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CHAPTER 8-3
TROPICS: EPIPHYTE ECOLOGY, PART 1

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Figure 1. Celaque cloud forest in tropical Honduras. Photo by Josiah Townsend, with permission.

Barkman (1958) has contributed the definitive work on cryptogamic epiphytes (bryophytes, lichens) in 628 pages. It provides an account of the ecology and adaptations as they were known at the time and is the "bible" on cryptogamic epiphyte ecology. The work is restricted to temperate regions and does not treat tropical epiphytic bryophytes, which were very little known at the time. Nevertheless, much of the ecological information provided in this book is also valid for the tropics.

I was surprised to learn that approximately 10% of the tracheophytes are epiphytes (Prosperi & Michaloud 2001). It was not a surprise to learn that these are almost exclusively tropical, where they represent up to 25% of the tracheophytes. Overall, bryophytes comprised 40% of the epiphytic biomass in a neotropical cloud forest in Costa Rica (Nadkarni 1984) compared to 6% in the leeward cloud forest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dryer 1980).

The epiphytic habitat (Figure 1) is the most diverse one for tropical rainforest bryophytes, with 14 of the 15 main bryophyte families being predominantly epiphytic (Figure 1) (Gradstein & Pócs 1989). This is where the greatest bryophytic biomass of the rainforests occurs (Hofstede et al. 1993). Not surprisingly, the dry weight of epiphytes in the tropics is generally less than that shown in a New Zealand study (Hofstede et al. 2001), where lower temperatures and shorter dry periods are more favorable for bryophytes. In a New Zealand lowland, a single tree supported 61 tracheophyte species compared to 94 non-tracheophytes (lichens included). Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates.

Among the early studies on bryophytic epiphytes, one must note the Japanese studies (Horikawa 1932, 1939, 1948, 1950; Kamimura 1939; Horikawa & Nakanishi 1954; Hattori & Noguchi 1954; Hattori & Kanno 1956; Hattori et al. 1956; Hattori 1966; Hattori & Iwatsuki 1970; Iwatsuki 1960, 1961, 1962, 1963a, b; Iwatsuki & Hattori 1955, 1956a, b, c, d, e, f, 1957, 1959a, b, 1965a, 1965b, 1966,

1968, 1970, 1987; Mizutani 1966). Hosokawa (1950, 1951, 1953, 1954) and coworkers (Hosokawa & Kubota 1957; Hosokawa & Odani 1957; Hosokawa & Omura 1959; Hosokawa *et al*. 1954, 1957, 1964) pioneered in describing epiphytic communities. Another important early study from Asia is the work by Tixier (1966) on epiphytic communities in Vietnam. Went (1940) discussed the sociology of tracheophytic epiphytes of Java.

Gradstein *et al*. (2007) compared the species richness on various substrates in southern Ecuador. This study demonstrated the preponderance of epiphytes there (Figure 2).
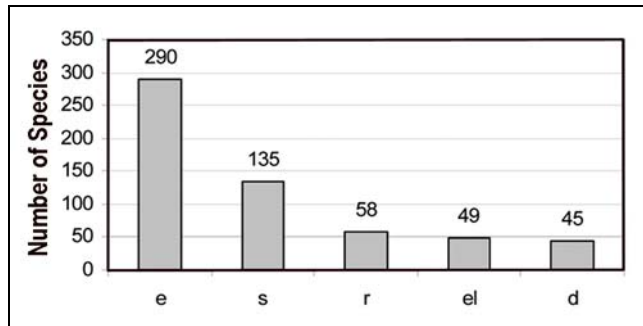

Figure 2. Substrate types of liverworts and hornworts at Reserva Biológica San Francisco, southern Ecuador. Number above each bar is number of species on that substrate type; e = epiphytic (bark); s = soil (incl. humus); r = rock; el = epiphyllous (living leaves); d = decaying wood. From Gradstein *et al*. 2007.

Frahm (1990a, 1994) found that in Borneo lowland and montane rainforests, even bark texture (smooth, fissured, flaky, or striped) made a difference in the epiphytic communities that developed. All bryophytes were considered to be acidophilic, with epiphytic bryophytes having no significant correlation with *p*H. On the other hand, rich concentrations of Na, K, and Mg seemed to be important in the substrate.

Akiyama *et al*. (2001) contributed to the knowledge of the Borneo bryophyte flora through two expeditions to the Kinabalu National Park in Malaysia. They reported 203 moss species and 31 liverwort species, with 25 species added to the checklist for the park and 17 new to Borneo.

Kürschner and Parolly (1998a) examined **pantropical** (covers tropical regions of both eastern & western hemispheres) features that determined distribution of the epiphytic bryophytes. They found that distribution is correlated with structural parameters of the tree stands and with temperature zone intervals. Using only **supraspecific** taxa (*i.e.*, above the species level) they concluded that communities at low altitudes and those at high altitudes, respectively, resemble each other more pantropically than do lowland and montane communities on the same continent. Kürschner and coworkers were instrumental in elucidating epiphytic bryophyte communities in Africa (Kürschner 1995a, b).

Kürschner and Parolly (1999) sought to derive a consistent system for classifying the tropical epiphytes on a pantropical basis. Instead of using species, they used higher classification levels. For the lowland and submontane tropics they recognized the **Coeno-Ptychanthetalia** (Figure 3), whereas in the montane zones they recognized the **Coeno-Bazzanio-Herbertetalia**

(Figure 4-Figure 5). Using this thinking, they found that the low-altitudinal and high-altitudinal communities are more silimar to each other pantropically than the communities of lowland and montane vegetation units occurring on the same continent.

Figure 3. *Ptychanthus striatus*; the *Pychanthalia* synusia is typical in the lowland and submontane tropics, with pantropic distribution. Photo by Li Zhang, with permission.

Figure 4. *Bazzania* sp. from the Neotropics, a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Michael Luth, with permission.

Figure 5. *Herbertus aduncus*, in a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Barry Stewart, with permission.

Much remains to be found among the tropical bryophytes. Lee and Pócs (2018) have recently added to our knowledge of the distribution of the large genus *Lejeunea* (Figure 6), describing the new species *Lejeunea konratii* from Fiji.

Figure 6. *Lejeunea flava*; *L. konratii* was a new species in Java in 2018. Photo by Jia-dong Yang, through Creative Commons.

Some epiphytic bryophytes are **facultative**, growing on other types of substrate. Ando (1969) reported that the epiphytic bryophytes on *Buxus microphylla* var. *insularis* (=*B. sinica* var. *insularis*; Figure 7) also grew on limestone ridges in Taishaku.

Figure 7. *Buxus microphylla*. Epiphytic mosses of this species also grow on limestone ridges. Photo by Sage Ross, through Creative Commons.

Frahm and Kürschner (1989) investigated factors related to bryophyte success on trees. Rhoades (1995) provided an extensive review on the nontracheophyte epiphytes of the canopy, including distribution, abundance, and ecological roles, but this paper mainly focuses on temperate forests.

Water Relations

The distribution of epiphytic bryophytes in the tropics seems to be all about water. The bryophytes in the crowns of the trees generally are more desiccation-resistant than are those at the tree base (Hosokawa & Kubota 1957; Hosokawa *et al.* 1964).

Water is always a primary limiting factor for epiphytes, and in the tropics the daily change from wet to dry can be particularly problematic (Johnson & Kokila 1970). For some species in the saturated rainforests, as little as 4 hours of exposure to a relative humidity of 63% or less can result in damage. Thus, such sensitive species often live on the wettest sides of the trees. Within a range of 10-76% humidity for four hours, two groups of mosses emerged. One group had low resistance, but the other had a high resistance to desiccation. This latter group of species grew in microhabitats of the forest with low humidity.

Löbs *et al.* (2019) opined that our understanding of the role of the extensive epiphytic bryophyte cover was largely unknown, noting their potential importance in biosphere-atmosphere exchange, climate processes, and nutrient cycling. Their water content could have important impact on local, regional, and even global biogeochemical processes. The researchers measured a vertical gradient from the Amazon Tall Tower Observatory in the Amazonian rainforest and determined that only minor variations occurred in the monthly average ambient light intensity above the canopy, but that different patterns emerged at different heights. At 1.5 m, the values were extremely low, exceeding 5 μmol m^{-2} photosynthetic photon flux density only 8% of the time. These values differed little throughout the year. The temperatures likewise showed only minor variation throughout the year, with larger values and more height dependence during the dry season. Water levels, on the other hand showed more variability. At higher levels they were affected by the frequency of wetting and drying; at low levels near the forest floor they retained water over a longer time period. They concluded that water content is the deciding factor for overall physiological activity, with light intensity determining whether net photosynthesis or dark respiration occurs. Temperature was of only minor importance. Light was limiting on the forest floor; in the canopy the bryophytes had to withstand a larger variation in microclimatic conditions.

Water Content

Klinge (1963) reported on the epiphyte humus from El Salvador. Their role in forest water and nutrient dynamics, however, seemed to attract little attention. Water content of bryophytic epiphytes in an old-growth forest in Costa Rican cloud forest reached maximum values of 418% of dry weight, with a minimum of 36% (Köhler *et al.* 2007). The epiphytic bryophytes experienced more dynamic wetting and drying cycles than did the canopy humus. The maximum water loss from bryophytes through evaporation was 251% (dry weight), whereas it was only 117% from the canopy humus, following three days of sunny weather with no intervening precipitation.

Pócs (1989) estimated that high altitude epiphytic bryophytes in Tanzania can absorb up to 30,000 L ha^{-1} of water during one rainstorm. When high humidity and high

temperatures occur at the same time, as they often do, they cause respiratory losses that cannot be balanced by photosynthesis in these C_3 plants, thus limiting their productivity, especially in the lowland forests (Richards 1984, Frahm 1990b).

Karger *et al.* (2012) measured the relationship of bryophyte cover to air humidity at two elevation ranges in the tropics. When the highland site (1800-3500 m asl) was considered separately from the lowland site (<1800 m asl) there was a significant relationship between bryophyte cover and relative air humidity. Temperature related to cover in the lowlands only. They confirmed that bryophyte cover is a good proxy for relative air humidity along the elevational gradient in the tropics, proposed earlier by van Reenen and Gradstein (1983).

Müller and Frahm (1998) compared the water-holding capacity of epiphytes in a montane rainforest in the Andes of Ecuador. They found an average of 0.57 L m-2 on the trunks, 19.51 L m-2 on branches, and 4.16 L m-2 on twigs. This is ten times the dry weight on branches, but only three times on twigs. Using a representative tree of 27 m height, which has an average of 65.4 kg dry weight of epiphytes, , they calculated that the epiphytic bryophytes on one such tree could store 669 liters of water.

Growth Forms and Life Forms

Several life forms and their role in water relations have already been discussed in an earlier chapter. For definitions, illustrations, and examples, see Chapter 4-5 in the Physiology volume.

Kürschner (1990) looked at the distribution of life forms and water-bearing and water-storing structures in epiphytic moss communities on Mt. Kinabalu, North Borneo. Norris (1990) concluded that water relations must be understood along at least four dimensions: hydration/dehydration frequency; duration of hydration; duration of dehydration; degree of water loss. More recent studies of xerophytic bryophytes suggest that the rate of drying is also important (Greenwood & Stark 2014). Norris further concluded that **large colonies** generally maintain hydration longer than do smaller colonies. Water can be conducted laterally among contiguous clones. Separated **tufts** and **cushions**, on the other hand, may store more water, but they contribute little to transfer of water over the surface of the host tree. In the tropical rainforests, the mass of the bryophytic epiphytes is typically larger than that found in temperate forests. The biomass is reduced as a result of disturbance, probably due to increased opportunity for desiccation with increased isolation and wind movement. This further results in the loss of water transfer and reduction in both water and mineral retention. Norris cited the **Braunfelsia** (moss; Figure 8) community in Papua New Guinea as an example of sensitivity to deforestation and resulting increase in dehydration frequency of adult plants.

