.55 years, compared to 1.55–2.0 years for litter from the three main tree species.

7.2.3. Douglas Fir (*Pseudotsuga menziesii*)

Climate makes a difference. The moss *Eurhynchium oreganum* in a **Douglas fir forest** in Oregon, USA, became brown and senescent in 3-year-old portions, with no branches older than that [7]. However, in Washington, USA, the same species commonly exhibited 6 years of green growth [242], hence sequestering nutrients for a longer time.

7.2.4. Tropical Forests

Fallen epiphytic material in a **Neotropical montane forest** was $50 \text{ g m}^{-2} \text{ yr}^{-1}$, a figure more than twice that reported previously for other tropical cloud forests [243]. However, this represents all epiphytes, not just bryophytes. Nevertheless, turnover times for nutrients were four to six times longer than that for nutrients in terrestrial rooted plants, except for K, a water-soluble nutrient. K turnover was 10 times as fast, suggesting the role of bryophytes in rapid capture and release. In a **moist evergreen, broad-leaved mossy forest** on Ailao Mountain, Yunnan, China, dominant bryophytes were mixed and decomposition rate constants were lowest compared to trees and bamboo [244]. Despite the large cover of epiphytic bryophytes and the wide range of forests, we are lacking quantitative studies on bryophyte decomposition rates throughout most of the tropics.

7.3. Nutrient Pulses

The nature of bryophyte physiology in response to weather events creates pulses of nutrient release. Leakage and repair of bryophyte cell membranes is a well-known phenomenon in desiccation studies [245]. Dry epiphyllous bryophytes have lower associated N fixation rates than hydrated ones; moist conditions are more suitable for microorganisms that conduct fixation [246]. Hence, there should be pulses in **tropical forests** where these epiphyllous species occur.

Nutrient pulses are only slightly better known in **boreal** ecosystems. *Pleurozium schreberi* can serve as a nutrient sink. *Pleurozium schreberi* absorbs N in quantities apparently beyond its needs [247,248]. At the other end of the spectrum, K^+ is easily leached out of *Pleurozium schreberi* under stress of simulated acid rain or desiccation [248]. In **Jack pine (*Pinus banksiana*)** and other **northern and boreal forests**, *Pleurozium schreberi* often reaches 100% cover and could have a major impact on nutrient flux. As an accumulator of N, it can become a sink, releasing its excess load in pulses slowly over time.

In a **subalpine spruce-fir forest** in western Alberta, Canada, feather moss mats serve as nutrient sinks [249]. They experience wetting and drying events throughout the growing season. In *Hylocomium splendens*, pulse release of organic C occurs during rehydration, reaching as high as 1544 mg m^{-2} total organic C. Using artificial mats as controls, the researchers determined that 23–75% of this pulse release originated in moss mats. K was likewise released during these pulses.

In **spruce forests** that have *Sphagnum* groundcover, mosses sequester K from through-fall and dust [250,251]. As summer weather becomes drier, cell membranes become damaged. When rain returns, K^+ leaches from leaky cells before membranes can be repaired. In northern spruce forests where this is a typical weather pattern, it means that nutrients, particularly K^+ , are released near the end of the growing season when they have been depleted from the soil, thus creating a late pulse when buds are forming for the next year of growth. In other cases, perhaps including *Pleurozium schreberi*, thick mats could slow runoff, causing slow release of K^+ to soil as the rainfall event progresses. This autumn pulse is a little-known phenomenon that could have important implications for nutrient signals in high-latitude conifer forests. It gives a boost at the end of the growing season that could permit underground storage organs to prepare for the coming spring.

7.4. Nitrogen Fixation

N fixation may be one of the more important roles of bryophytes in the forest. This is not accomplished by bryophytes themselves, but usually by associated Cyanobacteria that benefit from the moist environment that dries more slowly than the surrounding bare substrata. N fixation is strongly depressed by N deposition, as found in air pollution [252–256].

In old-growth **Douglas fir** forests in Oregon, the epiphytic leafy liverwort *Porella navicularis* (Figure 3) (6.98 g m^{-2} standing crop) with associated *Nostoc* Vaucher, 1888, Ex Bornet and Flahault accounted for a yearly contribution of at least $0.0015 \text{ g N m}^{-2}$ [257].



Figure 3. *Porella navicularis* growing on a tree in western USA. Photo with permission from Botany Website, UBC.

In coniferous forest sites in Sweden, only low N fixation was known, and this was only associated with *Sphagnum* [258]. The fens, on the other hand, had high levels of N fixation activity on *Sphagnum* as well as on *Drepanocladus* (Müll. Hal.) G. Roth *s.l.* and *Calliergon* (Sull.) Kindb. By contrast, the traditional view for **boreal forests** has been that these communities have no significant N fixation input [259].

Although N fixation was known in *Sphagnum* habitats [258] and Costa Rican **rainforests** [216], it was typically not mentioned for other ecosystems (e.g., [216]). “Significant” N fixation occurs among epiphyllous communities in Costa Rican **rainforests**, especially liverworts, due to favorable moisture conditions created by them [246]. Those measured on dried leaves reached $0.66 \mu\text{g N m}^{-2} \text{ h}^{-1}$, whereas on leaves that had been kept continuously wet, the rate was $18.69 \mu\text{g N m}^{-2} \text{ h}^{-1}$. The epiphylls maintain a moist environment on leaves, making it possible for N fixers to thrive there. In Costa Rican cloud forests, more N can be lost in stream discharge than that gained from atmospheric deposition [62]. Epiphytes in these forests that harbor N-fixing Cyanobacteria may compensate for these losses. N fixation in these canopies reached a mean rate of $5.04 \mu\text{g N g}^{-1} \text{ d}^{-1}$ during the wettest season, reaching a yearly fixation rate of $0.61 \text{ g N m}^{-2} \text{ yr}^{-1}$. Of that, 78% came from bryophyte associations. Only 2% of fixation occurred on the ground.

By 1985, the epiphytic liverwort *Porella navicularis* in western North America was known to have N-fixing colonies of *Nostoc* [260]. This association was found consistently throughout the broad geographic range of the liverwort. These *Nostoc* colonies were external, nestled in crevices and curled margins formed by leaves.

N-fixation rates in *Pleurozium schreberi* and *Hylocomium splendens* in the **boreal forest** were greater in mosses with higher C:N ratios and in green upper portions compared to brown lower portions [255]. The Cyanobacterium *Nostoc* and fungus *Nidularia* Fr. & Nordholm were predominant associates.

Despite these findings, N fixation was still not considered in the N budget of most forest ecosystems. However, the numbers did not add up. N reaching the soil was greater than could be measured in known inputs. Finally, researchers began to explore N fixation among feather mosses.

7.4.1. Boreal Forests

In the **boreal forest** *Hylocomium splendens*, when light supply is adequate, nutrients become limiting factors [261]. Abundant atmospheric N_2 is not usable by plants unless they have an N-fixing partner. Nutrients are available from those leached from tree crowns, dust, and atmospheric ammonia and nitrate. At the time Tamm [258] wrote the treatment of *H. splendens* nutrition, the role of Cyanobacteria as N-fixing partners was still unknown in its boreal ecosystems. However, Tamm recognized that N from the known sources was not enough to account for all N present in the moss.

In a **black spruce** (*Picea mariana*) forest in Alaska, mosses comprised 96% of plant ground cover, and most of these exhibited N-fixation activity [262]. However, the researchers were unsure of the organisms involved. They suspected epiphytic algae, but these were often absent, causing them to consider aerobic and facultative bacteria. Moisture seemed to be important in greater activity. At two sites in a subarctic **black spruce** (*Picea mariana*) forest, lichens had a lot of N-fixing phycobionts, but it was moss cover with its associated Cyanobacteria that had the highest overall proportion of activity. Moisture was the limiting factor controlling activity.

Clearly, the traditional absence of bryophyte-associated N fixation in the **boreal forest** needed to be re-evaluated, as it had been previously considered unimportant [259]. *Sphagnum capillifolium* had 11 times as great an N-fixation rate at its peak in summer when compared with that of *Pleurozium schreberi* in boreal forests in central Canada [259]. Increased temperature was much more beneficial (four times as much) to *S. capillifolium* fixation than to that of *P. schreberi*, suggesting that the maximum contributions of these two species occur at different times. The seasonal fixation rate for *S. capillifolium* was 193 mg N m^{-2} and for *P. schreberi* it was 23 mg N m^{-2} . We have learned relatively recently

that N fixation by Cyanobacteria associated with feather mosses makes a major contribution to N in boreal forests [263]. There is a high degree of host specificity among mosses by Cyanobacteria, but specificity and community composition and diversity did not differ among 30 forested islands in two adjacent Swedish lakes in the northern **boreal** zone, despite great variability in resources [263].

While all mosses in a **boreal forest** study induced hormogonia (filaments that detach) of the Cyanobacterium *Nostoc*, only *Hylocomium splendens* and *Pleurozium schreberi* were colonized; *Dicranum polysetum* and *Polytrichum commune* were not [254]. Researchers interpreted this to mean that feather mosses secreted species-specific chemo-attractants when N-limited, guiding Cyanobacteria toward them. Through this species-limited N-fixation mechanism they control N input into the **boreal forest** ecosystem. Feather moss–Cyanobacteria associations furthermore mediate N levels by slowing down as atmospheric N input increases, causing N availability and acquisition by woody plants to remain constant up to N addition rates of $1.2 \text{ g m}^{-2} \text{ yr}^{-1}$ or more [253]. About 71.8% of the boreal forest receives reactive N deposition at rates at or below $0.3 \text{ g m}^{-2} \text{ yr}^{-1}$, a level that is likely to limit anthropogenic N affecting trees throughout most of the **boreal** forest.

Species differ in response to climate change. *Pleurozium schreberi* had higher N fixation rates with warmer temperatures when compared to *Hylocomium splendens* [264]. At the highest warming treatments of $30.3 \text{ }^\circ\text{C}$, both species exhibited a decline in their N-fixation rates. Light levels had positive effects at low and intermediate temperatures (16.3 and $22.0 \text{ }^\circ\text{C}$), but damaged fixation production at the highest temperature. **Boreal forest** N relationships could benefit from climate warming, but increased shading and extreme temperature events could limit those benefits.

All studied *Hylocomium splendens* and *Pleurozium schreberi*, as well as a group of *Dicranum* bryophytes and two liverworts from **boreal forests** exhibited biological N fixation in Finland, with feather mosses exhibiting the most [256]. Addition of inorganic N of 0.08 to $0.44 \text{ g m}^{-2} \text{ yr}^{-1}$ depressed fixation of N in feather mosses and *Dicranum* species. At concentrations of 0.3 – $0.4 \text{ g m}^{-2} \text{ yr}^{-1}$, N fixation stopped completely. In southern spruce stands, N content was modified by tree canopies, with leaching resulting in compensation of inorganic N that was retained by the canopy. As in the more northern site, N fixation associated with *Hylocomium splendens* was negatively affected.

Increases in N fixation by *Sphagnum capillifolium*, with increases in global temperatures, are likely to increase the decomposition rate [259]. Thus, warming could act synergistically to convert **boreal** ecosystems from C sink to C source, further exacerbating climate change. These studies contributed to the important realization of the sometimes critical role of feather moss–Cyanobacteria associations in boreal forests.

7.4.2. Temperate and Deciduous Forests

Our earlier ignorance regarding the role of bryophyte–Cyanobacteria N fixation in **boreal forests** is easily surpassed by our ignorance of that in **temperate forests**.

In the **boreal forests** of Alaska, N-fixation rates in feather moss habitats were low in **deciduous** stands while being high and variable in **coniferous forests** [265]. Leaf litter was the major factor causing diminished cover by *Hylocomium splendens* in deciduous forests.

Labelled N in a **temperate forest** in New York, USA, revealed Cyanobacteria associated with three (*Fissidens taxifolius* Hedw., *Marchantia polymorpha* L., and *Thuidium delicatulum* (Hedw.) Schimp.) soil bryophytes of the seven bryophyte taxa examined, with colonization in 15–85% of their leaves [266]. These three taxa had $\delta^{15}\text{N}$ values 3.9% higher than those lacking cyanobacterial partners. However, the question remains, how important is this production of more usable N forms to **temperate forests**?

