

Chapter 23

Nonvascular Epiphytes: Functions and Risks at the Tree Canopy

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1 Research on Nonvascular Epiphytes

In the frame of current discussions on the value of forest canopies, a short introduction and recent advances of nonvascular epiphyte (NVE) research are presented here regarding a novel canopy access facility to study mechanisms and functions of carbon and water exchange as well as impacts of climate and land-use change on NVE.

Sometimes inconspicuous, but highly diverse and omnipresent in tree tops are microorganisms and nonvascular plants occupying plant surfaces (Lakatos 2011). The communities are composed of bacteria, fungi, cyanobacteria, lichens, algae, and bryophytes in variable proportions. The first four groups are generally categorized as microbes, whereas the latter are regarded as cryptogams and often subsumed as nonvascular epiphytes (NVE) due to the dominance of photoautotrophic organisms and the lack of lignified vascular water conduction system. They cover almost every spot of bark (corticolous) and develop from thin green biofilms comprising mainly cyanobacteria, algae, and fungi with a thickness of less than one millimeter to well visible and colorful epiphytic cryptogamic crusts or mats of several centimeters, dominated by lichens and bryophytes (Fig. 23.1). Biofilms also occur as epiphylls on the surface of long-living and evergreen leaves in the phyllosphere (Coley et al. 1993; Furnkranz et al. 2008; Sonnleitner et al. 2009; Rigonato et al. 2012). As corticolous and epiphyllic photoautotrophic communities, they influence important ecological processes

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Fig. 23.1 Colorful lichen assemblage in the Mata Atlantica, Brazil (*left*), and canopy studies on bryophytes in the lowland cloud forest of French Guiana

such as carbon, nitrogen, and water cycles (reviewed: Rhoades 1995; Sillett and Antoine 2004; Elbert et al. 2012); represent a large pool of species diversity (e.g., Mandl et al. 2010; Sporn et al. 2010; Ellis 2012); and effect trophic cascades as a food resource and as hosts for microbes, protists, and invertebrates in the phytosphere and phyllosphere. Despite their omnipresence and numerous roles occupied in the canopy, researchers have focused on macroscopic vascular plants and animals, whereas the direct and indirect impacts of NVE remain relatively understudied.

Most investigations on NVE are restricted to the tree base or lower stem of trees although several studies indicate that this limitation may underestimate species diversity by 30 % (for lichens in temperate forests; John and Schröck 2001) or even 50 % (for bryophytes in tropical forests; Cornelissen and Gradstein 1990b; Wolf 1995; Costa 1999; Gradstein et al. 2001). In entire vertical assessments of NVE assemblages, fallen trees were often examined (Jarman and Kantvilas 1995; Fritz 2009). However, epiphytic surveys for cyanobacteria are scarce (12 species in the tropical lowland forest, Singapore, Neustupa and Škaloud 2010) as well as for green algae, which range between 20 species (temperate forest, Germany, Freystein et al. 2008) and 40 species (tropical: Neustupa and Škaloud 2010; Lemes-Da-Silva et al. 2010) mainly from the families of Chlorophyceae, Trebouxiophyceae, and Ulvophyceae. Diatoms are common as epiphytes on epiphytic lichens (18 species in the tropical *Coenogonium linkii*; Lakatos et al. 2004) and also on mosses (Foerster 1971). Lichen diversity ranges from 36 to 76 species and bryophyte diversity from 28 to 55 species in Australia (Jarman and Kantvilas 1995; Milne and Louwhoff 1999), but with values of 88–100 bryophyte species reported in tropical lowland forests of Guiana and French Guiana (Cornelissen and Gradstein 1990; Gradstein 1995) and 153–190 bryophyte species in tropical montane forests (Wolf 1993; Gradstein et al. 2001). One single tree (*Elaeocarpus*) in Papua New Guinea boasted 173 lichen species (Aptroot 1997). Such high species diversity is one of the reasons that most studies on NVE in the canopy occur in tropical canopies, using single rope techniques (e.g., Nadkarni 1984; Wolf 1995; Freiberg and Freiberg 2000;

Nadkarni et al. 2004; Holz and Gradstein 2005; Gehrig-Downie et al. 2011), walkways, aluminum towers (e.g., Zotz and Winter 1994), and construction cranes (e.g., Komposch and Hafellner 2000). These studies mainly documented species distribution, cover, and biomass of NVE. In temperate and boreal regions, several studies documented biomass and species distribution on canopies largely consisting of conifers (e.g., McCune et al. 1997; Clement and Shaw 1999; Ellyson and Sillett 2003; Williams and Sillett 2007). One constraint of canopy research is the limitation of noninvasive accessibility that permits studying organisms in their natural undisturbed environment. This might explain why ecophysiological and long-term studies on NVE in the canopy are infrequent (but see Renhorn et al. 1997; Zotz and Schleicher 2003; Zotz et al. 2003; Antoine 2004; Lakatos et al. 2006; Romero et al. 2006; Gauslaa et al. 2012; Pardow and Lakatos 2013).