Working in the tropical montane oak-bamboo forest of Costa Rica, Romero *et al.* (2006) conducted investigations on four **pendent** bryophyte species, listed from most protected to most exposed: *Phyllogonium viscosum* (Figure 9), *Pilotrichella flexilis* (Figure 10), *Dendropogonella rufescens* (Figure 11), and *Frullania convoluta* (Figure 12). They found that the most exposed species had higher light saturation and compensation

points, higher dark respiration rates, more chlorophyll, higher chlorophyll $a:b$ ratios, and higher N concentrations. Contrary to expectations, the most exposed species had the lowest water content at full saturation. Rate of water loss differed little among the species. The rather exposed moss *Dendropogonella rufescens* had a substantially higher moisture compensation point for carbon uptake than did the other three species. The researchers concluded that density, size, and arrangement of leaves, as well as clump architecture, defined the physiological patterns of water storage and transport they observed.

Figure 8. *Braunfelsia dicranoides*. The *Braunfelsia* community is especially sensitive to deforestation in Papua New Guinea. Photo from the Natural History Museum, London, through Creative Commons.

Figure 9. *Phyllogonium viscosum*, a **pendent** species requiring the most protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 10. *Pilotrichella flexilis nudiramulosaa*, a **pendent** species requiring a protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Claudio Delgadillo Moya, with permission.

Figure 11. *Dendropogonella* sp.; *D. rufescens* has a substantially higher moisture compensation point for carbon uptake than the other three tropical species tested. Photo by Claudio Delgadillo Moya, with permission.

Kürschner and Parolly (1998b) discussed adaptations to water conduction and storing. The **mat** life form that is typical of lowland habitats correlates with such water-holding structures as leaf lobules (Figure 13) [especially **Lejeuneaceae** (Figure 6)] and water sacs as well as rhizoids that can act like sponges to hold and move water in capillary spaces. In addition to these, Frey *et al*. (1990) included **alar cells** (Figure 14), **vittae** (row of elongated cells down center of leaf, only one cell deep; Figure 15), and **ocelli** (darkened cells in row in leafy liverwort leaf; Figure 13, Figure 16) as characteristic of epiphytic

bryophytes in the lowland forest of Mt. Kinabalu, North Borneo. Rhizoid discs (Figure 17) maintain attachment. In areas with high humidity in the montane belt, the **mat** form is replaced by **fan** (Figure 21), **weft**, and **pendant** (Figure 9-Figure 12, Figure 34-Figure 35) life forms that are able to obtain water from fog and mist (**fog-stripping**). Fine leaves (Figure 10) or deeply divided leaves are able to capture this water.

Figure 12. *Frullania convoluta*, a **pendent** species requiring the least protection by the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 13. *Frullania tamarisci* with **ocelli** (dark lines of leaf cells) and leaf **lobules**. Photo by Hermann Schachner, through Creative Commons.
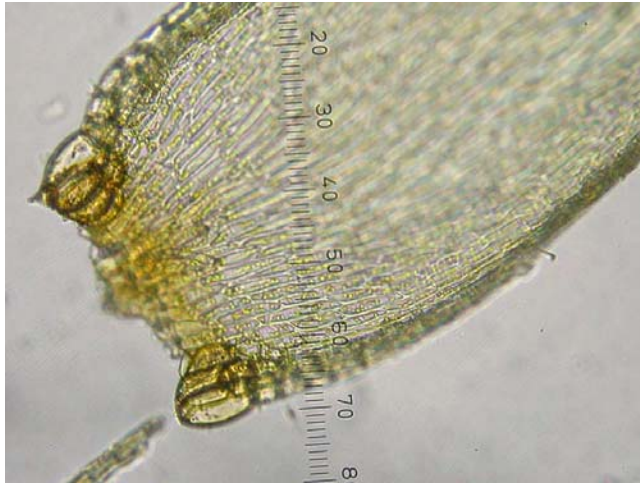
Figure 14. *Pylaisiadelpha tenuirostris* with inflated alar cells. Photo by Bob Klips, with permission.

Figure 15. *Herbertus aduncus* leaf vittae (note longer cells running down midleaf. Photo from Botany Website, UBC, with permission.

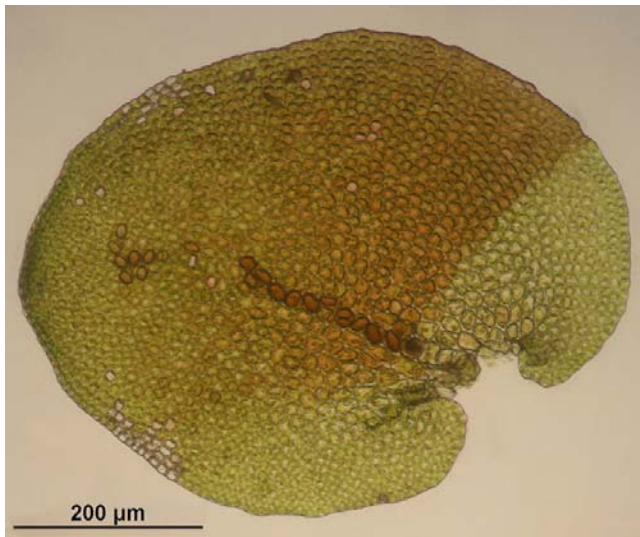Figure 16. *Frullania tamarisci* with **ocelli** (row of brown cells). Photo by Hermann Schachner, through Creative Commons.

Figure 17. *Frullania* rhizoids. Photo courtesy of Andi Cairns.

Frey *et al*. (1990) suggested three principles of water conduction and storing mechanisms: draining surplus water, storing water in dry seasons, and condensing water vapor. They cited the "groovelike" arrangement of leaves as a mechanism to permit water support as well as drainage of water surplus. They found a significant correlation between water sacs (Figure 13), **mat** life form, and smooth bark in the epiphytic bryophyte communities of the lowland forest, facilitating water availability during short periods of dryness.

Parolly and Kürschner (2004) noted that the adaptive trends of functional types (life forms, life strategies, water conduction, and water storage) among the **oreal** (pertaining to mountains) trunk epiphytes at various elevations of southern Ecuador were distinct. They further concluded that these trends occur worldwide among tropical trunk epiphytes.

Kürschner (2003) conduted a phytosociological analysis on the epiphytic Afromontane bryophytes of southwestern Arabia. These epiphytes are affected by monsoons, but at the same time must be drought-tolerant. *Orthotrichum diaphanum* (Figure 18) and *Syntrichia laevipila* (Figure 19) provide "character species" that define alliances. As in other studies, life forms and life strategies correlate with the ecological site conditions. The *Orthotricho* (Figure 18) – *Fabronietum socotranae* (see Figure 20) is a drought-tolerant, light-tolerant, and xerophytic alliance. It is dominated by cushions, short turfs, and mats of perennial stayers that regularly produce sporophytes. In contrast, the alliance in the shaded, subhumid habitats are described as the *Leptodonto* (Figure 21) – *Leucodontetum schweinfurthii* (see Figure 22) association. This association is comprised of **tail** or **fan**-forming **pleurocarpous perennial shuttles** that have large spores. This life strategy adapts them for short-range dispersal and moderately limited reproduction, with large spores more likely to survive and germinate than would smaller ones. Furthermore, this more humid atmosphere supports a much higher diversity in life forms and life strategies.

Figure 18. **Orthotrichum diaphanum**, member of a drought-tolerant, light-tolerant, and xerophytic alliance. Photo by Michael Lüth, with permission.

Figure 19. **Syntrichia laevipila** with capsules, a character species that defines an alliance of epiphytic Afromontane bryophytes in southwestern Arabia. Photo by Michael Luth, with permission.

Figure 20. **Fabronia pusilla**; **Fabronia** forms a drought-tolerant, light-tolerant, and xerophytic epiphytic alliance with species of **Orthotrichum** in Afromontane regions of southwestern Arabia. Photo by Michael Luth, with permission.

Figure 21. **Leptodon smithii**; **Leptodon** forms an epiphytic alliance with **Leucodon schweinfurthii** in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Note the **tail** or **fan**-forming **pleurocarpous** habit. Photo by Michael Luth, with permission.

Figure 22. **Leucodon sciuroides**; **Leucodon schweinfurthii** forms an epiphytic alliance with **Leptodon** in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Photo from Elurikkus, through Creative Commons.

In a similar study on Socotra Island, Yemen, Kürschner (2004) described the epiphytic **Lejeuneo rhodesiae** (see Figure 23) – **Sematophylletum socotrensis** (see Figure 24) from the upper parts of Haghier Mountains. This association characterizes the evergreen Afromontane forests where heavy fogs and mists are typical. Kürschner identified three subassociations [*typicum*, **Hyophiletosum involutae** (drought-tolerant; Figure 25), and **Papillarietosum croceae** (shade-loving humid; Figure 26).

These subassociations are dependent on altitude, forest structure, life conditions, and humidity. Both the *typicum* and *Hyophiletosum involutae* subassociations are characterized by **perennial stayers** or **perennial shuttle** species that form **mats** and **short turfs**. They regularly produce sporophytes. The *Papillarietosum croceae* subassociation is likewise characterized by **perennial stayers** and **perennial shuttle** species that are **pendant** or **mat**-forming, but these have large spores with moderate-low reproductive rates. As seen in the more humid areas in the 2003 study, the *Papillarietosum croceae* subassociation has a much higher species richness with more diverse life forms and life strategies.

Figure 23.   *Lejeunea* sp. growing as an epiphyll; *L. rhodesiae* forms an epiphytic alliance with *Sematophyllum socotrense* from the upper parts of Haghier Mountains, Yemen. Photo by Bramadi Arya, through Creative Commons.

Figure 24.   *Sematophyllum substrumulosum*; *S. socotrense* forms an epiphytic alliance with *Lejeunea rhodesiae*. Photo by Johathan Sleath, with permission.

For a comparative discussion of life strategies in bryophytes as functional types, see Kürschner and Frey (2013). This treatise addresses vegetation types and their associated bryophyte life strategies for both temperate and tropical systems, based on more than 140 bryophyte communities and 1,300 taxa for corticolous, saxicolous, and terrestrial bryophytes. Sporn (2009) compared life forms of bryophytes in various height zones in the forests of Central Sulawesi, Indonesia (Figure 27).

Figure 25.   *Hyophila involuta*, in the drought-tolerant subassociation *Hyophiletosum involutae*, drying. Photo by Bob Klips, with permission.