In **Sitka spruce** (*Picea sitchensis*) in the **temperate old-growth rainforest** of British Columbia, Canada, Cyanobacteria density was significantly greater among epiphytic bryophytes than among forest floor bryophytes, with higher N fixation rates at 30 m than at 15 m up or ground level ($26 \text{ mg N m}^{-2} \text{ yr}^{-1}$) [267]. Canopy bryophytes contribute $76 \text{ mg N m}^{-2} \text{ yr}^{-1}$.

In the Hoh Rainforest of the Olympic Peninsula, Washington, USA, **bigleaf maple** (*Acer macrophyllum*) bryophytic epiphytes had associated N-fixation organisms [268]. The highest fixation rates occurred in spring in *Isoetecium myosuroides*, with rates in the Hoh Rainforest at $113.0 \text{ mg N m}^{-2} \text{ yr}^{-1}$ in canopy branches and $0.9 \text{ mg N m}^{-2} \text{ yr}^{-1}$ on branches in a polluted Seattle site.

7.4.3. Post Fire

N fixation was responsible for significantly greater N content in the upper layer of bryophyte turfs, following the 1983–1985 experimental burns in a **Mediterranean forest** of southeastern Spain [269]. These were primarily in locations with *Funaria hygrometrica*, a moss species already known to have Cyanobacteria as associates [270].

N fixation following fires in southern Tasmania increased from 43 mg N m^{-2} in the second year, to 99 in the third, and to 152 in the fourth year after burning [270]. Three fire-follower bryophytes—the liverwort *Marchantia berteroana* Lehm. & Lindenb. and mosses *Ceratodon purpureus* and *Funaria hygrometrica*—exhibited high rates of N fixation. These rates were much greater than those of mosses from unburned forest.

N fixation in Cyanobacteria–bryophyte associations is responsible for a significant amount of total N recovery in recovering northern **boreal forests** [252]. In 12 forests, ranging 35–355 years since the last fire, N fixation rates increased linearly with time since fire. This trend most likely reflects increased colonization by bryophytes during this time period and would depend on the degree and type of burning. N fixation is more important in late succession, when N availability is otherwise low due to use by the mature forest.

In *Hylocomium splendens* and *Pleurozium schreberi* in the **boreal forest**, N fixation increased both in unit land area and per unit moss, as time since fire increased [271]. In unburned areas, N has been accumulating in the humus layer at $1.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ $0.18 \text{ g m}^{-2} \text{ y}^{-1}$ over the past 5000 years. This study contradicted several claims and demonstrated that N fixation is important both in early succession and in late succession systems that are nearing recovery. Nevertheless, much of N may exist in forms unavailable to rooted plants.

With estimates of only $0.05 \text{ g m}^{-2} \text{ y}^{-1}$ of fixed N in northern European **boreal forests**, $\sim 3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ N accumulation could not be accounted for [272]. *Nostoc* associated with *Pleurozium schreberi* fixes $0.15\text{--}0.2 \text{ g N mg}^{-2} \text{ yr}^{-1}$ in **mid- to late-successional forests** in northern Scandinavia and Finland [272,273]. After including moss-associated Cyanobacteria in their model, researchers found accumulation of N that was six times that which had been estimated previously. Organic N accumulates in these ecosystems at a rate of $\sim 0.3 \text{ g m}^{-2} \text{ yr}^{-1}$, accounting for the missing N [273]. In late successional boreal forests *Pleurozium schreberi*–Cyanobacterial associations contribute high rates of N fixation and high numbers of Cyanobacteria on moss shoots, but provide only low levels of available N [274]. On the other hand, early successional forests have higher available N and low rates of N fixation, and only limited colonization by Cyanobacteria.

7.5. Cold Hardening

There has been considerable controversy over the effect of atmospheric inputs of N pollution on trees, particularly the effects on preparation for winter (cold hardening). It appears this controversy stems largely from differences among the trees and the signals they use to begin cold hardening. Many conifers use low temperatures and shortening photoperiods to initiate cessation of growth, bud dormancy, freezing tolerance, and metabolic changes [275].

Freezing injury alone due to pollutants was insufficient to explain forest decline in **red spruce** (*Picea rubens* Sarg.) [276]. However, there have been other indications that air pollution, particularly acid rain, affects cold hardening in some conifers, and particularly in high-elevation **red spruce** (*Picea rubens*) in eastern North America [277–281].

For those trees that use diminishing nutrient levels to signal that the growing season is ending, bryophytes and their associated Cyanobacteria can play a mediating role. In mountainous areas of eastern North America, **red spruce** (*Picea rubens*) uses diminishing

nutrient levels as one of its signals to begin cold hardening [282]. Lack of preparation for winter is manifest in poorly developed phellum layers to protect overwintering buds, causing damage at higher winter temperatures than those temperatures causing damage in fully protected plants [282,283]. Since low soil N levels can signal boreal trees to prepare for winter, mediation by bryophytes can help to keep forests safe by trapping excess nutrients from pollution. However, this phenomenon of using low soil N as a signal that winter is approaching, while widespread in **red spruce** (*Picea rubens*) in northeastern USA and Canada [282–284], does not seem to be widespread among conifers [285–287]. Nevertheless, the feather moss association with N-fixing epiphytes seems to be critical in low-nutrient **black spruce** forests due to low-temperature, permafrost-dominated soil and consequent slow breakdown, especially in carpets of *Pleurozium schreberi* [286].

Thus, the role of bryophyte–Cyanobacteria N fixation may be detrimental to some species, while being beneficial or neutral to others [288,289]. Could it be that a fall pulse when bryophytes come out of desiccation [250] is part of this cold hardening signalling in these forests?

7.6. Fungal Interactions

The role of fungi and their interactions with bryophytes and tree species cannot be ignored in any forest ecosystem. For example, as many as 3000 different types of fungi support tree growth in Washington and Oregon, USA [290]. These help trees to obtain water and nutrients through mycorrhizal associations and influence community development, water relations, and aboveground productivity, while providing bioprotectants against pathogens and toxic stress [291].

Significantly more fungal biomass was associated with bryophytes (*Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*) in two mature *Picea abies* forests in south-east Norway than with co-occurring tracheophytes [292]. More fungal biomass was associated with senescent tissues of mosses than with green tissues. Release of ergosterol (component of fungal cell membranes—used as indicator of fungal biomass), while being relatively similar among tracheophytes, varied widely among species of bryophytes. Nevertheless, fungal biomass associated with mosses did not vary significantly between localities, whereas that associated with tracheophytes did.

At least 158 operational taxonomic units (~number of species) of fungi were associated with three dominant **boreal forest** bryophytes (*Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*) in Norway, indicating a need for further study [293]. The community of fungi associated with bryophytes in the **boreal forest** is dynamic, changing both species and abundance with seasons [294]. In four vegetation types in Tasmania, species composition of woody plants and other tracheophytes were the best predictors of taxon composition of mosses and macrofungi (which often are fruiting bodies of mycorrhizae) [295]. Do bryophytes make a difference in the success of these relationships? How do climate, seasons, and weather affect these relationships? Are they necessary to sustain the forest?

In the Cascade Mountains of central-western Oregon, USA, in just one year, ectomycorrhizal fungi suffered significant decrease in the soil of plots in which mosses had been removed, whereas ectomycorrhizal fungi in non-manipulated plots increased [296]. Moss-removed plots had a negative correlation between soil phosphatase activity and ectomycorrhizal root tips (EMT), whereas the correlation in moss-covered plots was positive. Mosses (mostly *Eurhynchium oreganum* and *Hylocomium splendens*) apparently provide needed microclimate for proliferation of EMT.

When activity of mycorrhizae was reduced, phosphates tended to have greater retention in mosses (*Sphagnum subsecundum*, *Hylocomium splendens*, and *Pleurozium schreberi*) [170]. Mycorrhizae apparently move P from mosses to areas where **black spruce** (*Picea mariana*) can obtain it, thus permitting **spruce** to compete with mosses. Tracers with nutrients fed to *Pleurozium schreberi* were transferred by mycorrhizal fungi to seedlings of *Pinus contorta* Douglas ex Loudon [297]. In contrast, in a different case, seedling growth and N

content increased significantly when mycorrhizal connections were disrupted, reducing the influence of *Pleurozium schreberi* and the shrub *Empetrum nigrum* L., and suggesting that fungi facilitated transfer of nutrients to mosses [298].

On decaying logs in old-growth **subalpine coniferous forest** in Japan, bryophytes harbored predominantly saprotrophic Ascomycota, whereas **spruce** roots had predominantly ectomycorrhizal Basidiomycota [299]. Furthermore, fungal communities differed significantly between two bryophyte species, *Scapania bolanderi* Austin and *Pleurozium schreberi*. However, some ectomycorrhizal fungi occurred in association with both bryophyte and spruce seedlings; the dominant fungi differed between the two bryophyte systems.

Association of *Pleurozium schreberi* with ericaceous plants and fungal hyphae exerts “powerful control” over tree regeneration from seeds in *Pinus sylvestris* by inhibiting seedling establishment and causing strong interference with nutrient availability to new seedlings [300].

7.7. CO₂ Trapping

By sequestering CO₂, bryophytes can help to sustain forests by reducing global warming. Bryophytes do not follow productivity patterns typical of most plants. Warm, dry summer weather is often a period of intermittent or sustained dormancy. For example, woodland bryophytes near Sheffield, UK, had peaks of standing crops in May and December—the beginning and end of the growing season [301]. Hence, they are able to contribute to ecosystem net primary productivity when other plants are not contributing at their peak [302].

Bryophytes have different growth behavior from that typical of tracheophytes. Frequently (perhaps always), bryophyte growth in length does not occur at the same time as increase in biomass [302,303]. Hence, these must be measured at two different points in time and can lead to errors in comparisons between species when different types of measures are used. Bryophytes also differ in having their living parts on top, while the bottom parts senesce, die, and decay. Older parts are brown and may sequester some nutrients and products, but soluble nutrients such as K can move to growing portions, regardless of translocation strategy.

Annual production of bryophytes in forests can reach ~100 g m⁻² [216]. In **white spruce** (*Picea glauca* (Moench) Voss) forests in the taiga, daily soil respiratory CO₂ can average 450 mg m⁻² h⁻¹ [304]. When adequate light is present, bryophytes are able to sequester a good portion of this soil CO₂ and become C sinks. In the **tundra**, release of more than 1000 ppm of CO₂ can occur in and around the bryophyte layer under snow in early spring [305], resulting from plant and soil respiration [306]. This spring phenomenon needs investigation in forests.

Increased atmospheric CO₂ is causing climate change on planet Earth. A **global** model of C uptake predicted 0.34–3.3 Gt yr⁻¹ C uptake by bryophytes and lichens [307]. Bryophytes played a role in global chemical weathering in Late Ordovician, reducing atmospheric CO₂ and contributing to climate cooling. Weathering is highly sensitive to atmospheric CO₂, implying strong negative feedback between weathering by bryophytes and climate.

7.7.1. Boreal and Conifer Forests

Boreal **black spruce** (*Picea mariana*) forests typically have dense ground cover of bryophytes and typically dominate understory biomass for the first century after logging in northern forests such as the **Sitka spruce-western hemlock** forests of Alaska [308]. Turnover rates of moss segments in Scandinavian **boreal** forests are actually rapid and are likely to be comparable to that of shrubs [12]. Net primary productivity of upland vs. lowland mosses differs greatly, with that of lowland *Sphagnum* (77 g C m⁻² yr⁻¹) being three times that of upland feather mosses (24 g C m⁻² yr⁻¹) [65]. However, since feather mosses were the dominant ground cover, overall net primary productivity was only

25 g C m⁻² yr⁻¹. Feather mosses and *Sphagnum* occupy quite different functional groups and their contributions need to be measured separately.

CO₂ levels diminished with distance from forest floor in a **mixed forest** in New England, USA [309]. High forest floor CO₂ concentration should be an advantage for seedlings and bryophytes. There is also often a CO₂ gradient within bryophyte mats, as seen in the **black spruce** forest of Alaska [305].

Boreal forests should become even greater C sinks with global warming [310]. In boreal forests, bryophytes can be a considerable portion of the ground-layer C pool [252]. Work in Alaskan **boreal forests** also points to high net primary productivity of mosses relative to that of associated trees [10,166,311]. These studies are encouraging because, until relatively recently, the contribution of bryophytes in forests to C sequestration has been largely ignored.