2 The “Biosphere Tower”: A Novel Canopy Access for Long-Term Research on Microbes and Nonvascular Epiphytes

One critical issue of investigations on microbes and NVE is that most canopy access methods are invasive and harm the ensembles of bark-dwelling (corticolous) organisms, particularly for long-term studies that require repeated access. To reduce the destructive impact of access, a new canopy tower was developed to conduct long-term studies. The “Biosphere Tower” (Fig. 23.2) is a wooden canopy access



Fig. 23.2 A novel canopy access: the wooden 36 m tall Biosphere Tower – the Biosphere Reserve Palatinate Forest–Northern Vosges, Germany

tower with mobile cantilevers, installed in a representative old-growth (170 years) and commercial oak forest in the Biosphere Reserve Palatinate Forest–Northern Vosges, Germany. The construction has a basal area of 3×3 m plus 6 platforms each ascending 6 m reaching a total height of 36 m. The structure surmounts the treetops and the cantilevers of 5–10 m in length reach each strata of adjacent oaks (*Quercus robur*) and beeches (*Fagus sylvatica*), which comprise economically the two most important broadleaf tree species in Europe. To emphasize abiotic canopy processes, a micrometeorological monitoring system was installed at the ground level, and both within and above the canopy, providing continuous measurements of abiotic conditions (e.g., light, temperature, humidity, turbulences), including UV and global radiation. All impregnation of the wood was avoided, because volatile substances may affect the target organisms of the epiphytic community. This interdisciplinary project is a partnership of the University of Kaiserslautern (Departments of Plant Ecology and Systematics, and Architecture), the Kaiserslautern forestry office, and the Rhineland-Palatinate Foundation for Innovation.

The Biosphere Tower facilitates long-term research on forest canopy biodiversity, ecology, and global climate change with the focus on microbial ecosystems. NVE are not often studied in silvicultural forests, despite their economic importance for wood production and water balance. Moreover, noninvasive long-term canopy research offers new insights into seasonality, succession, and long-term changes. Owing to its innovative design (renewable primary products, low-invasive construction method, microbial canopy research), the Tower will expand the novel field of microbial canopy ecology, promote ecologically and economically relevant long-term-research in the “silvicultural canopy biosphere,” and provide an attractive platform for environmental education.

3 Mechanisms and Functions of Nonvascular Epiphytes

The mechanisms and ecological impacts of NVE are still poorly understood (Cornelissen et al. 2007). In some ecosystems, they contribute a substantial proportion to primary production (Rhoades 1995; Lakatos 2011; Elbert et al. 2012), influence nutrient fluxes (Forman 1975; Knops et al. 1996; Sillett and Antoine 2004; Clark et al. 2005), and promote animal life (Pettersson et al. 1995; Richardson et al. 2000; van der Wal 2006). Two main aspects involved in understanding the NVE mechanisms and functions are the exchange of carbon and water.

Carbon exchange of NVE is closely bound with water availability. NVE are desiccation-tolerant organisms suspending metabolism when dry and recover after hydration by liquid water or high humidity (Proctor and Tuba 2002). They are capable of efficiently exploiting several liquid water sources such as rain, fog, and dew which are absorbed by their whole “plant” surface to activate metabolism and photosynthesis. This independence on permanent water supply enables them to photosynthesize and grow at sites inhospitable for vascular plants. Given NVEs’ poikilohydric strategy, they successfully inhabit almost all terrestrial habitats from the tropics to cold and hot deserts.