Figure 26. *Papillaria crocea* in cloud forest – a species that prefers humid shade, found in the *Papillarietosum croceae* subassociation.   Photo by Peter Woodard through Creative Commons.
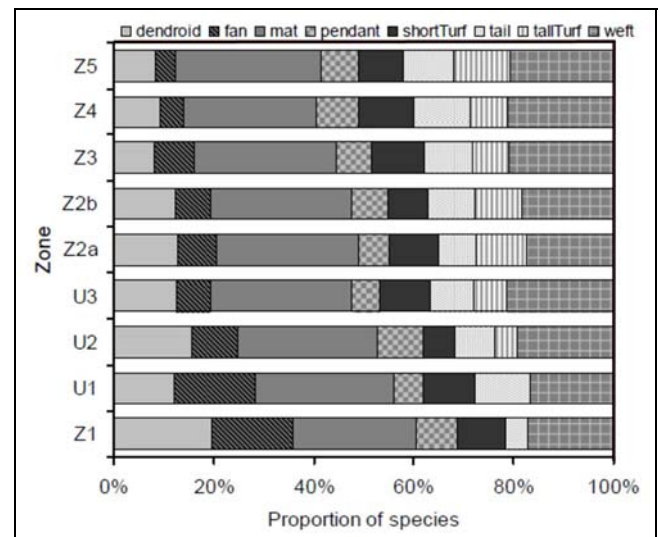

Figure 27.   Comparison of eight life forms of bryophytes among five zones (Z1-Z5) of canopy trees and 3 zones of understory trees (U1-U3) in southwestern Nigeria. See Figure 28 for location of zones. From Sporn 2009.
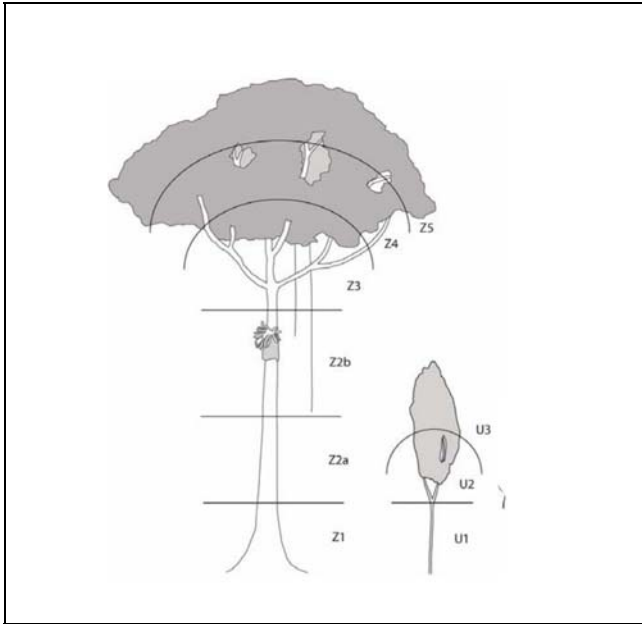
Figure 28. Epiphyte zones from Sporn 2009.

Osmotic Potential

Experimental studies on tropical bryophytes are still rare. However, several have looked at **osmotic potential**. This is the potential of water molecules to move from a **hypotonic** solution (more water, less solutes) to a **hypertonic** solution (less water, more solutes) across a semi permeable membrane. The osmotic potential becomes more negative as solutions become more concentrated.

Hosokawa and Kubota (1957) discussed the resistance to desiccation of epiphytic mosses from a beech forest in southwest Japan and related this to osmotic pressure. They found that the amount of time adult bryophytes could tolerate desiccation varied by species, but also by season of collection.

Akande (1984) looked at the use of **anhydrobiosis** (strategy that permits organisms to survive severe dry and/or extreme cold or hot conditions they often encounter) by corticolous tropical bryophytes as a means of surviving dry periods.   Akande (1985b) also demonstrated the importance of **osmotic potential** (measure of tendency of solution with dissolved salts to withdraw water from pure water by osmosis, across differentially permeable membrane) as a factor in resistance to water stress in four Nigerian corticolous species.   Using the mosses *Stereophyllum nitens* (see Figure 29-Figure 30) and *Calymperes palisotii* (Figure 31-Figure 32) and the leafy liverworts *Spruceanthus floreus* (syn. = *Mastigolejeunea florea*; see Figure 33) and *Frullania spongiosa* (see Figure 12) he found that the osmotic potentials of the corticolous mosses are higher than those of the tested liverworts. These osmotic potentials increase from wet to dry season. *Spruceanthus floreus* is less desiccation tolerant than the two mosses, but all three of these taxa could survive desiccation of 0%, 32%, and 54% relative humidities for six months at room temperature.

Figure 29.   *Stereophyllum radiculosum.*   In Nigeria, *Stereophyllum nitens* is a moss in which osmotic potential increases from wet to dry season. Photo by Juan David Parra, through Creative Commons.

Figure 30.   *Stereophyllum nitens* herbarium specimen. Photo from Natural History Museum, London, through Creative Commons.

Figure 31. *Calymperes palisotii* on bark, a species with high osmotic potential.   Photo by Scott Zona, through Creative Commons.

Figure 32. *Calymperes palisotii*, a species with high osmotic potential. Photo by Scott Zona, through Creative Commons.

Figure 34. *Pilotrichella ampullacea*, a species in Uganda that holds large quantities of external water. Photo by Jan-Peter Frahm, with permission.

Figure 33. *Spruceanthus planiusculus* in a genus where some of the tropical African species are less desiccation tolerant than mosses. *Sprutheanthus floreus* has a demonstrated low osmotic potential. Photo by Claudine Ah-Peng, courtesy of Robbert Gradstein.

Proctor (2002) measured water relationships in two **pendent** mosses [*Pilotrichella ampullacea* (Figure 34), *Floribundaria floribunda* (Figure 35)] in Uganda. The estimated osmotic potential at full turgor in *P. ampullacea* was -1.82 MPa and in *F. floribunda* it was -1.43 MPa. Based on the definition above, net diffusion of water occurs from regions of less negative potential to ones of more negative (or lower) potential. Hence, in this case, more water would move into *P. ampullacea*. Both species are able to hold large quantities of external capillary water, up to *ca*. 12 in *P. ampullacea* and *ca*. 6 in *F. floribunda*. *Pilotrichella ampullacea* has a very rapid initial recovery (30-60 minutes after 20 h air drying at -37 MPa), but as desiccation time increased from 20 hours to 12 days recovery became less complete and full recovery time was slower. This osmotic relationship is well suited to its humid tropical forest environment. *Floribundaria floribunda* requires more continuously moist conditions.

Figure 35, *Floribundaria floribunda*, a species in Uganda that holds large quantities of external water, but requires nearly continuously moist conditions. Photo through Creative Commons.

Desiccation Recovery

One advantage that bryophytes have following desiccation is that liverworts and some mosses recover their full photosynthetic capacity within hours of rehydration, whereas resurrectable ferns such as *Polypodium* (Figure 36) need at least a full day (Peterson *et al*. 1994). On the other hand, liverworts and most mosses lose water very quickly, whereas orchids, bromeliads, and other succulent tracheophytes lose water slowly. But some mosses also are able to retain their water for a longer time, as, for example, *Leucobryum* (Figure 37). *Leucobryum* has several adaptations that facilitate its water storage. It has a tight, compact cushion life form (Figure 37); its leaves are several cells thick (Figure 38); and it has **hyaline** (colorless – lacking chloroplasts; Figure 38) cells that permit water storage. Peterson and co-workers found that plants in the understory and gaps dried more slowly than did plants in their box treatment that simulated the canopy. Those in the gap dried slightly faster than did those in the understory.

Figure 38. *Leucobryum glaucum* leaf cs showing the outer hyaline cells surrounding the green chlorophyllous cells, typical of *Leucobryum* leaves. Photo by Walter Obermayer, with permission.

In French Guiana (Figure 39), 13 of 18 tested bryophyte species were able to maintain more than 75% of their photosynthetic capacity, as indicated by chlorophyll fluorescence, after 9 days of desiccation at 43% relative humidity (Pardow & Lakatos 2012). However, species from the understory required maintenance at 75% or higher relative humidity in order to recover. The researchers reactivated these bryophytes with water vapor only, a condition that is common in many tropical habitats, but which has been largely ignored in physiological ecology studies. The researchers concluded that tolerance to desiccation is of utmost importance as climatic changes occur (see also Wagner *et al.* 2013 and pertaining discussions in the subchapters on Tropics: Altitude).

Figure 36. *Polypodium polypodioides*, a resurrection fern that requires a full day to recover from desiccation. Photo by Korall, through Creative Commons.

Figure 39. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

Rainfall Interception

Frahm (2003a) compared the microhabitats of epiphytic bryophytes and lichens to determine why some trees were covered by lichens and others by bryophytes

Figure 37. *Leucobryum boninense*, showing the cushion life form. Photo by Tomio Yamaguchi, through Creative Commons.

(Figure 40) or others where lichens were in the crowns and bryophytes were on the trunks. Using humidity data loggers for one year, he used periods when the plants were wet and the relative humidity was at least 80%. He found that bryophytes typically thrive where there is a 20-30% longer duration of the wet period than where the lichens thrive. He cautioned that when doing pollution studies, such humidity differences should be considered.

Figure 41. Uluguru Mountains, Tanzania. Photo by Aleksip, through Creative Commons.

Figure 42. Tanzania forest in fog. Photo by pxhere, through public domain.

Figure 40. Moss forest Mt. Ruwenzori Africa. Photo by G. Miehe, courtesy of Robbert Gradstein.

Pócs (1980) in the Uluguru Mountains, Tanzania (Figure 41), East Africa, examined the effect that epiphytic biomass (all kinds of epiphytes) had on the water balance of two rainforest types. With 2,130 kg ha^{-1} dry matter in the submontane rainforest, the rain interception capacity was approximately 15,000 L ha^{-1}. By contrast, the mossy **elfin forest** (cloud forest; Figure 42) at 2,120 m altitude had approximately 14,000 kg ha^{-1} with an interception capacity of 50,000 L ha^{-1} during a single rainfall. Aerial humus accounts for a large portion of the interception capacity of the elfin forest, with ca 4,700 kg ha^{-1} compared to ca 375 kg ha^{-1} in the submontane rainforest.

Hölscher *et al*. (2004) examined the importance of epiphytes to rainfall interception in a tropical montane rainforest of Costa Rica. These canopy epiphyte masses are comprised mostly of mosses, liverworts, and lichens, all known for their ability to intercept rainfall. Biomass of all epiphytes was 1.9 t ha^{-1} dry weight in the studied 35-m-tall old-growth oak (*Quercus*) forest. The monthly moss water contents measured *in situ* ranged 24-406% of moss dry weight. This contrasts with sums of observed throughfall, stemflow, and interception measurements of 70, 2, and 28%, respectively, of the associated 2,150 mm of rain. Cloud water was not a factor in this ecosystem. This study suggested that mosses contributed only about 6% to the interception total, making the bryophytes much less important than in many rainforest ecosystems.

In central Veracruz, Mexico, Holwerda *et al*. (2010) assessed rainfall and cloud-water interception in a mature forest (Figure 43) and a 19-year-old secondary lower montane cloud forest. The researchers used separate calculations for events with rainfall only. They estimated cloud-water interception at 6% of dry-season rainfall (640 mm on average) for the secondary forest and 8% for the mature forest. On the other hand, annual values of cloudwater interception were less than 2% of the total rainfall (3,180 mm). The researchers considered the higher

loss in the mature forest to be the result of a higher canopy storage capacity, reflected in the greater tree leaf area and more epiphyte biomass.

Figure 43. Cloud forest, Bosque Comaltepec, Mexico. Photo by Prsjl, through Creative Commons.

In Colombia, Veneklaas and van Ek (1990) found that rainfall interception was 262 mm (12.4%) of the 2,115 mm of annual precipitation at 2,550 m elevation and 265 mm (18.3%) of the 1,453 mm precipitation at 3,370 m elevation. They found no evidence of fog precipitation. Most of this rainfall interception was accomplished by the epiphytic bryophytes. They attributed the higher rainfall retention at 3,370 m to differences in rainfall distribution and canopy storage capacities. They considered epiphytes to have an important role in this retention. The total epiphyte mass was approximately 12 **tonnes** (metric ton = 1,000 kg) dry weight per hectare, with most of it consisting of bryophytes and dead organic matter. In experiments, Veneklaas *et al.* (1990) found that epiphyte-covered branches were efficient in capturing rainfall. Most of this capture was accomplished by bryophytes. Release of this rainwater was very gradual, as was loss by evaporation.