Some researchers suggest that mosses in **boreal** communities may have a large effect on the tracheophyte community, creating a cold, nutrient-impooverished soil system that supports progressively less productive forests [10]. At the same time, bryophytes are unaffected by these belowground conditions. This is an unusual way of competing, but it works for boreal mosses. Mosses may even be the cause of decreases in older forest productivity in central Alaska by creating these impooverished soil conditions [160].

Patterns of C translocation differ among bryophyte species. In a **black spruce** (*Picea mariana*)-dominated forest in interior Alaska, *Polytrichum commune* retained the greatest levels of labelled C after two hours; *Sphagnum subsecundum* retained least [312]. *Sphagnum subsecundum* had the highest fraction of labelled C in its brown tissues after 35 days, with *Polytrichum commune* having the second highest. *Hylocomium splendens* and *Pleurozium schreberi* had no consistent translocation patterns. All four species accumulated labelled C in both growing shoot tips and brown (senescent) tissues. All four species also exhibited high loss of labelled C through respiration. In mature **black spruce** forests (including *Sphagnum* and *Polytrichum*) with permafrost in Alaska, the overall annual productivity of the mosses was ~120 g m⁻¹ yr⁻¹, a value about twice that of **spruce** trees [313], and annual moss production can be twice that of foliage production in boreal forests in Alaska [66].

Most of the productivity (84%) in **black spruce** forests in Alaska occurred within 20 cm of the moss surface, although it extended deeper into the ground-layer profile as the ground system slowly warmed during summer [314]. Mosses accounted for the largest component of aboveground productivity (73 ± 14 g biomass m⁻² yr⁻¹) compared to that of trees and shrubs.

In a **black spruce** forest with ground flora dominated by feather mosses, live mosses dominated loss of C through respiration, with decomposition of litter contributing less than 30% and spruce root respiration less than 10% of the total [315]. Both spruce and mosses exhibited decreasing net primary productivity as warmer temperatures of summer progressed. Moss net primary productivity ranged 19–114 g C m⁻² y⁻¹; that for spruce was 81–150 g C m⁻² y⁻¹. In an old **black spruce** BOREAS site (53.985° N, 105.12° W) there was no seasonal variation in maximal rates of carboxylation in *Pleurozium schreberi*, with values of 7, 5, and 7 μmol m⁻² s⁻¹ during the spring, summer, and autumn, respectively [316].

In maturing 117-year-old **boreal** forest with **black spruce**, *Sphagnum* bog, and fen systems, plants sequester ~0.01–0.03 kg C m⁻² yr⁻¹ [311]. Soil drainage controls C storage and flux by controlling feather moss input and decomposition rates, as well as through fire. Stands that have been recently burned are net sources of CO₂, whereas maturing stands become increasingly stronger sinks of atmospheric CO₂.

Traditional methods of measuring forest productivity may not be adequate to measure that of the feather moss component by underestimating productivity of lateral branches, with a 25% underestimation (~73 g m⁻² yr⁻¹) of annual production of *Pleurozium schreberi* [317]. These mosses dominate the ground layer of upland boreal forests and account for 50% of photosynthesis there. Thus, their contribution to soil C accumulation is significant. The underestimation can account for 14 Tg C yr⁻¹ across the boreal region.

Mosses in **boreal** ecosystems have a strong influence on C cycling [20]. Models suggest that loss of mosses would reduce soil C by influencing decomposition rates and soil N availability. Despite our recognition that species differ in their contributions and responses, we lack sufficient knowledge to describe functional groups among them. Mosses in general are opportunistic in CO₂ exchange. They are able to respond immediately to increased light, as in sunflecks (Figure 4) [318], or to revive quickly from desiccation and to fix CO₂ through photosynthesis; there are no stomata to open, and they are able to photosynthesize at low temperatures, in some cases below freezing [319]. Sunflecks can provide considerable PAR (photosynthetically active radiation) to mosses. In a mature **black spruce forest** in Alaska, sunflecks provided an intensity on the forest floor of about 76% of incident radiation and occurred on up to 35% of the ground surface [320]. The flickering behavior most likely prevents the high light intensity damage that occurs when the canopy is destroyed.



Figure 4. Forest floor with *Hylocomium splendens* showing sunflecks. Photo by Janice Glime.

Saturation of photosynthesis of the ground layer in a Finnish **boreal forest** was relatively low at 50–400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light levels [321]. Ground layer vegetation was primarily mosses (*Dicranum polysetum*, *Hylocomium splendens*, and *Pleurozium schreberi*), comprising a cover of ~60%. C fixation was $\sim 131 \text{ g C m}^{-2}$ for the growing season. *Hylocomium splendens* growing in sparsely **forested fens** had net productivity of 79 g m^{-2} ; growth correlated with length of time the moss was wet [322].

In a **black spruce** (*Picea mariana*) forest in Alaska, the moss *Polytrichum commune* had a maximum net photosynthetic rate of $2.7 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$, whereas *Sphagnum capillifolium* (Ehrh.) Hedw. had only $0.6 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ [313]. The overall moss production ($120 \text{ g m}^{-1} \text{ yr}^{-1}$) was about twice that of **spruce** production and was primarily limited by leaf water content. *Sphagnum* was also limited by N and P. For 2-year-old shoot sections of five common mosses from **taiga** ecosystems in Alaska, the highest net CO₂ exchange rates were for *Polytrichum commune* ($2.65 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) and the lowest were for *Sphagnum nemoreum* ($0.25 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) [323]. Dark respiration of CO₂ loss increased during periods of growth or recovery from desiccation. Photosynthetic rates decreased greatly in

winter. Moisture was again the limiting factor, and at permafrost-free sites, photosynthesis was frequently inhibited by moisture stress.

Midday gross photosynthetic CO₂ exchange at ground-layer moss surfaces in a **black spruce** (*Picea mariana*) forest in Manitoba, Canada was 0.5–1.0 μmol m⁻² s⁻¹ for feather mosses and 0.5–2.5 μmol m⁻² s⁻¹ for *Sphagnum* [324]. Loss of C from soil and moss respiration was 1–2.5 μmol m⁻² s⁻¹ above feather mosses and 0.5–2.5 μmol m⁻² s⁻¹ above *Sphagnum*. Even at 0 °C, *Sphagnum* accomplished 30% of its normal photosynthetic rate. The maximum rate occurred at 8 °C. Mosses accounted for 10–20% of whole forest gross CO₂ uptake. Its contribution to respiration was higher, accounting for 50–90% of whole forest respiration. For **black spruce** forest in Alaska, where *Hylocomium splendens* and *Sphagnum* spp. dominate ground cover along with lichens and shrubs, total aboveground biomass on the forest floor was 132 g m⁻², and mosses comprised one-third of this [325]. However, despite this portion of the vegetation, they contributed to ~40% of forest floor gross primary productivity. *Sphagnum* and tracheophytes had the highest net productivity on days with high light availability. However, *Hylocomium splendens* and lichens lost CO₂ during mid growing season, showing net gain at the end of the season, after the soil had cooled down. *Hylocomium splendens* was limited by moisture availability, whereas *Sphagnum* was not. Species composition was important in understory contributions to CO₂ and water vapor exchange.

Turnover rates of *Hylocomium splendens* segments in the **boreal** forests of Scandinavia were rapid and comparable to those of shrubs [326]. As patches of bryophytes developed, density also increased and 100% increase in density was associated with doubling in mean size. Increase in segment size corresponded with improved moisture conditions that permitted longer periods of net photosynthetic gain. However, in *H. splendens*, mean size was not significantly related to density of growing points. Rather, these density and moisture conditions are apparently due to interactions between bryophytes in the stands, regardless of species of neighboring plants. However, greater density means that growing tips can receive reduced light, and this seems to account for decreases in branching and regeneration in older stands of this moss. Nevertheless, such high densities only occur ~10% of the time.

Moss respiration rates in the **boreal** forest of interior Alaska corresponded to 60% of total soil respiration under dry weather conditions and 40% under wet weather conditions in unburned forest [327]. Thick moss layers make a significant contribution to the C cycle in this forest. **Boreal** forests are highly susceptible to wildfire, an event that changes them from net sinks to net sources of C [328]. Among the responses to fire, bryophytes follow a distinct successional pattern for the first five decades after fire, corresponding to decreasing soil temperature and contributing to increasing C accumulation in soils. Potential rates of C exchange by mosses were highest in early successional species, declining as the stand matured. It is the interactions of mosses, plant succession, soil temperature, and soil moisture that account for regulating C source–sink dynamics during the first century following fire in **black spruce** systems. It is bryophytes, not tracheophytes, that often are the dominant source of C accumulation in **boreal black spruce** forests.

Mosses are important in regulation of CO₂ exchange in the forest floor of boreal black spruce forests [329,330]. Moss production in a black spruce (*Picea mariana*) forest in Alaska equals that of trees and exceeds that of tree foliage by 3:1 [329]. Mean CO₂ efflux from the forest floor was ~7 μmol m⁻² s⁻¹ for both feather mosses and *Sphagnum* areas [330]. Nevertheless, *Sphagnum* had higher maximum rates of gross photosynthesis than did feather mosses. Mosses lost a net of 140.7 g C m⁻²; total forest floor respiration was 396.1 g C m⁻² during May–October. Mosses contributed about 13% to total ecosystem gross productivity, with *Sphagnum* making the greater contribution (228 g C m⁻²) compared to feather mosses (80 g m⁻²).

In an old **black spruce** (*Picea mariana*) forest in Canada, A_{max} (max rate of photosynthesis per unit foliage area at saturating irradiance) of feather moss *Pleurozium schreberi* was only 1.9 μmol m⁻² s⁻¹, compared to that of the highest in the forest, **aspen** (*Popu-*

lus tremuloides) of $16 \mu\text{mol m}^{-2} \text{s}^{-1}$ [331]. **Black spruce**, however, was even lower at $1.8 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Hylocomium splendens in a subalpine **spruce-fir** forest serves as a C sink, providing pulse releases during rewetting episodes when membranes are leaky [249]. It released 1544 mg m^{-2} of total readily soluble organic C during a single rehydration pulse; 23–75% of this pulse originated from moss mats. Both rapid drying and high-intensity rain events caused larger releases of C.

In **boreal** forests, bryophyte productivity is considerable [332] and often appears to be comparable to that of trees [12]. At the same time, bryophytes have a strong influence on underground processes of decomposition, nutrient flow, and soil nutrient accumulation. Mosses can dominate primary productivity in northern ecosystems, contributing to 20% of aboveground net primary productivity in **boreal** forests [18,20].

Mosses make substantial contributions to CO_2 emitted by respiration at night in **boreal** forests. In a **mixed boreal spruce-pine forest**, mosses explained 29% of variation in CO_2 exchange at night [333].

The moss-dominated forest floor lost 33.8 g C m^{-2} in **sub-boreal** forests in central British Columbia, Canada [334]. Moss productivity was CO_2 -limited by ambient atmospheric levels of CO_2 ($430 \mu\text{mol CO}_2 \text{ mol}^{-1}$) and benefitted from elevated CO_2 of $700 \mu\text{mol CO}_2 \text{ mol}^{-1}$. The CO_2 saturation point for bryophytes is high, further permitting them to take advantage of soil respiration and sunflecks to achieve “substantial” biomass productivity.

Ground bryophytes are regulators of soil C efflux in a **subalpine ecosystem** dominated by **conifers** on the Tibetan plateau [335]. Removal of bryophytes lowered CO_2 efflux from mineral soil, SOC (soil organic carbon), DOC (dissolved organic carbon), microbial biomass, and concentrations of phospholipid fatty acids. Furthermore, removal caused changes in the soil microbial community. These changes were not correlated with temperature or soil water content, but rather with higher SOC, DOC, microbial biomass C, and phospholipid fatty acid concentrations. Hence, it appears that bryophytes were ecosystem engineers that regulated C efflux.

CO_2 efflux from the forest floor in a 69-year-old **Scots pine** (*Pinus sylvestris*) forest in Belgium was $1.2\text{--}1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ [336]. The moss layer apparently influenced turbulent fluxes of CO_2 during the daytime.