In southeast Queensland, Ford (1994) found that epiphytes could absorb water 6-7 times their dry weight. This absorption affects stemflow and throughfall. The increased weight can cause outer, thin branches to break.

Other sources may prove helpful in understanding the water relations of tropical bryophytes. Pócs (1976) elaborated on the role of epiphytic bryophytes and other plants in the water balance of rainforests in the Uluguru Mountains, East Africa. Thompson *et al.* (1994) described the water-holding capacity of subtropical epiphytic bryophytes. Bergstrom and Tweedie (1995) described the hydrologic properties of epiphytic bryophytes. Kürschner and Parolly (1998b) described life forms and adaptations to water conduction and storage in North Peruvian epiphytic bryophytes. Other studies that pertain to rainfall interception are those of Kürschner & Parolly (2004) and Fleischbein *et al.* (2002).

Fog Interception

Some areas that receive little rainfall do experience fog on a regular basis (Lakatos *et al.* 2012). Fine wires and thin leaves are able to collect this fog water (Figure 44). Lakatos and coworkers measured dew formation on bark and lichens to be 0.29-0.69 mm d^{-1}. This water aids in cooling and provides enough moisture to prolong photosynthetic activity.

Figure 44. Spider web with fog drops; a similar appearance of water drops occurs on spider webs, fine wires, bryophyte leaf awns, and other thin structures in fog. For mosses, this is a source of water. Photo by Janice Glime.

Fog is able to provide sufficient water to many kinds of bryophytes in areas with low rainfall. Santon and Horn (2013) demonstrated this in lichens in a shrubland of northern Chile. They compared the ability to harvest fog water to the biomechanical mechanisms of filter-feeding aquatic invertebrates. Greater branchiness, as measured by fractal dimensionality, indicates greater fog-harvesting ability. Fractal dimension of the foliose and fruticose lichens increased significantly as fog availability increased.

Fog (Figure 45) is an important contributor to the cloud forest (elfin forest) (Camilo *et al.* 2008). The abundant epiphytes in these forests benefit from this fog input, especially during periods of lower rainfall. Camilo and coworkers suggested that it is especially important when wind speed is high and leaf water content has intermediate values, but that at both low and high leaf water content the interception of fog water is constrained.

Figure 45. Cloud forest showing fog, Ella, Sri Lanka. Photo by Kenny OMG, through Creative Commons.

In a subtropical montane forest in northern Taiwan, Chang *et al*. (2002) estimated fog deposition rate on epiphytic bryophytes by measuring the increase in plant weight when exposed to fog. Fog duration in this forest averaged 4.7 hours per day in summer months and 11.0 hours per day in other months. The maximum duration was 14.9 hours per day in November. The bryophytes experienced an average fog deposition rate of 0.63 g water g^{-1} dw h^{-1}.

Many bryophytes in the cloud forest and some tropical rainforests are **pendent** (Figure 34-Figure 35). Renner (1932) referred to these as dripping liquid water under various conditions in Javanese forests. León-Vargas *et al*. (2006) demonstrated the humidity stratification in the lowland Amazonian forest in upper Orioco (Figure 46). They found that all six species of **pendent** bryophytes in their Venezuelan cloud forests could survive at least a few days of desiccation. High humidities supported more recovery than low humidities. They considered droplets of cloudwater to be important sources of water for **pendant** and other bryophyte life forms, particularly during periods of low rainfall.
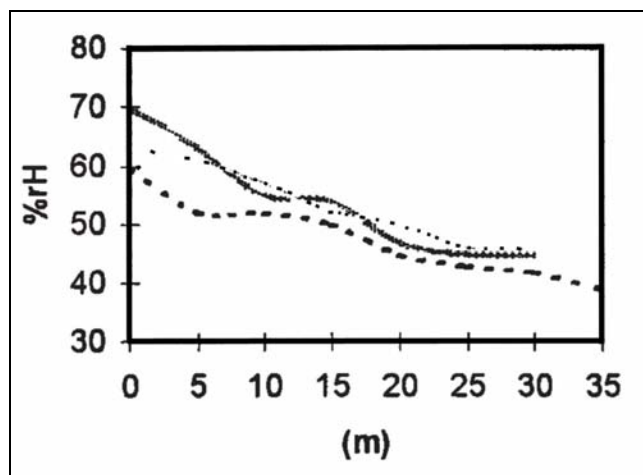

Figure 46. Relative humidity profile in meters above the ground in an Amazonian lowland forest of Surumoni, upper Orinoco. Modified from León-Vargas *et al*. 2006.

Pardow *et al*. (2012) described a recently discovered tropical lowland cloud forest type in the Guianas (Figure 47), originally discovered by Gradstein (2006) (see

Gradstein *et al*. 2010; Obregón *et al*. 2011; Gehrig-Downie *et al*. 2013). This habitat is created by frequent early morning fog events in the valleys, providing suitable habitat for a richer epiphytic species diversity compared to the common lowland rainforest. In the French Guiana (Figure 39) they compared the distribution of functional groups of epiphytes by height zone in the lowland cloud forest and lowland rainforest. These forests differed in composition of epiphytes in the canopy, especially in the mid and outer canopy, with the cloud forest exhibiting both a higher biomass and cover of both bryophytes and tracheophytes. Furthermore, the cloud forest had a richer bryophyte life-form composition. The cloud forest frequently exhibited tails, wefts, and pendants, life-forms that were nearly absent in the canopies of the common rainforest.

Figure 47. Canopy of a lowland cloud forest, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Microclimate

In any ecosystem, a diversity of microclimates can increase the diversity of species. These provide differences in substrate, temperature, light, and moisture availability. With their many layers of canopy, the tropical forests provide a wide range of microclimates and niches.

One might expect that gradients in light and humidity would affect species diversity and richness. In a Brazilian Atlantic Forest remnant, Silva and Pôrto (2013) found the highest diversity and richness in the trunk zone. But they found no significant difference of bryophyte total richness or diversity along edge distance or vertical zonation gradients. However, at the species level, they found that shade epiphytes decreased significantly along vertical gradients, while sun epiphytes increased. They concluded that the bryophyte distribution in the forest is more related

to the microenvironmental gradation than to such landscape characteristics as edge distance.

Early studies by Biebl (1964, 1967) attempted to relate success of the tropical species to water and temperature. Wolf (1993a) recognized that some species from the Colombian lower montane rainforest were able to occupy the more exposed habitats in the warmer lowland rainforest of Guyana where they could receive more radiant energy. Furthermore, the epiphytes in the northern Andes tropical montane rainforests were divided by height on the tree, occupying a gradation of microhabitats characterized by differences in moisture (Figure 46) and light (Figure 48).
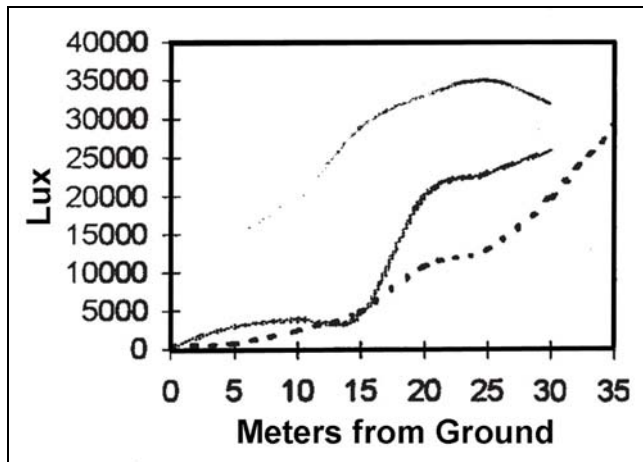

Figure 48.   Light gradation from ground to canopy in an Amazonian lowland forest. Modified from León-Vargas 2001.

Temperature is one of the important aspects of microclimate.   As noted by Wagner *et al*. (2013), bryophyte biomass and diversity both decrease dramatically as one goes from high to low altitudes in the tropics. They surmise that high respiration rates at high temperatures may at least in part explain this decrease. They transplanted two bryophyte species from 1,200 and 500 m asl to 500 m and sea level, respectively, in Panama and studied the short-term temperature acclimation of CO_2 exchange for 2.5 months. They also compared survival and growth for 21 months. Mortality was highest and growth lowest in transplanted samples, with no evidence of short-term acclimation.

Whereas the Wagner *et al*. (2013) study implies that temperature is important in altitudinal distribution of species, Wolf (1993c) suggests that it is a moisture gradient that accounts for epiphyte community differences in the northern Andes.   Nevertheless, in a study in Panama, Zotz *et al*. (1997) found a strong diurnal variation in water content of tropical bryophytes in a lower montane rainforest. Both low and high water content limited carbon gain. More than half of the daily carbon gain was lost during the night as respiration, suggesting that temperature also was important.

Hosokawa and Odani (1957) tied the limits on the period of assimilation to the loss of carbon from respiration. They found that those species at the tree base (***Thuidium cymbifolium*** (Figure 49), ***Loeskeobryum cavifolium*** (Figure 50), ***Thamnobryum subseriatum*** (Figure 51), ***Homaliodendron scalpellifolium*** (Figure 52) had a minimum light requirement of 400 lux, whereas those species higher in the trunk had a higher **light**

compensation point (light level at which photosynthetic gain = respiration loss on daily basis). On cloudy days, only the mosses at the tree base could reach their compensation point.

Figure 49. ***Thuidium cymbifolium*** with capsules, a tree base species with minimum light requirements. Photo by Li Zhang, with permission.

Figure 50.   ***Loeskeobryum cavifolium***, a tree base species with minimum light requirements. Photo by Digital Museum Hiroshima, with permission.

Figure 51.   ***Thamnobryum subseriatum***, a tree base species with minimum light requirements. Photo by Michael Luth, with permission.

Figure 52. *Homaliodendron scalpellifolium*, a tree base species with minimum light requirements. Photo by Taiwan Biodiversity, through Creative Commons.

The CO_2 levels differ throughout the canopy. In a subalpine forest of Taiwan, higher CO_2 levels occur in the lower canopy (Kao *et al*. 2000). Low CO_2 levels can limit photosynthesis, but higher levels can help to compensate for limited light.

Cao *et al*. (2005) found a correlation between epiphylls and light, moisture, habitat, and disturbance due to human activities. They found that the number of epiphytes increased from the center of the city to the outer suburbs. In the city, 67.4% of the epiphytes had a Levin's niche width of less than 0.1.

Gehrig-Downie *et al*. (20110 found that the lowland cloud forest had significantly more epiphytic biomass than did the lowland rainforest without fog in French Guiana (Figure 39). The lowland cloud forest is characterized by the high air humidity and morning fog that characterize river valleys in hilly areas, explaining the higher epiphytic bryophyte biomass.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) conducted the first study comparing tracheophytic epiphytes and bryophytes along a disturbance gradient in a dry forest. They compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland (Figure 53). They found that density of bryophytic epiphytes on 100 trees of *Acacia macracantha* (in northern Ecuador; Figure 54) was significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge was more impoverished than semi-closed woodland and had similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types varied, contributing to the diversity. As they pointed out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density was closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determined most of the epiphyte assemblage. Their most important conclusion is that in these dry environments, tracheophytic epiphyte diversity is not affected by disturbance, whereas bryophyte diversity is clearly affected. They attribute this to the poikilohydric

bryophyte condition that is more sensitive to changes in microclimate as compared to that of the homoiohydric tracheophytic epiphytes. The importance of microclimate for niche assembly of epiphytic bryophytes and absence of dispersal constraints is further supported by Oliveira *et al*. (2009) in the Guianas.