Tracheophytes in the understory of a **Douglas fir** (*Pseudotsuga menziesii*) forest were replaced by mosses in the later stages of stand development [337]. Decomposition on the forest floor seemed to decrease with age. After 22 years, mosses comprised 0.4% of ground-layer aboveground productivity, but after 73 years they represented 82%. In old-growth **Douglas fir**, mosses added 20% to total biomass and 95% to photosynthetic tissue biomass [7]. However, moss production added only 5% to aboveground estimates of net primary productivity. Including trees, mosses comprised only 0.13% of aboveground biomass, yet they contributed substantially to ecosystem processes.

Most of the C found in ground surface mosses has accumulated there from the atmosphere since the end of thermonuclear weapons testing in 1963 [227]. Turnover times range 36–250 years for C in uplands with thick moss cover and **black spruce** trees. Although fires and controlled burning can offset sequestered C gains in moss layers, we cannot ignore the role of bryophytes in sequestering C, especially in **boreal forests** where bryophyte species are adapted to photosynthesis at cool temperatures and low light levels.

7.7.2. Temperate Forests

Our knowledge of productivity and C sequestration in **temperate forests** is meager compared to that of **boreal forests**. Annual net production of bryophytes in temperate forests is estimated to be $400\text{--}2500 \text{ kg m}^{-2}$ [338]. In a North Wales **sessile oakwood** (*Quercus petraea*) woodland, bryophytes provided ~90% of standing crop of ground vegetation [67]. Epiphytes formed ~4% of total bryophyte standing crop.

7.7.3. Tropical Forests

In the **tropical montane cloud forest** of Peru, diverse bryophyte communities sequester considerable C [61]. In these forests, epiphytic bryophytes have an estimated 4500 g m⁻² dry mass—one of the highest cover values reported here (Table 2)—and provide substantial contributions to C sequestration.

Bryophytes can also contribute to the C budget by harboring photosynthetic microorganisms that also sequester CO₂ in both boreal and tropical forests. In boreal peatlands, microorganisms can take up twice the C (~4.4 mg CO₂ m⁻² h⁻¹) compared to that in tropical rainforests (~2.4 mg CO₂ m⁻² h⁻¹) [339]. This is only 4% and 2% of bryophyte uptake, respectively. Contributions of these microorganisms is dependent on moss water content and available light, particularly in tropical rainforests. Bryophyte secretions such as polyphenols, carbohydrates, and tannins could foster differences in microbe species among bryophyte species.

In a **tropical montane forest** in Monteverde, Costa Rica, epiphytic bryophytes had net productivity of 122–203 g m⁻² yr⁻¹, representing estimated growth of 30.0–49.9% y⁻¹ [192]. Accumulated C by these epiphytic bryophytes was 37–64 g C m⁻² yr⁻¹.

In a **submontane tropical rainforest** of Panama, there is pronounced daily water content fluctuation in bryophytes [340]. Both low and high water content were limiting to C gain. More than half the C fixed during the day (2.9 mg C g⁻¹ plant tissue) was lost at night through respiration. Net primary productivity was ~45% of initial plant C content.

Based on models, bryophytes in the **temperate rainforest** in New Zealand took up 103 g m⁻², whereas CO₂ efflux from the forest floor was 1010 g m⁻² [90]. Hence, bryophytes were able to use about 11% of soil respiration.

Magnitude and type, but not frequency, of precipitation events affect bryophyte C fluxes [341]. Increases in drought could negatively impact bryophytes and their C storage, having far-reaching consequences for ecosystem processes.

7.7.4. Peatland Forests

In **peatland forests**, *Sphagnum* modulates long-term accumulation of C [342,343]. As keystone species, these mosses present a variety of phenolic profiles that in turn affect colonization by mycorrhizal fungi on shrubs and trees. *Sphagnum* acids and phenolics play different roles in this interaction, and interactions vary with moss species, season, and microhabitat [342]. Cell wall polysaccharides contribute to decay resistance of *Sphagnum*, causing it to form one of the largest known reservoirs of organic C [344]. Most of this C occurs as decomposition-resistant litter, and when these *Sphagnum* systems become forested, a large store of C lies beneath them. Phenolics have only a minor role in decay resistance but cell-wall polysaccharides have a major role, providing resistance to and active inhibition of microbial mineralization of *Sphagnum* litter. However, positive correlations of decay resistance can occur not only with polysaccharides (sphagnum), but also with phenolics [345]. The effects of *Sphagnum* on decay are affected by habitat nutrient availability.

Although the occurrence of *Sphagnum* in northern forests tends to be patchy, it can make significant contributions in those locations [346]. *Sphagnum* is represented by four functional groups that relate to growth, biomass, defense, and water stress tolerance. It is important to understand biochemical traits (including defense) in order to assess their role in the ecosystem. These permit them to compete with trees and other plants, enabling them to control the ecosystem. This lends support to other recent studies that have shown that phenolics in mosses are important in other functions such as protection from high light and antibiotic activity [347–349].

7.7.5. Under the Snow?

One aspect that has not been explored is productivity of bryophytes under snow. Four arctic evergreen tracheophyte species exhibit photosynthetic activity under springtime snow [350]. In this season, the subnivean environment has elevated levels of CO₂, temperatures often above freezing, and sufficient light for photosynthesis. For the moss *Roellia roellii*

(Broth.) A.L. Andrews ex H.A. Crum (syn. = *Bryum sandbergii*), the minimum temperature for photosynthesis is below $-5\text{ }^{\circ}\text{C}$ [319]. In the Antarctic mosses *Bryum subrotundifolium* A. Jaeger, *B. pseudotriquetrum* (Hedw.) G. Gaertn., B. Mey. & Scherb., and *Ceratodon purpureus*, net photosynthesis remained substantial at $0\text{ }^{\circ}\text{C}$, but was strongly decreased below that temperature [351]. The latter two mosses can be found in temperate and boreal forests, with *Ceratodon purpureus* being common after fire. *Hylocomium splendens* removed from beneath snow showed positive net photosynthesis within 332 s when placed in light at $+5\text{ }^{\circ}\text{C}$ [352].

I find it very likely that bryophytes find suitable conditions for photosynthesis under snow, at least under early snowfall in autumn and during spring melt, times when CO_2 is emanating from soil due to soil respiration [306] and temperatures and light are sufficient. However, we need measurements.

8. Seedbeds

One might think that one of the most direct benefits of bryophytes in forests is to serve as a seedbed for the trees. They can hide seeds from herbivores, provide a more moist environment, hold seeds in place, and prevent competition from tracheophytes—or can they?

As ecosystem drivers in the **boreal** forests of Sweden, bryophytes interact with seedlings [12]. When seedlings are planted into dense feather moss layers, they usually establish and grow very poorly despite the more moist environment. This seems to be due to effective competition for nutrients by mosses, although competition for light can also be a problem. This is exacerbated by roots of shrubs that readily access nutrients through mycorrhizal fungi. However, mosses are able to build up thick moss litter layers beneath themselves, and greater retained moisture can promote decomposition of other types of less recalcitrant litter from tracheophytes [221]. Suppression of fire permits greater buildup of bryophytes in **boreal** forests, and this in turn increases suppression of many kinds of seedlings.

Gause's hypothesis (every species must occupy a different niche) may be valid in many circumstances, but it seems to ignore regeneration in plant communities [353]. Grubb feels that the plant niche has four components: habitat, life form, phenology, and regeneration. While I would consider the first three to all be part of the species niche, one might argue that conditions for germination and seedling development can in fact require a different niche than that which is favorable for mature plants. In some cases, germination and mature niches can be made compatible by timing. In other cases, they may be incompatible, such as in those trees that cannot germinate and succeed in the shade of their own species. Since bryophytes in mature forests generally differ from those in early succession [18], the available tree regeneration niche is likely to be changed by changes in bryophyte species and cover. Hence, understanding of niche factors created by those changing bryophytes is important to understanding regeneration of forest trees.

Possible interactions between bryophytes and tracheophyte seeds are allelopathy, mechanical obstruction, soil moisture, and temperature control [354]. All six bryophytes tested suppressed regeneration of tracheophytes, but there were significant differences among bryophyte species. These differences were primarily related to control over soil temperature regime, with cushion thickness being the primary variable; temperature depression during germination was most detrimental.

When bryophytes enhance seed germination, it is not always beneficial for forests. For example, in southwest Ireland, seedlings of **common rhododendron** (*Rhododendron ponticum* L.) are closely associated with slopes covered with bryophytes that do not exceed 1 cm depth [355]. Hence, bryophytes, combined with slopes, provide safe sites for rhododendron. Oakwoods here are heavily grazed by sika deer (*Cervus nippon* Temminck) who at the same time aid dispersal of rhododendron seeds. The *R. ponticum* poses a threat to the oakwoods by shading ground flora and preventing regeneration.

Mosses significantly impact tree regeneration after fire [356]. Mosses can ameliorate the microclimate by remaining moist longer than soil. They also provide protection from predation and wind. Early fire succession mosses *Ceratodon purpureus* and *Funaria hygrometrica* (Figure 5) host associated Cyanobacteria, enabling the latter to provide fixed N that could serve as N “oases” for tree seedlings. On the other hand, burned feather mosses are hostile to some tree species. They have low absorptive capacity and can elevate emerging roots. For **spruce**, they made little difference; for **tamarack**, there was twice as much mortality on burned mosses compared to that on mineral soil.



Figure 5. Pine seedling with *Funaria hygrometrica* after fire. The reddish stalks on the right belong to *Ceratodon purpureus*. Photo from WNCOUTDOORS, through Creative Commons.

Early-seral tracheophytes, including pine seedlings, following fire in a pine forest in southwestern Oregon, USA, germinated but had lower growth on burned bryophytes than on other seedbeds [357]. Nevertheless, these early-seral bryophytes were critical to successional patterns and establishment of other vegetation.

Bryophytes, despite their diminutive size, can be effective competitors. In addition to trapping atmospheric nutrients and acquiring soil nutrients through mycorrhizal fungi, they can be allelopathic (see below) [358]. However, they can also compete with seedlings for suitable physical space and light.

Mosses also colonize bare rock surfaces, initiating soil formation. This new organic substratum permits seed plant colonists to become established. As succession proceeds, young trees and other tracheophytes provide shade and outcompete pioneer mosses, but new shade-tolerant mosses replace them. What happens, then, as mosses become more dense? Cushion mosses in high Andean communities enhanced diversity of tracheophytes [359]. However, is that also true for forest floor diversity, including tree seedlings?

8.1. Life Forms

One of the factors affecting survival of tree seedlings is the life forms (genetically determined morphological characters of individuals) of the bryophytes. Life forms change as bryophyte communities change from early successional stages to later ones. Bryophytes have a wide diversity of life forms [360–362], and these often correspond with their effects on the regeneration niche through differences in the effects on soil moisture and tempera-

ture. In the **boreal spruce-fir** forests of North American **taiga**, the most common life forms are short turfs, smooth mats, threaded mats, and tall erect turfs in terms of number of species; however, wefts dominate cover [8,66,286], especially in **black** and **white spruce forests**. Competition from weft mosses may account for low diversity of other bryophytes in those two community types. They affect which tree species can succeed in germination and establishment.

In the **temperate forests** of Argentina, germination of some woody species was favored, but others were affected negatively by the presence of mosses [363]. Burned or cutover early forest successional stages typically have tight, acrocarpous mats. In later stages, pleurocarpous mats or wefts tend to predominate. These life forms can have pronounced effects on the success of seedlings and even differential effects on germination.

8.2. Boreal Forests

With a thick layer of weft feather mosses on the forest floor, the boreal forest can experience severe competition for nutrients by mosses against seedlings. Sequestering of recalcitrant nutrients by bryophytes is not the case in all forest situations. In **boreal forests** of northern Sweden and elsewhere, tree seedlings frequently access these sequestered nutrients by way of mycorrhizae [364]. However, this mycorrhizal relationship has not been documented in most of the boreal forest. N fixation by Cyanobacteria (*Nostoc*) is common among feather mosses, especially *Pleurozium schreberi*, resulting in a buildup of organic N in the soil [273]. This buildup increases in the later stages of succession [252]. The ability of boreal tree seedlings to survive differs among species of both bryophytes and trees. Understanding the reproductive biology of these tree species is important in order to sustain production [365]. The ever-present feather mosses can be key to that understanding [366].

Due to its high water-holding capacity, *Sphagnum* is a superior substrate for seedling emergence, but it causes high seedling mortality due to smothering because it can grow faster than seedlings of *Picea abies* and *Picea mariana* [126]. Similarly, “smothering” of young seedlings of *Picea abies* was greatest in *Sphagnum* habitats and lowest in *Hylocomium splendens* and *Pleurozium schreberi* [127]. Mortality is highest in plots originally dominated by *Sphagnum*, but because germination is higher there, the number of surviving seedlings is still greater than in feather mosses after 2–3 years.

8.2.1. Feather Mosses

Feather mosses are large mosses, which often make thick carpets (Figure 6). They have a loose structure. Some researchers have attributed low seed success among feather mosses to their dryness due to fast evaporation and insufficient contact between seeds and soil substrate [66,367–371]. Many kinds of seedlings are shorter than mosses and cannot reach both light and soil.

Mosses can be detrimental to the growth of seedlings in Swedish **boreal** forests [12]. When seedlings were planted in dense feather moss layers, their establishment and growth exhibited poor responses. Although mosses often absorb and retain moisture [372], when seedlings are transplanted into moss layers, mosses are effective in absorbing nutrients but are not very effective at sharing them with tracheophytes [10,373].

Timing is important for nutrient release. *Pleurozium schreberi* releases significant quantities of both N and P after drying, with more N coming from senescing portions than either dead or green portions [297]. Drying causes membranes to leak, resulting in loss of inorganic nutrients, proteins, and sugars. These nutrients can facilitate growth of mycorrhizal fungi in culture, and mycorrhizae of associated plants are able to colonize mosses, especially in senescent portions. These fungi can transfer labelled phosphate and C from moss shoots to *Pinus contorta* roots and these then travel to pine shoots. However, are these releases occurring at a time that is beneficial to seedlings? Mosses are likely to be hydrated, possibly under the snow, and active before seeds germinate. Are those early-released nutrients available to the seedlings?



Figure 6. (Left): Feather moss carpet of *Pleurozium schreberi* on forest floor in Europe. (Right): *Hylocomium splendens* on forest floor, showing the loose structure of this feather moss. Note the upright stems of *Polytrichum* at the arrow. Photos by Michael Lüth, with permission.

8.2.2. Picea

The **black spruce** (*Picea mariana*) forest is the most fire-prone forest type in Alaska [329]. These forests have low productivity, are very limited in nutrients, with nutrient limitation controlled largely by temperatures of soil and forest floor [329,374,375]. **Black spruce** dominates on north-facing slopes where permafrost persists and mosses dominate the forest floor [376]. Bryophytes are ecosystem engineers for these nutrient limitations. These ecosystems are adapted to fire and if fire is excluded, it will result in major changes in the ecosystem [377]. Hence, to sustain these forests, it will be necessary to understand the important roles that bryophytes have in this fire cycle (Figure 7).



Figure 7. *Pleurozium schreberi* in a Douglas fir forest, showing healthy green mosses within centimeters of burned soil, and seedlings surviving among the mosses, but not in the burned soil. Wet mosses are resistant to burning. Note the brown and black decay layers of mosses. Photo by Janice Glime.

In Ontario, Canada, *Picea mariana* had the best regeneration after fire when patches of *Sphagnum* remained [378]. Both *Picea glauca* and *Picea mariana* benefitted from burning, with increased seed germination and net seedling establishment after three years, even on severely burned soils [379]. On the other hand, without fire there was a steep decline in conifer establishment when organic soils were deeper than 2.5 cm. Seedlings from small seeds experienced greater mortality on lightly burned organic soils than did those from large seeds.

In eastern Canada, young (burned or harvested) **black spruce** forests had a ground layer comprising a “mosaic” of different bryophyte species, primarily *Sphagnum* and feather mosses [380]. These patches were intermixed with exposed mineral soil and disturbed organic matter that originated mostly from mosses at different stages of decay (Figure 7). Three years after disturbance, **black spruce** seedlings experienced the greatest annual increment on substrates of feather mosses (mostly *Pleurozium schreberi*), fibric material (having at least three-quarters of identifiable plant remaining after rubbing) originating from *P. schreberi*, or a mixture of fibric *P. schreberi* and humic materials. Seedling growth increments were lowest when seedlings were associated with fibric *Sphagnum* spp., mineral soil, or decaying wood. **Black spruce** trees with better N and P leaf status occurred on those sites favoring seedling growth. These results led the researchers to recommend fill-planting seedlings in substrates that originated from *P. schreberi* and to use management techniques that would favor this moss species.

In a **tundra-forest ecotone**, seedbed removal increased **black spruce** recruitment [381]. In that case, seed emergence was highest on *Pleurozium schreberi* (6.3%), followed by bare ground (4.6%). The success of seedlings among mosses was apparently due to the facilitation response of the seedlings, causing increased seedling height (31%) and survival (55%). Furthermore, herbivory and over-wintering mortality were lowest among mosses. Surprisingly, nutrient availability was higher on *Pleurozium schreberi* seedbeds. They attributed protection from predators and temperature extremes in the first three years to the physical structure of the moss.

In the **black spruce** (*Picea mariana*) forest in Alaska, sexual reproduction (i.e., by seeds) required decades to occur post-fire [382]. Rather, these trees reproduced largely by branch layering in non-fire years. In northernmost sites, sexual reproduction requires periodic fires. Seedling numbers (60%) were disproportionately large on *Sphagnum*, despite its occupancy of less than 15% of the surface. On the other hand, fast-growing *Sphagnum* species can out-grow slow-growing seedlings of **black spruce** [383,384], but their growth and establishment are enhanced on partially decomposed or slower-growing *Sphagnum* in some cases [385–387], and seedlings can survive on surviving unburned mats of *Sphagnum* [387]. However, **spruce** regeneration can be limited to areas with herbs as ground cover and live feather mosses can retard seedling development [384]. *Sphagnum* peat can be the best seedbed for **black spruce**, but it should be sheared off to avoid outgrowing seedlings while retaining greater moisture [386]. However, is this an advantage or disadvantage for the next fire? I would guess that if any living branches are retained, *Sphagnum* would resume growth from at least some of those; this is most likely an advantage.

In forested wetlands near Quebec City in Canada, both *Picea mariana* and *P. rubens* were unable to maintain a good presence following clearcutting [388]. Instead, dominance shifted to *Abies balsamea* (L.) Mill., *Larix laricina* (Du Roi) K. Koch, and *Thuja occidentalis* L. *Abies balsamea* fared much better near the edges than in middle of the clearcut. Slow-growing year-old seedlings can be overgrown by *Sphagnum*.

Vegetation was absent on hummock tops after fire near Inuvik, NWT, Canada [389]. Hollows, however, had luxuriant growths of mosses that competed with seedlings of *Picea mariana*. These **black spruce** seedlings were generally favored by mineral soil or moist mosses, with fire generally improving their seedbeds. However, seedlings are sensitive to water stress and low temperatures. Similarly, feather mosses and cushion formers *Dicranum* spp. were poor seedbeds for *Picea abies* [390]. However, after two to three seasons, survival of those that did germinate was nearly equal on various substrates. Seedlings of

this species can adjust by forming adventitious roots when they become established on fast-growing *Sphagnum* [383].

Mosses appear to be responsible for the frequent failure of both seed germination and survival in **black spruce** (*Picea mariana*) forests [391]. The presence of mosses may have contributed to excess moisture and increase in fungal pathogens, as well as nutrient competition. On the other hand, pioneer mosses were good seedbeds and compensated for losses of seedbeds [385]. *Sphagnum* seedbeds, in particular, were able to maintain good coverage in lowland depressions for a longer time than seedbeds in upland soil strata.

White spruce pioneering in pastures in Nova Scotia, Canada, germinated most prolifically in carpets of *Polytrichum* [392]. In other experiments, seeds and seedlings of **white spruce** using *Polytrichum* spp. (Figure 8) moss cushions exhibited the highest seedling emergence on mineral soil, but there were no differences in emergence among moss, litter, and burned litter [393]. However, under short drought treatment, survival was significantly better in mineral soil and among *Polytrichum* when compared to litter and burned litter. Differences in success related to above- and belowground biomass of competing species on litter and burned litter seedbeds, reaching 10 times that on mineral soil and in moss seedbeds. Seedlings grown on these mosses were taller, with smaller epicotyls and stem diameters, typical characteristics of etiolation resulting from insufficient light for normal growth. On the other hand, seedlings among *Polytrichum* exhibited better-developed roots.



Figure 8. Cushions of *Polytrichum commune*, a suitable habitat for germination and survival of pines and some spruce species. Photo by Janice Glime.

Feather mosses do not favor the **white spruce** seedlings [394]. **White spruce** on the Mackenzie Delta, NWT, Canada, was limited to areas with periodic flooding and absence of feather mosses.

8.2.3. *Abies*

Fir tree (*Abies*) seedlings were affected by moss cover in the Murmansk area, Kola Peninsula, Russia [395]. Species matter. In North America, in a minerotrophic peatland in central New York, USA, **balsam fir** (*Abies balsamea*) germinated better on mat-forming *Hypnum imponens* than on *Hylocomium splendens* or *Sphagnum girgensohnii* in the field, but these differences did not occur in the greenhouse, suggesting the two mosses may have had differential roles related to microclimate [396].

Similarly, on Isle Royale, Michigan, USA, the best performance of seedlings of **balsam fir** was on hypnaceous mosses, with the highest mortality occurring on broadleaf litter [397]. The presence of vegetation benefitted seedling recruitment on rotten logs. There is heavy browsing by moose on the island, and they postulated that seedlings are likely to be protected by mosses.

Bryophyte-covered hummocks were important regeneration sites for *Abies balsamea* in a coniferous forested wetland in central New York, USA [398]. These and other raised surfaces elevate young seedlings above the competition on the forest floor.

In boreal forests, bryophyte cover has positive effects on **balsam fir** seedling density [399], being critical to both the establishment and continued success of regeneration. Lack of availability of optimal seedbeds (*Dicranum* sp, *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Rhytidiadelphus* sp. and other low-growing plants), combined with lack of broadleaf litter, grasses, or large shrubs, proved to be limiting to recruitment.

8.2.4. Larix

In Alaska, **tamarack** (*Larix laricina*) seeds had greater 1-year survival on mineral seedbeds than on feather mosses [369]. However, in northern Québec, in a transition zone between forest and tundra, **tamarack** seedlings and saplings became established mostly among mosses [400]. In Minnesota, USA, more seedlings of this species occurred on fine mosses (i.e., *Mnium affine* (Blandow) T.J. Kop., *Drepanocladus s.l.*, and *Helodium* Warnst.) than elsewhere; this is consistent with the observations that these seedlings cannot grow through thick mats [401]. Mosses helped to protect seeds from rodent herbivory; when plots were protected from rodents, seed germination fared better on bare mineral soil than in non-*Sphagnum* moss plots. However, compressed *Sphagnum* that was protected from herbivory gave the best results. *Sphagnum* was a good germination medium with favorable moisture and temperatures, but later it out-competed seedlings by growing faster and taller and by drying out. Hence, it is beneficial for these seeds when *Sphagnum* is compressed or the tops sheared off. The moss *Mnium s.l.* was beneficial for seedlings, apparently because the soil beneath it retained moisture longer into the season than did bare soil.

8.2.5. Tsuga

Eastern hemlock (*Tsuga canadensis*) frequently has successful regeneration in moss mats on soil, rocks, and fallen trees [402,403]. Eastern hemlock uses bryophyte-covered hummocks (microsites created by natural or human disturbance) as important regeneration sites [398]. These raised areas avoid much of the competition from taller moss mats.

Similarly, *Tsuga diversifolia* (Maxim.) Mast. seedlings are too small to survive among bryophytes on the ground, helping to explain differential survival between *T. diversifolia* and *Abies veitchii* Lindl. seedlings [404,405]. In a subalpine coniferous forest on Mt. Fuji, Japan, the ground layer was dominated by *Hylocomium splendens* and *Pleurozium schreberi* [406]. *Tsuga diversifolia* seedlings had a distinct preference for elevated substrates such as fallen logs and convex ground such as that at tree bases. Nevertheless, since there was much higher presence of flat ground, this species reached frequencies of 54–77% there. Thus, the researchers concluded that flat ground should be considered the most important seedbed for *T. diversifolia* in forests with extensive moss cover on the ground. This preference for flat ground, where mosses dominate, was not reported in previous studies where herbs and dwarf bamboo comprised the ground layer. There, only raised microsites provide suitable habitat for seedlings.