Figure 53. *Acacia koaia*. Degree of disturbance affects density of bryophytic epiphytes in forests of *Acacia macracantha*. Photo by Forest and Kim Starr, through Creative Commons.

Figure 54. *Acacia macracantha*, an Ecuadorian species with lower density of bryophytes at forest edges and on isolated trees. Photo by Vladeq, through Creative Commons.

Oliveira (2018) noted that the major differences from base to outer canopy are those of relative abundance. She then tested character traits of 104 species of epiphytic **Lejeuneaceae** (Figure 6, Figure 23) in the Amazonian terra firme forests. She examined dispersal ability, dark pigmentation of leaves, ability to convolute leaves when

drying, possession of thickened cell walls, monoicous vs dioicous reproduction, and facultative epiphyllous habit. Four of these six traits proved useful in separating canopy and/or understory communities. Interestingly, high dispersal ability did not vary much along the height gradient. She further noted that asexual propagules were not over-represented in the dynamic environment of the canopy, seemingly challenging the bryophyte life strategy theory.

Oliveira (2018) found that facultative epiphylls were over-represented on the tree bases. Dark pigmentation and convolute leaves were significantly more common in the canopy and less common at the base. These two traits can protect against high light intensity and prolong periods of hydration, respectively. The paucity of these species at the bases of trees may be the result of high temperatures and low light, made lower by the pigmentation, while the prolonged hydration in these conditions would add to a high rate of respiration relative to photosynthesis.

Stuntz *et al*. (2002) noted that microclimate goes two directions. Bryophytes not only respond to the microclimate around them, but they can have a major impact on the microclimate of the forest around them. To put it in the descriptive wording of the researchers, they "air-condition the forest."

Although their study included only two orchids and a bromeliad, Stuntz *et al*. (2002) showed that the space around these epiphytes had significantly lower temperatures than did areas of the same tree with no epiphytes. Evapotranspiration was reduced almost 20% compared to microsites with no epiphytes. This study would suggest that the effect of bryophytes on the microclimate in tropical forests could likewise be significant.

Understanding of the microclimate is important in management strategies if one wants to protect the bryophytes (Sporn 2009; Sporn *et al*. 2009). These researchers sampled understory trees in a natural forest and in two types (natural shade trees and planted shade trees) of **Theobroma cacao** (cacao; Figure 55) agroforests in Central Sulawesi, Indonesia. The two agroforests had low air humidity and high afternoon temperatures. Although bryophyte species richness differed little among the habitats, the species composition was markedly different between the natural forest and the agroforests. These differences were most likely the result of microclimate differences.

Nutrient Dynamics

Akande *et al*. (1985a) found that the nutrients in the tested corticolous bryophytes increased from the dry season to the wet season. The nutrient fluctuations were more pronounced in mosses than in the liverworts tested. They concluded that bryophytes must be significant in the nutrient cycling of tropical ecosystems.

We are beginning to understand now how bryophytes play a major role in nutrient dynamics in the tropical forest. Their ability to sequester rain and fog water consequently means that they can sequester the nutrients dissolved in this water. When they dry out, damaged membranes release the nutrients, and the early stages of precipitation dissolve these released nutrients and carry them downward.

Figure 55. Cacao plantation in Sulawesi, showing trunk epiphytes. Photo courtesy of Robbert Gradstein.

Vitousek (1984) summarized known nutrient relationships in lowland tropical forests, based on published studies from 62 tropical forests. He found that these forests and higher nitrogen levels lower ratios of dry mass to nitrogen in the litterfall compared to that ratio in most temperate forests. Nevertheless, the nitrogen return is comparable to that of temperate forests. Phosphorus return is very low in many of these tropical forests, whereas calcium return is high. The phosphorus cycling seems to be very efficient.

Sometimes the nutrients in the host affect the colonization by epiphytes. Benner (2011) found that epiphytes in the unfertilized Hawaiian montane forests (Figure 56) colonized high-phosphorus (fertilized) host trees more frequently than they did unfertilized trees. Mosses were less responsive to the fertilization than the cyanolichens. The cyanolichens were good predictors of chlorolichen and bryophyte abundance at three out of four Kauai, Hawaii, sites, indicating high bark and leaf phosphorus. Benner and Vitousek (2007) found that after 15 years of P fertilization in the forest, there was a "dramatic increase" in both abundance and species richness of the canopy epiphytes. There was, on the other hand, no response to fertilization with nitrogen or other nutrients.

Figure 56. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Nadkarni (1983, 1986) noted the importance of epiphytes in making a significant contribution to the overall nutrient cycling in both temperate forests and tropical rainforests. In both forest types they absorb nutrients collected from the atmosphere during the dry season. The net release from branches with epiphytes during the wet season is greater than that from branches stripped of their epiphytes. Chang *et al*. (2002) measured ion input in a subtropical montane forest in Taiwan and found that more than 50% of the ecosystem input arrived in fog deposition, suggesting that fog is an important nutrient contributor in some tropical ecosystems.

Nadkarni *et al*. (2004) found that the primary forest canopy of a cloud forest in costa Rica had 63% of its organic matter as dead organic matter (DOM). Bryophytes comprised 12%. By contrast, the canopy organic matter of the secondary forest was 95% bryophytes, with only 3% DOM. Different locations within the primary canopy varied, with branch junctions having only dead organic matter and roots. Rather, bryophytes were the only organic matter at branch tips, subcanopy, and understory substrates. The trunks had diverse organic matter, but were dominated by tracheophytes and bryophytes; little dead organic matter was present. The secondary forest differed in having little difference in organic matter between trunks and branches. Canopy organic matter was high because of the strong presence of bryophytes. One surprise was that bryophytes were absent in branch junctions, although that is a likely place for them in other ecosystems. The researchers recommended transplant studies to try to determine the causes of the bryophyte distribution on the trees.

Rainfall vs Throughfall

Not all nutrients respond to their trip through the bryophyte sponges in the same way. Clark *et al*. (1998b) assessed net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. They found that phosphate, potassium, calcium, and magnesium were leached from the canopy, but nitrogen compounds were retained.

Hölscher *et al*. (2003) determined that differences in the canopy structure of predominately ***Quercus copeyensis*** (Figure 57) forests and epiphyte (mosses, liverworts, and lichens) abundance in old growth vs two ages of secondary growth in Cordillera Talamanca, Costa Rica, resulted in large differences in the way nutrient transport was divided into stemflow and throughfall. Nevertheless, the nutrient transfers reaching the soil were similar. Significantly higher litterfall of non-tracheophyte epiphytes indicated the higher epiphyte load in the old-growth forest.

In seeming contrast to the findings of Clark *et al*. (1998b), in a Venezuelan rainforest with a low-nutrient forest floor, the fluxes in calcium, sulfur, and phosphorus in the rainfall were greater than those in the throughfall (Jordan *et al*. 1980). Other elements occasionally had greater fluxes in the rainfall than in throughfall. Jordan and coworkers suggested that the canopy epiphylls (algae, lichens) intercepted and modulated the nutrients, resulting in their conservation in the canopy. Phosphate, potassium, calcium, and magnesium were at sometime later leached from the canopy. Seasonal data suggest that biomass burning increased concentrations of NO_3^- and NH_4^+ in cloud water and precipitation at the end of the dry season.

Regardless, a large majority of the inorganic N in atmospheric deposition was retained by the canopy at this site.

Figure 57. ***Quercus copeyensis*** with trunk epiphytes. Photo through Creative Commons.

To help us understand the effects the rainforest has on the nutrients, Wilcke *et al*. (2001) established five 20-m transects on the lower slope of a tropical lower montane rainforest in Ecuador. In the soil, they found the total Ca (6.3-19.3 mg kg^{-1}) and Mg concentrations (1.4-5.4) in the O horizon were significantly different between the transects. The throughfall ranged 43-91% of the rainfall; cloudwater inputs were less than 3.3 mm yr^{-1} except for one of the five transects where it was 203. Even the *p*H was affected by filtering through the canopy and associated epiphytes, increasing from a mean of 5.3 in the rainfall to 6.1-6.7 in the throughfall.

The leaves in this rainforest increase the element (Al, TOC, Ca, K, Mg) concentrations in the throughfall due to leaching from the leaves and washing off the dry deposition (TOC, Cu, Cl$^-$, NH4$^+$-N) (Wilcke *et al*. 2001). This could be an advantage for inner canopy bryophytes that receive these nutrients from the top of the canopy. Only Mn, Na, and Zn escape enhancement as a result of throughfall contacts. However, in high flow events, even Mn and Zn are elevated in the throughfall.

The nutrient input to forest bryophytes is higher at 2,250 m than at 3,370 m asl in two montane tropical rainforests of Colombia (Veneklaas 1990) attributed this to the greater precipitation volume at the lower altitude. The losses of nutrients from the canopy were likewise higher at 2,550 m. Veneklaas considered the differences between forests to be related to differences in precipitation, geographical situation, and soil nutrient availability.

Bryophytes can alter the nutrient dynamics of the forest in a variety of ways. They act as sponges, absorbing rainfall, and with it the nutrients carried by that rainwater. Epiphytes furthermore trap water and nutrients as they flow down branches and tree boles, retaining nutrients leached from bark, leaves, and other kinds of epiphytes or collected in their dust. They host a variety of nitrogen-fixing bacteria, most notably the **Cyanobacteria (**Figure 58**)**.

Figure 58. *Scytonema*, a genus that performs nitrogen fixation in the phyllosphere. Photo by Yuuji Tsukii, with permission.

Nitrogen Dynamics

Bergstrom and Tweedie (1998) found that epiphytes were able to access at least three sources of nitrogen, including atmospheric, the phorophyte through decomposed litter, and a source of nitrogen fixation. The ^{15}N exhibited considerable spatial heterogeneity within the tree.

Clark and coworkers (Clark 1994; Clark *et al.* 2005) reminded us of the large role bryophytes can have in nitrogen dynamics of a tropical forest. The assemblages of epiphytic bryophytes, vascular epiphytes, litter, and associated humus harbor ~80% of the inorganic nitrogen retained in the canopy (Clark 1994). The forest canopies are able to trap and retain inorganic nitrogen from rainfall, dry deposition of gasses, vapors, and particles, and nitrogen previously trapped by clouds. Because they form much of the surface area in the canopy and lack a thick cuticle (many, perhaps all, bryophytes have a waxy cuticle, but it is very thin) and epidermis, they are able to trap and retain this nutrient much more effectively than the tree leaves. Clark and coworkers compared nitrogen retention of field samples of epiphytic bryophytes, epiphytic assemblages, epiphytic tracheophyte foliage, and host tree foliage to cloud water and precipitation in a tropical montane forest canopy in Costa Rica. They estimated, using models and field data, that epiphytic bryophytes and epiphyte assemblages retained 33-67% of the nitrogen deposited by cloud water and precipitation. The model predicted an annual retention of 50% of the inorganic nitrogen that arrived through atmospheric deposition. The bryophytes are important in the transformation of inorganic nitrogen such as nitrates to less mobile forms such as ammonia, but also deposit some of it in **recalcitrant** (unresponsive to treatment; resistant, *i.e.*, it doesn't break down easily, if at all) forms of biomass, litter, and humus.

The collected nitrogen that is added to the epiphytic biomass, litter, and canopy humus (Vance & Nadkarni 1990, 1992) is eventually added to the very large pool of nitrogen in the soil organic matter (Edwards & Grubb 1977; Grieve *et al.* 1990; Bruijnzeel & Proctor 1995). Clark *et*

al. (1998b) found that the net nitrogen accumulation was ~8-13 kg ha^{-1}.