8.3. Pines

8.3.1. *Pinus sylvestris*

Conifers are common in most northern and high-elevation forests. In northern Sweden, when seeds of **Scots pine** (*Pinus sylvestris*), **lodgepole pine** (*Pinus contorta*), **Norway spruce** (*Picea abies*), and **black spruce** (*Picea mariana*) were planted on a variety of

moss substrates, *Sphagnum angustifolium* was most favorable for germination, *Pleurozium schreberi* least, and *Sphagnum fuscum* intermediate [126]. The reverse order was true for survival. Among tree species, nonindigenous *Pinus contorta* and *Picea mariana* exhibited the lowest average mortality. Nevertheless, native seeds of *Pinus sylvestris* were most able to germinate in *Pleurozium schreberi* habitats, but their seedling mortality was strongly increased. Native *Picea abies* was least affected by type of seedbed.

Even though *Pleurozium schreberi* covered 10–20% of the ground in two **Scots pine** (*Pinus sylvestris*) forests in northern Sweden, it covered less than 3% of microhabitats where seedlings/saplings less than 10 years old occurred [372]. For older seedlings, cover of the lichen *Cladina* (Nyl.) Nyl. spp. decreased them significantly, while that of *Pleurozium schreberi* increased them slightly. *Pleurozium schreberi* impeded germination and establishment of **Scots pine** (*Pinus sylvestris*), but temporary disruption of mycorrhizal fungi did not impede development [298]. However, when hyphal connections were disrupted and covering by *P. schreberi* and the shrub *Empetrum nigrum* were removed, seedling growth increased significantly, as well as having higher seedling N content and shoot/root ratios. If mosses were left undisturbed, but *E. nigrum* was reduced, seedlings had low shoot/root ratios (1.6). Later experiments with *Pleurozium schreberi* and shrubs showed that *P. schreberi* apparently interfered with uptake of nutrients from dead seeds to **Scots pine**; nutrients were taken up by seedlings when the moss was disturbed experimentally [373]. *Pleurozium schreberi* took up 80% of N released from dead seeds. The fungi facilitated transfer of nutrients to mosses. Many kinds of studies have indicated that mosses are able to live in low-nutrient conditions, but they can compete against seedlings for nutrients [407]. Could it be that they are just very efficient at getting those meager nutrients into the plants?

There seem to be no advantages for seedlings of Scots pine in feather moss seedbeds [370,371,408]. The highest germination occurred on humus (~40%), but there was germination on all tested substrates, including mosses. Reduced success also occurs when ericaceous shrubs are present; they are able to take nutrients from dead moss tissues through mycorrhizal hyphae, preventing those nutrients from reaching the seedlings [298].

In a forest with dominants of *Betula pubescens*, *Pinus sylvestris*, and *Picea abies*, removing feather mosses (*Pleurozium schreberi*, *Hylocomium splendens*) had positive effects on regeneration [409]. The greatest effects were rendered by these organisms that occupied only a small proportion of the biomass. On small islands, removal of mosses had the greatest effect on seedling survival and regeneration of *Pinus sylvestris*. These results emphasized the importance of resident flora at the “functional group” (bryophytes) or species level, especially on small islands. While mosses provided favorable conditions for survival, they also were competitors for space, light, and especially nutrients, thus also having negative effects.

In experiments with steam-killed ground vegetation, including mosses, regeneration of **Scots pine** (*Pinus sylvestris*) by seedlings increased [364]. When activated C was added to the soil surface, regeneration of pine seedlings increased even more. Activated C adsorbed and reduced phenolic levels leached from bilberry litter and humus (it could also have deactivated allelopathic substances left by mosses). On the other hand, ectomycorrhizal fungi seemed to be unharmed and colonized nearly all fine roots of pines. Seedlings had a higher nutrient content on the steam-treated substrate, indicating that resource competition with ground vegetation affected success and development of seedlings.

For germination of **Scots pine** following clearcutting in northern Sweden, *Pleurozium schreberi* created a favorable microhabitat for seedling regeneration following disturbance [410]. However, that advantage quickly diminished with time after disturbance, with the highest regeneration occurring the first year. Nutrients available to seedlings declined after the first year.

As the growth of mosses continues, mosses further immobilize nutrients, even affecting older seedlings and saplings [272,373,411]. In northern Sweden, after prolonged absence of fire in *Pinus sylvestris* forests, understory species composition shifted to *Empetrum nigrum*, *Calluna vulgaris* (L.) Hull, and feather mosses (especially *Pleurozium schreberi*), accompanied

by increased presence of *Picea abies* in the overstory [272]. Removal of *Sphagnum* was beneficial to success of *Pinus sylvestris* following forest harvesting [412]. When seeds of *Pinus sylvestris* were planted into cushions of eight common tundra bryophyte species, seedlings (also those of downy birch (*Betula pubescens*)) performed as well as or better in the presence of bryophytes compared to those in bryophyte-free soil [413]. Seedlings of both tree species grew largest in mats of *Hylocomium splendens*. However, their responses were different. *Betula pubescens* seedlings exhibited a much stronger response to higher temperatures when grown in bryophyte mats than in bryophyte-free soil, whereas for *Pinus sylvestris* the opposite was true. Available organic N also played an important role, with *B. pubescens* apparently needing a greater N supply at higher temperatures.

8.3.2. *Pinus contorta*

In a seeding experiment, significantly more **lodgepole pine** (*Pinus contorta*) seedlings became established in *Cladina* (lichen) habitats than in *Pleurozium schreberi* habitats, with significantly higher mortality in the latter [372]. In the laboratory, *Pleurozium schreberi* had a negative chemical effect on germination of *Pinus contorta* seeds. However, there was no effect on radicle growth of pregerminated seeds, explaining why germination was more successful with the lichen *Cladina*, but seedlings and saplings could survive as *Pleurozium schreberi* became more prevalent later in succession. Hence, pine seed germination and survival in the field were affected by moisture, chemical interference, and nutrient availability, all of which were engineered by mosses.

Lack of moss disturbance following mountain pine beetle (*Dendroctonus ponderosae* Hopkins) disturbance most likely was a major contributor to low seedling emergence in a **lodgepole pine** (*Pinus contorta* var. *latifolia* Engelm.) forest in central British Columbia [414]. The forest floor seed substrate cover was dominated by mosses. Instead of **lodgepole pine**, replacement trees were dominated by **subalpine fir** (*Abies lasiocarpa* (Hook.) Nutt.), a change also due at least in part to changes in light penetration.

8.3.3. *Pinus strobus*

Bryophyte-covered hummocks are important as regeneration sites for *Pinus strobus* L., among other conifer species [398]. In some cases, these are created by bryophytes, particularly *Sphagnum*, but in other cases they have been created through cutting, natural stumps, wind, or other disturbances. In an **eastern white pine** (*Pinus strobus*) forest, mosses and decayed wood were the most favorable substrata for seedling emergence for *Pinus strobus* [415]. Many North American conifer species experience natural regeneration in association with species of *Polytrichum* (Figure 8) [393]. In particular, *Polytrichum* provides a good seedbed for **eastern white pine** [416–420]. Most conifer seedlings experienced negative interactions with mosses, but *Polytrichum* provides better conditions for **white pine** seedlings than exposed, dry mineral soil or forest litter [416]. *Polytrichum* provides insulation and permits seedling roots to penetrate and get into the soil more easily than in tree litter. In experiments, *Polytrichum* beds reduced temperatures and provided moisture and nutrients during the seedling establishment phase, and provided a safe site nearly free of competition [421]. Moss seedbeds also supported higher seedling density than other seedbeds after various disturbances. Mosses could also act as seed traps and protect seeds from rodent browsing, suggesting that rodents might not like to walk on these mosses because they would make running more difficult. Carabid beetles avoid *Pleurozium schreberi*, apparently because they fall into the moss mat when they visit it [422].

Water content enhances seedling success in *Polytrichum* beds. In a boreal *Picea mariana* forest in central Alaska, *Polytrichum commune*, with its ability to move water through an internal vascular system, was able to avoid moisture stress more than did species such as *Hylocomium splendens* and other mosses that gained their water through their leaves [320]. *Polytrichum* has quick recovery from fire (Figure 9), an added advantage in fire-adapted conifer forests.



Figure 9. Charred *Polytrichum* stems and recovering stems, most likely from buried rhizomes. Photo by Janice Glime.

Other experiments in Madison County, New York, resulted in better germination of *Pinus strobus* on the moss *Hypnum imponens* Hedw. than on *Hylocomium splendens* or *Sphagnum girgensohnii* Russow in the field, but not in the lab [396,423]. It appears that improved growth on *Hypnum imponens* is due to its being shorter than other mosses. Better germination occurred on all mosses compared to the original substrate.

Even in peatlands, *Polytrichum* serves as a nurse plant [424]. Not only do members of *Polytrichum* trap seeds, but they also apparently also trap *Sphagnum*. After peat extraction, *Sphagnum* in these abandoned peatlands was always associated with carpets of *Polytrichum strictum* Menzies ex Brid. In field experiments, *P. strictum* kept *Sphagnum* fragments more humid than even bare peat, unless *P. strictum* was “bone dry”. Furthermore, *Polytrichum strictum* buffered temperatures, keeping it cooler in daytime and warmer at night. As with other species of *Polytrichum* noted here, *P. strictum* served as a seed trap, retaining more artificial seeds in experiments than did bare peat. Furthermore, tracheophytes planted into *P. strictum* carpets were healthier than those planted on bare peat.

8.3.4. *Pinus resinosa*

Mosses and decayed wood were most favorable substrata for seedling emergence for **red pine** (*Pinus resinosa* Aiton) [415]. **Red pine** seed germination was actually stimulated by moss mats, whereas **white pine** (*Pinus strobus*) was not [425]. The difference seemed to be in microclimate needs. *Pinus resinosa* benefitted from high temperatures and moisture among mosses, whereas *P. strobus* requires a period of stratification (cold period) before germination; thus, it is not stimulated to germinate early. Moss substrate had no significant effect on survival of *Pinus strobus* the first year; in *Pinus resinosa* only one treatment out of five—the plot that had been burned almost 60 years earlier—had significantly greater seedling survival on moss substrates than on other types. Low pine seedling density was associated with feather mosses, most likely due to competition and other forms of inhibition [426].

8.3.5. *Pinus banksiana*

Soaking **Jack pine** (*Pinus banksiana*) seeds in peat extract for 2–5 weeks inhibits germination, although short-term exposure enhances germination, perhaps due to presence of IAA in extracts [427]. Using seeds from nurseries, growth of 6-month-old seedlings, 2–3-year-old field seedlings, and belowground growth of 2-year-old seedlings planted in *Pleurozium schreberi* was significantly greater than when planted in lichens [428]. Germina-

tion was not affected. Ground-layer shading had no effect on seedling growth, i.e., there was no smothering effect. Lichens are known to produce inhibitory substances that inhibit seedling mycorrhizae [429].

8.3.6. *Pinus rigida*

In New Jersey **pinelands**, where **pitch pine** (*Pinus rigida* Mill.) dominates, bryophytes and lichens form mats that last for many decades following fire, and only scattered tracheophytes occur [420]. Moss dominance correlates with higher tracheophyte densities. Lichen extracts have a strong inhibitory effect on seed germination; moss extracts have none. It appears that mosses facilitate tracheophyte development, while lichens inhibit it. Furthermore, mycorrhizal infections by ecto- and endomycorrhizal fungi are greater among mosses than among lichens or bare soil. Nevertheless, both lichens and fungi inhibit seedling emergence. This is at least in part due to fluctuations between very hot and dry versus cool and moist conditions that cause lichens to overgrow mosses in the hotter conditions.