Cloud loadings can contribute to nutrient availability. Clark and Nadkarni (1992) experimented with excised epiphytes from Monteverde, Costa Rica, by subjecting them to NO_3^- loadings; from 0% to 90% of that NO_3^- is retained by the epiphytes. Ammonium (NH_4^+) is considerably more variable, ranging from a 200% loss to a 90% gain. These bryophytic epiphytes retain ca. 85% of the nitrate N from the atmospheric deposition to the canopy.

Wania *et al.* (2002) used ^{15}N levels to compare nitrogen in various positions within the forest canopy of a lowland rainforest in Costa Rica. The ^{15}N levels of canopy soils did not vary significantly, but the content in the epiphytes (including bryophytes) in different canopy layers did. The researchers concluded that epiphytes in different levels exhibited different ^{15}N during nitrogen acquisition.

Wanek and Pörtl (2008) examined nitrogen (NO_3^-, NH_4^+, and glycine) uptake in bryophytes of a lowland rainforest of Costa Rica. They found no significant differences between the epiphyllous and epiphytic bryophytes. The mean uptake rates for these bryophytes are 1.8 µmol g^{-1} dw h^{-1} for nitrate, 3.6 µmol g^{-1} dw h^{-1} for ammonium, and 3.4 µmol g^{-1} dw h^{-1} for glycine, suggesting that amino acids such as glycine significantly contribute to bryophyte nutrition in these epiphytes.

Most of the nitrogen fixation probably occurs on leaves with epiphylls. In any case, it is an important contributor to the tropical forest nitrogen dynamics. Matzek and Vitousek (2002) found that the total nitrogen fixation in a Hawaiian montane rainforest (Figure 59) was highest in sites having low N:P ratios in the leaves and stemwood. They suggested that epiphytic bryophytes and lichens depend on canopy leachate for their mineral nutrients, but the heterotrophic nitrogen fixation is controlled by the nutrient supply in the decomposing substrate. Differences in substrate cover had a larger effect on total N input from fixation than did fixation rates, a conclusion consistent with the low fixation rates observed in young forests. Nitrogen fixation in the **phyllosphere** (space surrounding a leaf) will be discussed under epiphylls.

Figure 59. Hawaiian tropical wet montane forest. Photo by Djzanni, through Creative Commons.

In 1998, Clark *et al*. (1998a) used epiphytic bryophyte samples in enclosures to estimate rates of growth, net production, and nitrogen (N) accumulation by shoots in the canopy in a tropical montane forest in Monteverde, Costa Rica. They also used litterbags to estimate rates of decomposition and N dynamics of epiphytic bryophyte litter in the canopy and on the forest floor. They estimated N accumulation at 1.8-3.0 g N m^{-2} yr^{-1}. The cumulative mass loss from litterbags in the canopy after one year was 17±2% (mean ± 1 SE) and after two years 19±2 % of initial sample mass. Mass loss from litter in litterbags after one year on the forest floor was 29±2%, and from green shoots 45±3%. On the forest floor, ca 47% of the initial N mass was lost within the first three months. The N that remained in the litter was apparently **recalcitrant** (resistant to microbial decomposition), although there was no evidence for net immobilization by either litter or green shoots. The annual net accumulation of N by epiphytic bryophytes was ca 0.8-1.3 g N m^{-2} yr^{-1}.

Akande and coworkers (Akande 1985a; Akande *et al*. 1985) concluded that the role of bryophytes in nutrient cycling of African tropics is significant and requires study. Nutrient contents of bryophytes fluctuate with season, and in three forests at Ibidan, Nigeria, the highest mean monthly nutrient composition of the bryophytes is in June to July, with the lowest in November to January. Magnesium is an exception, reaching its peak in October when the other nutrients are diminishing. There are considerable differences between species, although the phenological patterns are very similar, with mosses accumulating more than liverworts. Relationships of bryophyte concentrations to those of bark suggest that the bryophyte obtains its nutrients from stemflow containing leachates not only from the canopy leaves, branches, and canopy dust, but also from the bark, and that bryophytes do not get nutrients directly from the bark, but rather get them only from those leached out by rain. Akande *et al*. concluded that the predominant source of these nutrients was from dust and other pollutants such as smoke and sulfur dioxide.

Base cation and fluxes increase in throughfall, but NH_4^+-N and NO_3^--N decrease relative to that in rainfall in a subtropical montane moist forest in Yunnan, southwest China (Liu *et al*. 2002). The throughfall inputs of N, P, Ca, and S come primarily from precipitation, whereas most of the potassium and 2/3 of the magnesium in throughfall come from canopy leaching. The cycling rates for mineral elements are generally low compared to other tropical forests. Epiphytes are abundant on the bole and affect the chemical composition of the stemflow through selective uptake or release of elements. The total N, NH_4^+-N, Mg, Na, and SO_4^{2-}-S are enhanced, while NO_3^--N, K, P, and Ca are depleted in stemflow. Nitrogen from nitrogen-fixing organisms is low, most likely due to constraints by low temperatures.

In a study in the subtropical forest of northeastern Taiwan (Figure 60), Hsu *et al*. (2002) noted that nutrients in epiphytes and tree foliage are more readily available than those in the woody parts of the tree, making the tiny bryophytes proportionally more important than their size would suggest.

Figure 60. Taiwan blue magpie in subtropical rainforest of Taiwan. Photo by Gulumeemee, through Creative Commons.

Pulse Release

One mechanism by which the bryophytes help the forest floor plants is through pulse release of nutrients. This burst of nutrients occurs when dry bryophytes with damaged membranes first get water that wets them. This pulse is especially important for nutrients that are typically held in nutrient pools within the cells. The damaged membranes resulting from drying permits the rain to leach these nutrients from their otherwise safe interior locations. Coxson (1991) estimated the efflux of these solutes from stem segments of canopy bryophytes in tropical montane rainforest in Gaudeloupe (Figure 61). These reached 80.1 kg ha^{-1} yr^{-1} for potassium, 1.4 kg ha^{-1} yr^{-1} for phosphorus, and 11.8 kg ha^{-1} yr^{-1} for nitrogen in these rewetting episodes. On the other hand, estimates using intact bryophyte mats during natural field rewetting episodes were smaller, causing release of 28.7 kg ha^{-1} yr^{-1} for potassium and 0.2 kg ha^{-1} yr^{-1} for phosphorus. The lower numbers most likely result from internal recycling of released ions within the bryophyte mats.

Within the cloud forest canopy, and most likely elsewhere in the tropics, bryophytes accumulate considerable quantities of sugars (Coxson *et al*. 1992). In Guadeloupe, French West Indies (Figure 61), more than 950 kg ha^{-1} of sugars and polyols are released by epiphytic bryophytes per year as a result of wetting and drying cycles. The sugars come as a pulse during re-wetting, contributing to growth of the microbial flora both within and beneath the canopy. These sugars and polyols account for 17% of the dry weight of the upper canopy liverwort *Frullania atrata* (Figure 62), while providing less than 6% of the dry weight of the lower canopy moss *Phyllogonium fulgens* (Figure 63). (The name *Frullania atrata* may be incorrect as many species have incorrectly been identified as this one.)
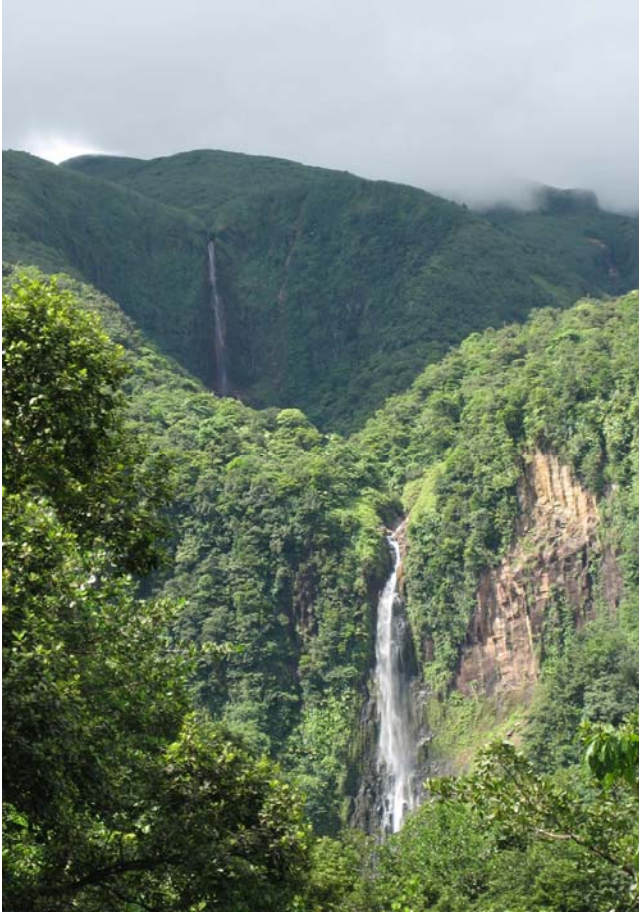
Figure 61.   Montane rainforest, Guadeloupe.   Photo by Bobyfume, through Creative Commons.
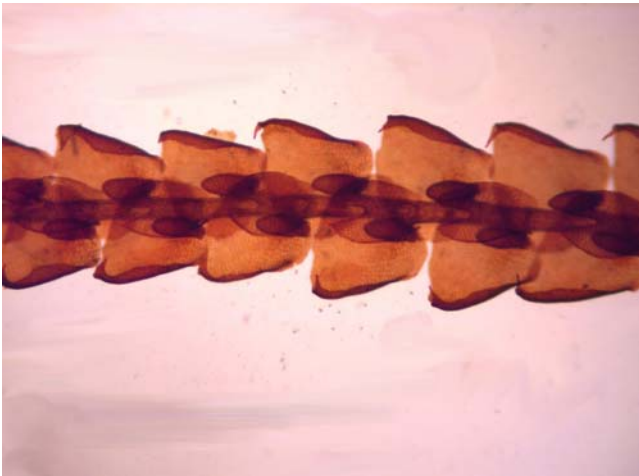

Figure 63. *Phyllogonium fulgens*, a lower canopy **pendent** moss.   Photo by Yelitza Leon, Venezuelan Flora, through Creative Commons.

In a subtropical forest of the Ailao Mountains in Yunnan, southwest China, Liu *et al.* (2002) found that bryophytes enhance the annual amounts of total N, NH_4^+-N, Mg, Na, and SO_4^{-2}-S but deplete NO_3^--N, K, P, and Ca in the stemflow.   Although many kinds of N-fixing organisms often are associated with epiphytic bryophytes, their contribution to total N in the mountains of Yunnan is most likely constrained by low temperatures.   In a montane rainforest of the warmer Hawaii, on the other hand, Matzek and Vitousek (2003) found that the potential nitrogen fixation ranges from ~0.2 kg ha^{-1} yr^{-1} in a 300-year-old site to ~1 kg ha^{-1} yr^{-1} in a 150,000-year-old site.   They felt that the dependence of epiphytic bryophytes and lichens on nutrients leached from the canopy might account for the fact that the highest fixation rates occurred in sites with low N:P ratios in the leaves and stemwood of the trees.   For heterotrophic fixation, the nutrient supply offered by the decomposing substrate is also important in controlling the fixation rate.   Thus, older substrata with more epiphytes are likely to contribute more nutrients to these N fixers, and indeed Matzek and Vitousek did find that the fixation rates relate to substrate cover.

With an epiphyte biomass and associated soil of 44 tons ha^{-1}, the epiphytes form a significant contribution to the Colombian upper montane rainforests (Hofstede *et al.* 1993).   The 20 kg of epiphytes exceeded the biomass of the

Figure 62.   *Frullania atrata*, an upper canopy liverwort. Photo by Juan Larrain, with permission.

Keystone Resource

Nadkarni (1994a) attributed to the canopy epiphytes the role of **keystone** resource in the nutrient cycling of tropical forest ecosystems.   That is, this is a resource that is critical to the structure and function of the ecosystem, without which the system would cease to function as it does.   The epiphytic bryophytes may have a key role in the nutrient dynamics of these forests.

part of the tree that supported them. In this epiphytic community, the researchers found 2,360 g N, 215 g P, 1,350 g K, and 99 g Ca. The epiphytes create large accumulations of bryophytes, favored by low temperatures, continuous high humidity, low air turbulence, and the structure of the forest. The water-soluble phosphorus stored in the epiphytic biomass is higher than that of the forest floor soil.

Pentecost (1998) assessed the cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains of Uganda (Figure 64). He found that the lichens contain ~2% of the total above ground nutrients, whereas 8% occurs in the bryophytes. The concentrations of the three "fertilizer" nutrients were N (10 kg ha^{-1}), P (1 kg ha^{-1}), and K (3 kg ha^{-1}).

Figure 64. Rwenzori Mountains, western Uganda. Photo by Agripio, through Creative Commons.

Nadkarni (1984) reported 141.9 kg of epiphytes on a single *Clusia alata* (Figure 65) in a Costa Rican cloud forest. The nutrients in these epiphytes were estimated as 1062 g N, 97 g P, 678 g K, 460 g Ca, 126 g Mg, and 207 g Na. This is significant because this relatively small component (less than 2%) of the forest biomass holds up to 45% of the nutrients found in the foliage of similar forests and stresses the importance of epiphytes as keystone resources in the nutrient dynamics of these forests.

Canopy Roots

To me, the most intriguing relationship is the relationship of bryophytes with canopy roots, first discovered and described by Nalini Nadkarni in her classical paper in Science (1981). Laman (1995) reported the improved germination of *Ficus stupenda* in moss beds associated with canopy knotholes, attributing their survival to good moisture retention. However, seed harvesting ants (*Pheidole* sp.; Figure 66) killed many of the seedlings later in development.

Figure 65. *Clusia alata,* a common epiphyte host in Costa Rica. Photo by Evaristo Garcia Foundation, through Creative Commons.

Figure 66. *Pheidole pilifera* minor (**left**) and major (**right**) workers. Some species of *Pheidole* kill *Ficus stupenda* seedlings in epiphytic moss beds. Photo by M. L. Muscedere and J. F. A. Traniello, through Creative Commons.

Epiphytic bryophytes also provide a rooting medium for **adventitious roots** (roots that arise from stem tissue; Figure 67) of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community (Nadkarni 1994b). The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al*. 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994b). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.

Figure 67. Adventitious roots of banyan tree (*Ficus benghalensis*). Photo through Creative Commons.

Nadkarni (1981) found that epiphytes, including bryophytes, stimulate the growth of adventitious roots. The bryophytes serve to trap nutrients for them, and the relationship is so strong that Nadkarni argues that evolution has selected for it.

In *Senecio cooperi* (Figure 68), a species in the tropical cloud forest, Nadkarni (1994b) experimented with epiphytes air-layered on stem segments. For comparisons, she used wet epiphytes or dry epiphytes plus associated humus, sponges wetted with either water or nutrient solutions, dry sponges, and controls with no added layering. The wet epiphyte-humus mix and sponges with nutrient solutions were most successful in producing roots. Nadkarni suggested that the epiphytes intercept nutrients that they retain and provide the "cue" for the host tissue to produce the roots.

Some adventitious roots take advantage of the microenvironment created by epiphytic bryophytes (Sanford 1987). The roots are able to grow upward, and can do this in as rapidly as 5.6 cm in 72 hours. The roots are less than 2 mm in diameter and grow on the exposed bark surfaces, in bark fissures, and beneath attached epiphytic mosses, ferns, and vines.

Epiphytes decompose in the canopy to form soil on the large branches (Hietz *et al*. 2002). Epiphyte groups differ, in part relating to uptake of N through mycorrhizae or nitrogen fixation. These different sources affect the highly

variable quantity of epiphytes, often depending on the systematic group and canopy position.

Figure 68. *Senecio cooperi* , a species that produces aerial roots in wet epiphytes. Photo by Dick Culbert, through Creative Commons.

In Hawaii, the koa tree (*Acacia koa*; Figure 69) takes advantage of the bryophyte mats for moisture and other favorable conditions (Leary *et al*. 2004). The roots of this tree actually grow upward and form **nodules** (Figure 70) with the bacterium *Bradyrhizobium* (Figure 71) in pockets of organic soils within the canopy. These organic soils in the tree contain significantly higher levels of exchangeable cations and total nitrogen, and significantly lower aluminum levels than the ground soils. Some of these mats have significant bryophyte presence.

Figure 69. *Acacia koa*, Maui, Hawaii, a species that forms adventitious roots in moss clumps on the trunk. Photo by Forest and Kim Starr, through Creative Commons.

Figure 70. *Acacia koa* nodules in a bed of mosses. Photo courtesy of Leary *et al.* 2004.
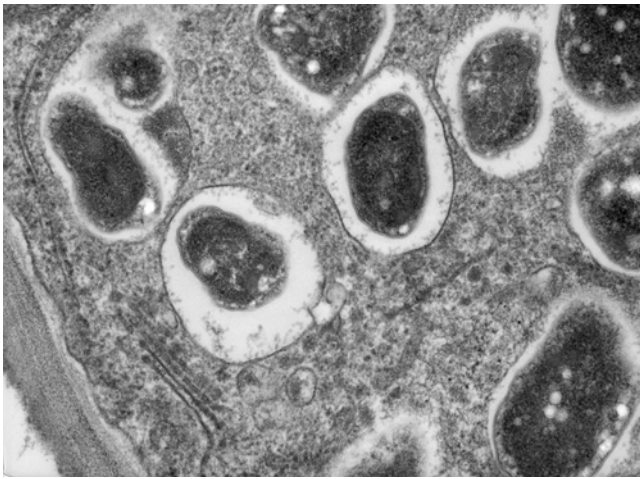

Figure 71. *Bradyrhizobium* from root nodule. Photo by Louisa Howard, through public domain.

Herwitz (1991) examined the aboveground adventitious roots of *Ceratopetalum virchowii* (see Figure 72) in an Australian montane tropical rainforest. These roots developed from stems and branches of this canopy species. In this case, Herwitz could find no evidence that this tree requires the epiphyte mats to stimulate its root growth. Instead, it appears that the stemflow of this species is particularly rich in Ca^{2+}, Mg^{2+}, and Na^+ compared to the soil. The bark of this species remains moist for a long period of time, providing a suitable environment for the adventitious root.

Productivity and Biomass

Studies on productivity in the tropics are rare. Jacobsen (1978) published one of the earliest studies. Most seem to be simply reports of standing crops. Several look at the effects of temperature on net carbon storage (see above under Microclimate).

Köhler *et al.* (2007) reported that bryophytes dominate the epiphytic vegetation in both an old-growth cloud forest and a 30-year-old secondary forest on slopes of the Cordillera in northern Costa Rica. The combined epiphyte biomass and canopy humus was 16,215 kg ha^{-1} in the old-growth forest and 1,035 kg ha^{-1} in the secondary forest.

Figure 72. *Ceratopetalum apetalum*; *C. virchowii* forms adventitious roots but shows no evidence of influence by epiphytic bryophyte mats. Photo by John Tann, through Creative Commons.

Van Dunne and Kappelle (1998) studied epiphytic bryophytes on five small stems of *Quercus copeyensis* (Figure 57) in a Costa Rican montane cloud forest (Figure 73). They found 22 species of mosses and 22 species of liverworts. Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass. Nearly 90% of the biomass is contributed by only 14% of the species, with the predominant contributors being the mosses *Pilotrichella flexilis* (Figure 10), *Rigodium* sp. (Figure 74), *Porotrichodendron superbum* (Figure 75), *Prionodon densus* (Figure 76), *Neckera chilensis* (see Figure 77), and the leafy liverwort *Plagiochila* (Figure 78).

Figure 73. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

Figure 74. ***Rigodium pseudo-thuidium***, in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.

Figure 75. ***Porotrichodendron superbum*** with capsules, a species that is a major biomass contributor to Costa Rican epiphytes. Photo Paris Cryptogamic Herbarium, through Creative Commons.

Figure 76. ***Prionodon densus***, a major biomass contributor to Costa Rican epiphytes. Photo by E. Lavocat Bernard, with permission.

Figure 77. ***Neckera scabridens***; ***N. chilensis*** is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.

Figure 78. ***Plagiochila*** sp., in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Jan-Peter Frahm, with permission.

Frahm (1987) raised the question of how altitude affected the biomass and productivity of epiphytes in the tropics. Researchers had typically assumed that it related to greater light and lower temperatures at higher altitudes, permitting greater photosynthesis, but no physiological studies had been used to support this hypothesis. In his study, he used a transect with sampling at 200-m intervals from 200 to 3,200 m asl in Peru. He determined biomass in the field and measured CO_2 gas exchange in a series of light and temperature combinations in the lab. The lab experiments used specimens from 2,300 m asl collected in Colombia in October. These were 150 cm^2 specimens of the mosses *Neckera* sp. (Figure 77), ***Heterophyllium affine*** (Figure 79), ***Porotrichum*** sp. (Figure 80), and the liverwort ***Metzgeria*** (Figure 81). These experiments support the

hypothesis that it is a combination of high temperatures and low light that limits most of these tropical bryophytes at lower elevations. They are unable to store enough carbon in the low light to balance that lost to respiration at the high temperatures of the lowland forest. This is supported by experiments with temperature on the moss *Plagiomnium rhynchophorum* (Figure 82-Figure 83), but unfortunately, no methods were provided.

Figure 79. *Heterophyllium affine*, a species in which high temperatures and low light limits these tropical bryophytes. Photo by Blanka Shaw, with permission.

Figure 80. *Porotrichum bigelovii*; a species in this genus has high temperature and low light limits in tropical habitats. Photo by Ken-ichi Ueda, with online permission.

Figure 81. *Metzgeria*, a genus that has high temperature and low light limits in tropical habitats. Photo by Michael Lüth, with permission.

Figure 82. *Plagiomnium rhynchophorum* with capsules, a mostly Asian tropical moss that has no net photosynthetic gain at 25ºC and above. Photo by Germaine A. Parada, through Creative Commons.
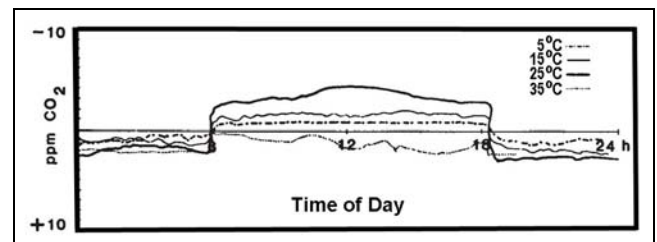

Figure 83. Photosynthesis of *Plagiomnium rhynchophorum* (Figure 82) under various temperature conditions at 1500 lux. The montane forest conditions of 5° and 15°C yield sufficient net photosynthesis; the lowland condition of 25°C permits photosynthesis throughout the day but no net photosynthetic gain. At 35°C no net photosynthesis occurs during the day. Graph modified from Frahm 2003b.