8.4. *Thuja occidentalis*

White cedar (*Thuja occidentalis*) germinates better on *Sphagnum girgensohnii* than on *Hylocomium splendens* [396]. When different moss solutions were applied to seeds, there was no statistical difference in germination; but growth regulatory compounds cannot be ruled out. The results support the hypothesis that tall mosses can keep seeds from reaching soil or if they fall to reach soil, the leaves are unable to reach light above the moss. However, the improved germination success seems to result from good moisture relations, with habitats on logs (with *Hypnum imponens*) experiencing less fluctuation. Coarse woody debris, including logs, is important in regeneration of *Thuja occidentalis* [430]. Similarly, *Thuja occidentalis* benefitted from raised bryophyte-covered hummocks created by disturbances [398].

8.5. *Chamaecyparis thyoides*

In New Jersey, USA, in the pinelands, **Atlantic white cedar** (*Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb.) occurs in swamps. *Sphagnum* has typically been considered to provide optimal seedbed conditions for this species [431]. There were no significant differences in seedling density when comparing low, medium, and high levels of disturbance.

8.6. Broadleaf Species

Broadleaf species often have small seeds. Organic soils tend to provide poor seedbeds for such species. Thus, mosses, which contribute to deepening of organic soils, tend to be poor seedbeds for these species [354,379,391,414]. Small-seeded species suffer greater mortality when organic soils are lightly burned than do large-seeded species such as pine [379]. Hence, mosses indirectly control tracheophyte regeneration (cf. [354,379,391,414]).

In an **oak-pine forest**, *Quercus velutina* Lam. and *Q. coccinea* Münchh. tended to occur more with moss-lichen cover where litter layers were shallow [432]. *Quercus alba* L., *Quercus michauxii* Nutt., and *Sassafras albidum* (Nutt.) Nees seedlings tended to avoid mosses, developing better in areas with taller ground cover. In a **hemlock-hardwood forest**, **red maple** (*Acer rubrum* L.) seedlings had survived only where there was moss cover; they had dried out in other types of locations [433]. In Lago Puelo National Park (Chubut, Argentina), mosses favored germination of many **temperate forest** tree species, but some were negatively affected [363].

Moss “mats”, particularly *Polytrichum*, were too dense for seed penetration in **Poplar** (*Populus*) stands in Michigan, USA [434]. Mosses absorbed water too quickly to allow seeds to soak; frequent wetting and drying caused seedlings to heave from the soil.

Bryophytes were one of three “functional groups” in understory vegetation on 30 lake islands in northern Sweden; when mosses were removed, the effects were positive [411].

The success of *Betula pubescens* seedlings was significantly increased by removal of mosses, and emergence was adversely affected by presence of mosses. In the **tundra**, as trees are forced farther north due to climate change, the suite of variables that control survival through the seasons will change. When seedlings of **downy birch (*Betula pubescens*)** were planted and snow cover manipulated, the milder over-wintering conditions resulting from increased snow cover tended to increase negative effects of bryophytes on seedlings immediately after winter, supporting the stress gradient hypothesis (plant interactions in tundra would become increasingly negative as climate warms and conditions become less harsh than we would predict in this situation) [435]. Although bryophytes had even more negative effects on seedlings at lower elevations, they had no significant impact on over-winter survival between elevations, a finding that contradicts the stress gradient hypothesis.

8.7. Tropical Forests

Researchers have lamented the lack of knowledge about bryophyte communities and ecology in the tropics [63,436]. In one study in restoration corridors of koa and 'ōhi'a, seedlings were commonly associated with bryophytes; bryophytes might be significant in improving forest seedling establishment in the tropics [436]. Nevertheless, bryophytes are relatively uncommon on the forest floor due to the combination of high temperatures and low light.

In the seasonally dry tropical **Brazilian Caatinga forest**, mats which include bryophytes increase soil organic C and may help to counterbalance disturbances in this ecosystem, particularly that by goats [437]. Bryophyte mats may play a “substantial” role in regeneration of vegetation. Clearly, we still need studies on the role of bryophytes in regeneration niches of **tropical forest trees**.

8.8. Allelopathy

The traditional definition of allelopathy is “an interference mechanism by which plants release chemicals which affect other plants” [438]. However, instead of the traditional application of the concept to plant populations and communities, it would be more appropriately applied at the ecosystem level. Secondary metabolites, those credited with allelopathic properties, are wide ranging in their effects, hence regulating ecosystem function, including herbivory, decomposition, and nutrient mineralization. The secondary compounds of bryophytes in many types of forest ecosystems seem to fulfill this latter definition of effects at the ecosystem level.

Bryophytes are well known for their resplendent array of antibiotic compounds. However, interest in these has been primarily for their potential uses as pesticides, herbicides, and human medicine. Certainly we should be asking how they are used in their own ecosystems. Several studies already mentioned have suggested allelopathy as a mechanism used by bryophytes that can interfere with seedling establishment.

Mosses appear to directly inhibit tracheophyte germination through allelopathy [20,372]. Nevertheless, although there is evidence of strong negative effects of bryophyte phenolics on seedling germination in the lab, these were not present in the field [354]. Could they be neutralized by the soil? Was it the wrong season? Despite the many biochemical studies describing antibiotics in bryophytes, their connections to ecology in the natural habitat have almost entirely been ignored.

Early studies on 12 mosses indicated that they produce growth inhibitors against various bacteria and fungi [439]. The study should have been a wake-up call because extracts did not exhibit consistent activity even against the same species. Are these inhibitors inducible, like the antiherbivory substances produced by many tree leaves?

Even epiphylls, including bryophytes, on **grapefruit** leaves and an understory *Cyclanthus bipartitus* Poit. ex A. Rich. discouraged attacks by the fungus-growing leafcutter ant *Atta cephalotes* Linnaeus from removing the leaves [440]. When epiphylls were removed, there was 2–3 times as much damage caused by these ants.

Bryophyte extracts can be used as antifungal agents [441]. *Rhynchostegium pallidifolium* (Mitt.) A. Jaeger extracts exhibit allelopathy against several herbaceous sun-loving plants, permitting the moss to form pure colonies [442]. However, what is their effect in forests? Are these substances leaked, and do they affect tracheophytes or their fungal partners?

Bryophyte water-soluble extracts can enhance seedling growth at low concentrations and inhibit it at higher concentrations [358]. Additionally, species differ. For the common New Zealand forest tree species *Melicytus ramiflorus* J.R. Forst. & G. Forst., such extracts from the leafy liverwort *Lepidozia concinna* Colenso inhibited germination; that from the moss *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer was strongly stimulatory. Both bryophyte species inhibited radicle growth. *Fuchsia excorticata* L. f. experienced inhibition of both germination and seedling radicle growth. The researchers found differences in toxicity among bryophyte species, and these were not consistent between mosses and liverworts. The bryophyte species that had the strongest inhibition effects were associated with significantly reduced densities of broadleaf tree seedlings in forests.

Although there are studies showing inhibiting effects on germination, growth, and establishment of nearby plants, other studies failed to demonstrate any effects [443]. Are water extracts used in these studies adequate since the allelopathic chemicals studied are lipophilic, thus likely having longer retention times in soil?

Three areas of focus in understanding the ecological impacts of allelopathy seem important [444]:

1. Variation in allelopathic expression within species;
2. Community-level variation in allelopathy across species;
3. Variation in impacts of allelopathy on associated species.

To these I would add the effects of the soil environment on activity of the purported allelopathic compounds and the seasonal and other inducible variations in expression.

Understanding these differences can help us to discover if bryophytes produce allelopathic substances seasonally, if they are induced by herbivory, competition, or other forms of interaction, and what differences do bryophyte allelopathies make in forest dynamics, in addition to the role of size.

As can be seen in Table 5, germination and survival success in bryophyte seedbeds can depend on both tree and bryophyte species.

Table 5. Forest tree seedling germination success and survival among mosses, based on the conclusions of the studies.

	Germination		Seedling Survival		Ref.
	High	Low	High	Low	
CONIFERS					
<i>Abies balsamea</i>		■			[396]
<i>Hylocomium splendens</i>		■			[396,397]
<i>Hypnum imponens</i>	■		■		[396]
<i>Sphagnum girgensohnii</i>		■			[396]
<i>Chamaecyparis thyoides</i>					
<i>Sphagnum</i>	■		■		[431]
<i>Larix laricina</i>					
<i>Hylocomium splendens</i>				■	[369]
<i>Drepanocladus s.l.</i>			■		[401]
<i>Helodium</i>			■		[401]
<i>Mnium affine</i>			■		[401]
<i>Picea abies</i>					
<i>Dicranum</i>		■	■		[390]
<i>Hylocomium splendens</i>		■	■		[127]
			■		[400,409]
<i>Pleurozium schreberi</i>		■	■		[126,127]
				■	[409]

Table 5. Cont.

	Germination		Seedling Survival		Ref.
	High	Low	High	Low	
<i>Sphagnum</i>	■			■	[126,127]
<i>Sphagnum angustifolium</i>	■			■	[126]
<i>Picea glauca</i>					
<i>Polytrichum</i>	■		■		[392]
<i>Picea mariana</i>					
<i>Hylocomium splendens</i>			■		[320]
<i>Pleurozium schreberi</i>		■	■		[126,381–387]
<i>Polytrichum commune</i>			■		[320]
<i>Sphagnum angustifolium</i>	■			■	[126]
<i>Pinus banksiana</i>					
<i>Sphagnum</i>		■			[427]
<i>Pinus contorta</i>					
<i>Pleurozium schreberi</i>		■	■		[126]
<i>Sphagnum angustifolium</i>	■			■	[126]
<i>Pinus strobus</i>					
<i>Hylocomium splendens</i>		■			[396,423]
<i>Hypnum imponens</i>	■				[396,423]
<i>Polytrichum</i>	■		■		[416–421]
<i>Sphagnum</i>	■				[398]
<i>Sphagnum girgensohnii</i>		■			[396,423]
<i>Pinus sylvestris</i>					
<i>Hylocomium splendens</i>				■	[409]
			■		[413]
<i>Pleurozium schreberi</i>				■	[300,409]
				■	[373]
	■				[410]
		■	■		[126]
<i>Sphagnum</i>				■	[412]
<i>Sphagnum angustifolium</i>	■			■	[126]
<i>Sphagnum fuscum</i>		■		■	
<i>Thuja occidentalis</i>					
<i>Hylocomium splendens</i>		■			[396]
<i>Hypnum imponens</i>	■				[396]
<i>Sphagnum girgensohnii</i>	■				[396]
DECIDUOUS TREES					
<i>Betula pubescens</i>					
<i>Hylocomium splendens</i>				■	[409]
			■		[413]
<i>Pleurozium schreberi</i>				■	[409]
<i>Fuchsia excorticata</i>					
<i>Dendrohypopterygium filiculiforme</i>		■			[358]
<i>Lepidozia concinna</i>		■			[358]
<i>Melicytus ramiflorus</i>					
<i>Dendrohypopterygium filiculiforme</i>	■				[358]
<i>Lepidozia concinna</i>		■			[358]
<i>Populus</i>					
<i>Polytrichum</i>		■			[434]

■ The black rectangles indicate the non-quantitative level of high or low success of germination and survival. Those located between the two levels exhibit intermediate success.

8.9. Layering

Plant nurseries often use air layering to propagate trees. The success often depends on use of mosses, especially *Sphagnum*, to keep rooting parts moist [445–447]. Some forest

trees use air layering naturally in the field, particularly where thick mats of mosses can maintain appropriate levels of moisture.

Natural layering occurs in **black spruce** in northern Ontario [448]. For air layering to occur in **black spruce**, there must be green branches present at the base and a moist rooting medium that can imbed them [448]. These adventitious roots grow above the initial root collar and into the organic soil–moss layer surrounding the tree [383,449]. Adventitious root development is stimulated by mosses and humus that cover stems [383,450]. In Québec, Canada, **black spruce** remaining from cutovers regenerates mostly by layering, with adventitious roots forming in mosses (mostly *Pleurozium schreberi*) along buried stems [451]. Hence, layering is more common on wet sites than well drained ones. Mosses provide a suitable medium for this layering.

Balsam fir (*Abies balsamea*) experiences air layering; increased snowfall may favor growth of *Sphagnum*, facilitating rooting of its basal branches [452]. Air layering also occurs in **eastern white pine** (*Pinus strobus*) and is frequent in *Tsuga*, *Picea*, *Abies*, *Chamaecyparis*, *Thuja*, *Juniperus* L., and *Taxus* L. [453].