Wolf (1993b) found that altitude explains most of the variation in the epiphytic bryophytes and lichens on selected bark types of canopy trees, using 15 sites on an altitudinal transect from 1,000 to 4,130 m asl in the Central Cordillera of Colombia (Figure 84). Species richness varies among the three groups (mosses, liverworts, and lichens). Liverworts reach their greatest species richness (ca 100 taxa) at mid-elevational sites (2,550-3,190 m asl). In this case, biomass of bryophytes and lichens increases with altitude, coinciding with an increase in humidity.

Figure 84. Cordillera in central Colombia. Photo by Samual Rengifo, through Creative Commons.

Hofstede *et al.* (1993) examined the relationship between the epiphytic biomass and the nutrient status in a Colombian upper montane forest near the treeline at 3,700 m asl with a massive presence of epiphytes. The amount of accumulated epiphytic mass, suspended soil, and living plants on a full-grown tree was 32.7 g dry weight per dm^2 surface area, the highest documented value ever. This high value is attributed to a combination of low temperatures, high humidity, low wind velocities, and structural characteristics of the tree.

Müller and Frahm (1998) sampled epiphytic bryophytes in a montane rainforest in the Andes of Ecuador at about 2,000 m asl. They measured the dry weight on various parts of the trees and found that on trunks it was 80 g m^{-2}, on branches 1,873 g m^{-2}, and on twigs 1,230 g m^{-2}.

Clark *et al.* (1998a) conducted one of the few studies on retention of carbon by the tropical epiphytic bryophytes. They found an annual net accumulation of carbon to be approximately 37-64 g C m^{-2} yr^{-1} in their study in a tropical montane forest in Monteverde, Costa Rica. Net production of epiphytic bryophytes in the forest was 122-203 g m^{-2} yr^{-1}.

In the upper montane forest of the Rwenzori Mountains of Uganda, Pentecost (1998) found that large cushion-forming liverworts are dominant in the lower canopy. These are predominately *Chandonanthus* (Figure 85), *Herbertus* (Figure 86-Figure 87), and *Plagiochila* (Figure 88) species. Their productivity is controlled by light intensity and substrate tree age. In total, he found 14 species of bryophytic epiphytes. The total epiphytic biomass, including bryophytes, lichens, and algae, contribute nearly 1 ton ha^{-1} standing crop, a figure that is approximately 10% of the above-ground standing crop.

Figure 86. *Herbertus aduncus* in BC, showing large "muffs" around branches. This genus forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Botany Website, UBC, with permission.

Figure 87. *Herbertus aduncus* showing dense cushions formed by this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo from Botany Website, UBC, with permission.

Figure 85. *Chandonanthus birmensis*, in a genus that forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Manju Nair, through Creative Commons.

Figure 88. *Plagiochila cristata* showing dense cushions like those formed by other members of this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Michael Lüth, with permission.

Lösch *et al.* (1994) describe differences in environmental conditions and photosynthetic rates for bryophytes in a rainforest (800 m asl), a bamboo forest, and a tree-heath (2,200-3,200 m asl) in east central Africa. In the lowland rainforest, the climatic conditions are a nearly constant 24°C, 100% relative humidity, and PAR below 100 µmol photons m^{-2} sec^{-1}. The mountain bryophytes exhibit approximately 6 times those daily sums of PAR while experiencing temperatures of 10-25°C and relative humidities of 60-100%. In the bamboo forest, the epiphytic mosses experience water loss down to less than 70% of their water content, but become saturated again from the vapor-saturated air at night. In these habitats, the photosynthesis peaks between 22 and 30ºC. The lowland species exhibit higher optima than do those of the mountain sites. The light saturation points for all species are below 400 µmol photons m^{-2} s^{-1}, but the slopes differ. Those bryophytes from the lowland have a smaller light compensation point (3-12 µmol photons m^{-2} s^{-1}), accompanied by a steeper slope in the low-light range. In the highland, the compensation point is 8-20 µmol photons m^{-2} s^{-1}.

Waite and Sack (2010) considered the relationship of moss photosynthesis to leaf and canopy structure. These include ground-dwelling species as well as branch and trunk dwellers: *Acroporium fuscoflavum* (Figure 89), *Campylopus hawaiicus* (Figure 90), *Distichophyllum freycinetii* (Figure 91), *Fissidens pacificus* (Figure 92), *Holomitrium seticalycinum* (see Figure 93), *Hookeria acutifolia* (Figure 94), *Leucobryum* cf. *seemannii* (Figure 95), *Macromitrium microstomum* (Figure 96), *M. piliferum* (Figure 97), and *Pyrrhobryum pungens* (see Figure 98) (all mosses). Interestingly, they did not find any correlation between light saturation for photosynthesis and habitat irradiance. The bryophytes have low leaf mass per area and a low gas exchange rate. The nitrogen concentration, as well as A_{mass}, (maximum assimilation per unit leaf mass) has a negative correlation with the canopy mass per area. *Campylopus pyriformis* (Figure 99) exhibits a high A_{max} (maximum assimilation) that could be the result of its high leaf area index. Anatomical factors such as smaller cells, thicker cell walls, or physiological adaptations such as higher osmotic adjustment could lower the potential for a higher A_{max} in sun mosses.

Figure 90. *Campylopus hawaiicus*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 91. *Distichophyllum freycinetii*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by John Game, through Creative Commons.

Figure 89. *Acroporium fuscoflavum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 92. *Fissidens pacificus*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 93. *Holomitrium trichopodum*; *Holomitrium seticalycinum* is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.

Figure 94. *Hookeria acutifolia*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.

Figure 95. *Leucobryum seemannii*, a moss for which is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.
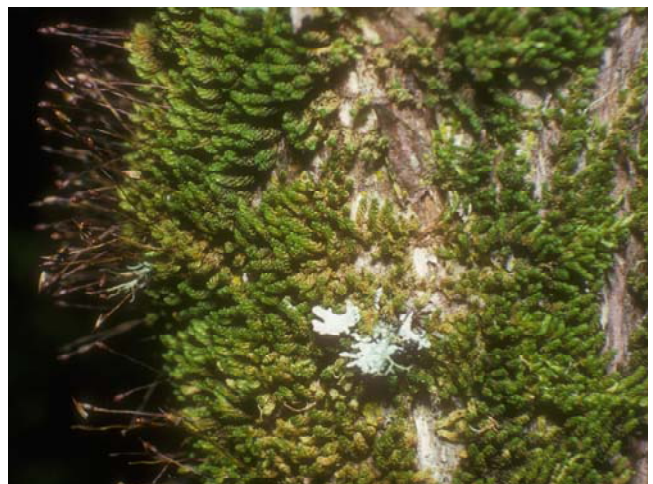

Figure 96. *Macromitrium microstomum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Janice Glime.

Figure 97. *Macromitrium piliferum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 98. *Pyrrhobryum* sp.; *Pyrrhobryum pungens* is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.

Figure 99. *Campylopus pyriformis*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.

Epiphyte Litterfall

Both bryophyte and tracheophyte litter can fall from the trees, especially during severe storms. This is a loss of canopy productivity, but provides a new source of nutrients for the soil, and in some cases these plants may continue growth on the ground.

Matelson *et al*. (1993) considered the rate of nutrient release from bryophytic and other epiphytic litter fall. They determined that it varies with microhabitat and suggested that both spatial and temporal distribution should be studied at the species level as they relate to microhabitat characteristics.

Köhler (2002) investigated total epiphytes in 10-15-year-old early secondary forest, a 40-year-old later-stage secondary forest, and an old-growth (primary) forest in Costa Rican mountain rainforests. Succession resulted in an increase in epiphytic litterfall. They estimated 4.8 g m^{-2} in early secondary forests (160 kg ha^{-1} at stand level), 12.0 g m^{-2} in later secondary forest (520 kg ha^{-1} at stand level), and 78.5 g m^{-2} in the old-growth forest (3400 kg ha^{-1} at stand level). Nevertheless, epiphytes constitute only a small part of the litter.

In a Neotropical cloud forest in Monteverde (Figure 100), Costa Rica, Nadkarni and Matelson (1992) found that epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter at that site. This litterfall contributes to the nutrients of the forest, with measurements (in kg ha^{-1} yr^{-1}) of N (7.5), P (0.5), Ca (4.2), Mg (0.8), and K (0.1). These epiphytic litter components have a higher annual rate than does the litter from plants rooted in the ground. On the other hand, the turnover time of all nutrients except potassium is 4-6 times slower in the fallen epiphytic litter. Potassium turnover is ten times as fast. In a later study, Nadkarni (2000) determined that epiphyte litterfall in a lower montane cloud forest in Monteverde, Costa Rica, occurs at a rate of 50 g dry wt m^{-2} yr^{-1}. This slow turnover of most bryophyte litter is most likely due to the high phenolic content that protects the bryophytes from herbivory and attack by fungi and bacteria.

When branches make contact with each other, by wind or storm, the impact can cause tiny branches at the tips to break, a phenomenon known as **crown shyness** (Figure 101) (Franco 1986). This can occur between the same species of tree, or among different species. The exact cause is not clearly known, but at least in some cases it appears that it is the result of **reciprocal pruning** as trees contact each other. It appears that lateral branch growth is usually not influenced by the neighbors until such mechanical abrasions occur. One such tree is *Clusia alata* (Figure 65). This branch breakage can cause any adhering bryophytes to lost from the canopy as the branch tips fall away.

Figure 100. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

Figure 101. Crown shyness in Buenos Aires, Argentina; branches break when they contact in wind events. Refractor, through Creative Commons.

Summary

Bryophytes in the tropics, particularly epiphytes, undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. They are adapted by their life forms and physiology to withstand desiccation. **Anhydrobiosis** and **osmotic potential** are typically used as means of surviving dry periods. Dry areas typically have **mats**; in areas with high humidity these are replaced by **fans**, **wefts**, and **pendants** that are able to obtain water from fog and mist (**fog-stripping**). Many are **perennial stayers** or **perennial shuttle** species.

Species of highly exposed locations have higher light saturation and compensation points, higher dark respiration rates, more chlorophyll, higher chlorophyll *a:b* ratios, and higher N concentrations than those of shade species. Some are able to retain water and nutrients in **hyaline** cells that hold water and surround photosynthetic cells. But most lose water easily and survive by their ability to recover quickly from desiccation, without the need to make new chlorophyll.

Substrate, temperature, light, and moisture availability are the microclimate variables that drive the community structure of epiphytic bryophytes. Their biggest physiological problem is the need to store more carbon than they lose to respiration.

Nutrients are obtained from the atmosphere, rain, and the bark and collected on the bryophyte surface until it becomes moist and can absorb them. Hence, nutrients in the bryophytes increase from the dry season to the wet season. **Cyanobacteria** living in the microenvironment of the bryophytes contribute to the usable nitrogen of the ecosystem. The ability of the bryophytes to leak nutrients but retain them on their surfaces permits external nutrient storage until rainfall returns, but releases them to the ecosystem as heavy rains carry them away. Light rains and fog permit the bryophytes to hydrate and absorb the nutrients. This makes the epiphytic bryophytes a keystone resource for the forest. These nutrient-rich, wet bryophytes furthermore provide a suitable substrate for canopy roots for some species.

Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass at higher elevations. Biomass increases with altitude, coinciding with an increase in humidity. At lower elevations, the combination of high temperatures and low light severely limit bryophyte productivity. Epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter in the cloud forests and only a small amount in the lowland forest. Whereas leaf litter decays rapidly in the tropics, bryophyte litter is slow to decay due to its many phenolic compounds that inhibit insects, bacteria, and fungi.

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