We know that *Sphagnum* serves as a good medium for layering because of its widespread use for that purpose in nurseries. However, it appears that we know little about the bryophytes involved or interactions needed for successful air layering of forest trees in nature [450].

8.10. On Logs and Stumps

There is concern about the number of original **deciduous forests** that are disappearing [454]. With current global climate change, this concern becomes even more urgent. Among a list of 10 possible properties that could be used to monitor the condition of **eastern deciduous forests** is the number of corticolous bryophyte species. The number of bryophyte species associated with logs and other convex surfaces was strongly decreased by clearcutting, and recovery was scant even after 30–50 years [147]. In spruce forests of South Tyrol, researchers expressed concern that there was insufficient deadwood to maintain the integrity of the forests [22]. These concerns apply to other types of forests as well; in addition to being indicators of forest health, logs are important in creating suitable germination habitats for some tree species.

Bryophytes commonly inhabit logs [455], and so do tree seedlings, but few studies have addressed their interactions. In a variety of **deciduous forests**, diversity and abundance of bryophytes relates to decay stages of logs and to stand age [456]. In **oak-hornbeam** forests, as in many others, most of the bryophytes in abundance are generalists [455]. These bryophytes typically provide 53–78% cover on logs.

Some seeds and seedlings do best on logs. The raised surface provides a refuge from falling leaves, particularly in **broadleaf forests**. Logs also typically develop bryophyte coverings that are important in establishment of seedlings on logs [457]. However, the mechanisms involved are poorly known. Unfortunately, many studies have simply referred to all of them as moss. Do these bryophytes help or hinder particular seedlings on logs? Do species of bryophytes matter?

For **conifer** seedlings in old-growth subalpine forests in Japan, logs are important in tree seedling establishment [458]. Yet logs form only a small percentage of ground cover, 4.5% in one site and 2.5% in the other. Unsurprisingly, there were no seedlings on freshly fallen logs. As logs aged, moss cover and occurrence of seedlings both increased, particularly as logs increased in decay. On one site, all conifer seedlings and saplings were on logs, and at the second site *Picea* and *Tsuga* seedlings were much more frequent on fallen logs than on soil, while *Abies* seedlings and saplings were able to establish on both soil and fallen logs. However, whereas seedlings were taller on decayed logs, saplings were almost absent on logs. Seedling frequency increased as moss cover increased, but at the same time decay stage increased, so both mosses and decay stage contributed to more moist environments. Mosses maintain a relatively humid environment that is favorable to seeds and seedlings, as well as protecting them from the impact of water drops [355].

In the **subalpine forests** of central Japan, seedlings of **northern Japanese hemlock** (*Tsuga diversifolia*) survived only on logs with small-statured bryophytes; apparently this is a function of sapling size [405]. **Veitch's fir** (*Abies veitchii*) seedlings were taller than any soil bryophyte community, enabling their radicles to penetrate into the moist humus, but the seedlings of *Tsuga diversifolia* were too short for roots to penetrate the soil and at the same time permit cotyledons to extend upward into sufficient light amid deep feather mosses.

On Mt. Ontake, Japan, the seedling density of **spruce** (*Picea*) on logs increased, as did cover of the leafy liverwort *Scapania bolanderi* and thickness of the liverwort colonies; but seedling shoot length was negatively associated with cover of *S. bolanderi* [457]. Seedling density was negatively associated with *Hylocomium splendens* cover. *Scapania bolanderi* continued to gain cover with time and stage of log decay, but in the final decay stage it was replaced with *Hylocomium splendens*. Transition from thin mats to thick is a common pattern for bryophytes on logs. In ***Tsuga-Abies* forests** of central Japan, there is a succession from *Heterophyllum* (Schimp.) Müll. Hal. ex Kindb. and *Scapania*, both relatively shallow mats, to *Hylocomium splendens* and *Pleurozium schreberi* that form deep mats [459]. *Picea* and *Tsuga* were restricted to the early thin mat stage, whereas *Abies* seedlings were able to grow in both thin and deep mats. Hence, there is an ideal “window of time” in which **spruce** seedlings can colonize decaying logs.

Picea abies regeneration in old-growth **boreal swamp forests** seems to depend on bryophytes and logs. In these forests in northern Sweden, seedlings were able to establish most easily in *Sphagnum* spp. and *Pleurozium schreberi* growing on logs, with the highest numbers in *Sphagnum* [127]. Establishment in *Hylocomium splendens* was lower than in the other two bryophytes. As in most studies of seedlings, they found that seedling mortality was usually caused by “smothering” by bryophytes that were taller than seedlings. This explains poor success among *Hylocomium splendens*, tallest of these three mosses, and reaffirms the importance of elevated microhabitats.

In the Hoh **temperate rainforest** in Washington state, USA, it was the moss *Rhizomnium glabrescens* (Kindb.) T.J. Kop. that appeared in an early decay stage and correlated with high tree seedling density [460]. In later stages of decay, *Hylocomium splendens* predominated, reaching a depth of more than 20 cm, and seedling density was at its lowest. Overall, seedling density was 4.5 times as high on nurse logs compared to the forest floor. As decay proceeds, interactions shift from facilitative to competitive. Nevertheless, logs provide a safe site from the competition with tracheophytes on the forest floor.

Not surprisingly, moisture matters on logs. There were both positive and negative effects of moss cover on *Picea abies* seedling establishment on logs, with moisture being an important factor [127,461–463]. However, this advantage can be overridden if mosses are too tall [464,465], a typical occurrence on the forest floor. Nevertheless, *Picea abies* had a positive relationship only with mosses [461].

The role of mycorrhizae in the bryophyte–seedling relationship on logs is not one we can overlook. In an old-growth subalpine coniferous forest in Japan, *Picea jezoensis* subsp. *hondoensis* (Mayr) P.A. Schmidt was the dominant seedling on conifer logs [466,467]. *Scapania bolanderi* and *Pleurozium schreberi* each exhibited about 33% cover on logs [467]. *Pleurozium* cover and basal area of adjacent *Picea* adult trees had a negative association with *Picea* seedlings. Brown-rot of sapwood inhibited *Pleurozium* cover, permitting the thinner mats of *Scapania bolanderi* to become dominant. There was also a positive correlation of bryophyte total cover, *Scapania* cover, and white-rot in heartwood. In this case, it appears that fungi have an indirect impact that favors seedlings by affecting the structure of the bryophyte community.

Moss beds on logs are often not beneficial to seedlings. On logs in ***Picea-Tsuga* forests** of Oregon and Washington, USA, seeds mostly failed to penetrate the bryophyte mat, with less than 1% of seedlings present having germinated within a moss mat [464]. However, competition with herbs and mosses in the ***Picea-Tsuga* forest** precludes germination on the forest floor for most of them, causing the greater proportion to germinate on logs. In

the field, seeds often fell through mats and reached soil; in the lab they did not. For *Picea sitchensis*, 80% of seedlings survived when the mat was only 380 g m⁻², but when mats were thicker, survival was greatly reduced; 50 mm seemed to be a critical depth. The mean height of *Tsuga heterophylla* (Raf.) Sarg. seedlings was 14 mm, making the 44 mm height of mosses too high. However, it appears that in some parts of the world, logs are suitable for regeneration of *Tsuga* species. The **eastern hemlock** (*Tsuga canadensis*) can experience regeneration not only on soil, but also on rocks and fallen trees [468]; it is likely that these are both moss-covered.

One difference in site suitability among logs is rate of loss of bark. In the Olympic National Park, Washington, USA, *Picea* and *Tsuga* lost their bark in 60 years, whereas *Pseudotsuga* required 190 [469]. Bryophytes covered 85–90% of all three log types in 11–19 years. As in other cases cited here, bryophyte species change as logs change. *Hypnum circinale* Hook., a thin-mat former, colonizes early and promotes seedling development. Later the arrival and establishment of *Rhytidiadelphus triquetrus* and *Hylocomium splendens* creates a mat that is too thick for seedlings to both root and reach light.

Japanese cedar (*Cryptomeria japonica*) became established on decaying logs covered with mosses [470]. In succession of bryophytes on fallen logs in **coniferous forests**, including *Cryptomeria japonica*, on Yakushima Island in Japan, the first colonizers were the moss *Hypnum densirameum* Ando and/or the leafy liverwort *Plagiochila semidecurrens* (Lehm. & Lindenb.) Lindenb., with some epiphytic species [471]. Once logs lost their bark, they were colonized by the leafy liverwort *Nowellia curvifolia* (Dicks.) Mitt. and then the moss *Wijkia deflexifolia* (Mitt. ex Renauld & Cardot) H.A. Crum. These were all relatively thin mats. Final stages of communities were dominated by *Pyrrhobryum spiniforme* (Hedw.) Mitt. (a much larger moss) and included not only bryophytes, but a much more diverse community with herbaceous plants, dwarf shrubs, and tree seedlings (including **Japanese cedar** (*Cryptomeria japonica*)). This final stage developed a structure of 2–3 height layers.

Bryophytes in forests that have been damaged by wind or salvage logging can not only exhibit greater overall species richness due to the more elevated substrates, but are able to support species that have high conservation value, particularly rare species [472]. In these disturbed habitats, the highest number of taxa is typically associated with dead wood. Hence, it appears to be better to let these forests recover naturally, maintaining the dead wood in place.

9. Summary, Conclusions, and Limitations

The neglected role of bryophytes in forests is slowly being remedied. Forest ecologists are beginning to recognize the roles of bryophytes as ecosystem engineers in many aspects of forest dynamics. In addition to their role in preventing erosion and slowing water flow, we now recognize that they play both positive and negative roles in forest maintenance and regeneration. They can comprise half the living biomass and net productivity in the forest and add considerable diversity themselves, while increasing the diversity of non-bryophytes. They slow soil evaporation, maintaining a more moist habitat, buffer the soil temperature, raise the level of permafrost, prevent frost heaving, trap seeds, smother small seedlings, and play major roles in nutrient trapping and cycling. Canopy bryophytes regulate water impacts and trap numerous nutrients that would otherwise be unavailable to the forest ecosystem. Both epiphytic and ground-layer bryophytes trap nutrients from rain and dry fall, sequester them, and release them when rewet following desiccation or when senescing. They harbor N-fixing Cyanobacteria and other bacteria that add usable N to the forest ground layer, and epiphylls even contribute N to tree leaves. Bryophytes decay slowly, taking years, sometimes more than 200 years, to reach an unrecognizable stage. They also can slow the decomposition of tree litter types through antibiotics, poor nutrient quality availability, and lowering soil temperatures. They readily lose K and sometimes Mg, but retain P and Ca. N might be contributed by N fixation, but can be retained in the bryophyte tissues, losing some forms and retaining others. They harbor fungi that in some cases benefit from the moist environment and transfer nutrients from senescing and

dead moss tissue to roots and seedlings, but in other cases help to transfer to and sequester nutrients in the bryophyte tissues, making them unavailable to trees for years or even decades. As **boreal spruce** forests age, bryophytes become more prominent, eventually depriving the trees of essential nutrients and limiting their growth. Especially in **boreal** forests, bryophytes can make a 50% or more contribution to sequestering CO₂, thus helping to reduce global warming. They protect tree seedlings from desiccation and herbivory, but they can overgrow and smother them.

The roles of the bryophytes vary with species, with thin moss mats on logs benefitting many types of seedlings while tall moss mats can trap the smaller seeds and seedlings and prevent them from getting both light and rooting substrate. Bryophytes are not a single functional group, with their roles varying with their life forms and biochemistries. Therefore, bryophytes have both positive and negative roles in the forest, and these depend on the tree species, its life cycle stage, the ecosystem conditions, and the species of bryophytes.

It is clear that bryophytes contribute many roles that cannot be attributed to all bryophytes, but must be examined by functional groups for a given function. By understanding the many potential interactions of bryophytes in forests, managers and forest ecologists can make more informed decisions as they manage forests through climate change and other environmental changes, including logging and fire. We lack studies on the roles of liverworts, especially in harboring nitrogen fixers and in allelopathy in the forest. We are, nevertheless, limited by the lack of bryologists on forest management teams and the paucity of experimental studies on forest bryophytes and their interactions, especially in deciduous and tropical forests.

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