The success of their poikilohydric was catalogued by biomass distribution and by their role in ecosystem carbon fluxes. In general, a clear pattern of biomass distribution occurs in tropical forests: biomass increases with altitude ranging from 10 gm^{-2} (relative to branch surface area) at lowland forests to almost $3,000 \text{ gm}^{-2}$ of bryophytes in upper montane forests at 3,700 m a.s.l. (Hofstede et al. 1993; Freiberg and Freiberg 2000). In contrast, the biomass of vascular epiphytes (usually between 400 and 900 gm^{-2}) seems not to increase with altitude (Freiberg and Freiberg 2000). Also, patterns of biomass distribution change within the tree – the biomass of NVE (dominated by bryophytes) decreases from the branches of the inner crown to the periphery of the canopy (Freiberg and Freiberg 2000; Romanski et al. 2011), whereas lichens and biofilms increase (Werner et al. 2012; M. Lakatos unpublished data). On a regional level, local studies revealed maximal NVE biomass of around $2,000$ – $16,000 \text{ kgha}^{-1}$ relative to ground surface area in tropical montane forests (Coxson et al. 1992; Köhler et al. 2007; Werner et al. 2012) compared to boreal and coastal forests where NVE biomass of up to $4,220 \text{ kgha}^{-1}$ was reported (Rhoades 1981). On an ecosystem level, calculated NVE biomass per biome was calculated to range from 470 to $2,120 \text{ kgha}^{-1}$ relative to ground surface area (Elbert et al. 2012). A global extrapolation of NVE approximates $\sim 3.1 \text{ Pg}$ (1.4 – 6.5 Pg) dry biomass on the basis of an global epiphytic area of $30.57 \times 10^{12} \text{ m}^2$ (Friedl et al. 2002). The calculated carbon uptake fluxes of NVE range from $5.8 \text{ gm}^{-2} \text{ year}^{-1}$ in extratropical forests to $10 \text{ gm}^{-2} \text{ year}^{-1}$ in tropical forests and correspond to an annual carbon net uptake of 0.45 – 0.95 Pgyr^{-1} (Elbert et al. 2012). In an ecosystem comparison, the total global carbon net uptake for NVE of 1.4 Pgyr^{-1} would be in the same range as that for tundra (1.83 Pgyr^{-1}) and desert ecosystem (1.72 Pgyr^{-1}) (Cleveland et al. 1999), accounting for 2.5% of the total net primary production of terrestrial vegetation (56 Pgyr^{-1} ; Zhao et al. 2005). By these rough calculations, NVE could compensate for almost half of the global annual carbon release from biomass burning (3.6 Pgyr^{-1}). Although these calculations are based on very few data, the function of NVE as part of global carbon fluxes nevertheless has been underestimated until now.

The contribution of NVE to the hydrological cycle is also often overlooked (Hölscher et al. 2004; Köhler et al. 2007). Poikilohydric NVE exploit nearly every available water sources and absorb rain, fog, dew, and vapor over their entire “plant” surface to activate metabolism and photosynthesis. Many lichens and bryophytes significantly alter water contents (WC) by as much as 250 – 400% of dry weight (DW) in green algal lichens (Blum 1973; Rundel 1988), 600 – $2,000 \%$ DW in cyanolichens (Lange et al. 1993), and $2,500 \%$ DW in bryophytes (Proctor et al. 1998). Optimal photosynthetic capacity is achieved between full turgor and turgor loss of the cells, varying between life-forms and species from 100% to $2,000 \%$ DW (e.g., Proctor et al. 1998; Hajek and Beckett 2008). During desiccation, photosynthesis decreases until cessation is reached at low water potential (-22 MPa) with a critical water content of 30 – 70% DW for bryophytes or even down at -38 MPa for lichens (Nash III et al. 1990) where WC ranges between 10% and 20% DW. For the reactivation of photosynthesis, green algae (Edlich 1936; Bertsch 1966) and green algal lichens require only relative humidity between 75% and 85% RH, corresponding to water potential of -37 to -22 MPa (Lakatos 2011). In contrast,

it was assumed that cyanobacteria (Lange et al. 1994) and bryophytes need liquid water for photosynthetic reactivation (Green et al. 1994). However, recent studies on bryophytes demonstrated for almost all investigated tropical mosses and liverworts the recovery of PSII already at around 85 % relative humidity (RH) (-22 MPa; Pardow and Lakatos 2013). The exchange of vapor with the organism occurs quite fast in NVE. Equilibration experiments during desiccation at 60 % RH and traced by the stable isotope ^{18}O demonstrated total exchange of thallus water with vapor within only 2 h for the fruticose *Usnea filipendula* and within 3–4 h for other lichen growth forms (Hartard et al. 2009). In comparison, the epiphytic vascular plant *Tillandsia usneoides* needed days for total equilibrium and only under RH above 95 % (Helliker and Griffiths 2007). Due to this rapid equilibration, lichens and other NVE may serve as prospective long-term proxies for water sources (Hartard et al. 2009). Moreover, their use as indicators for relative humidity and precipitation is important (Pardow et al. 2010; Obregon et al. 2011; Karger et al. 2012; Pardow and Lakatos 2013). The exploitation of vapor as a water source has several advantages: (i) the loss of CO_2 by respiration can be compensated to some degree; (ii) when liquid water becomes available, total recovery of metabolism happens faster; and (iii) some organisms perform photosynthesis with increasing efficiency at equilibrium with vapor because the absorption of liquid water reduces CO_2 diffusion and leads to higher respiration rates of the fungal partner (Pintado and Sancho 2002). Besides vapor, recent insights indicate that dew is another important water source. In particular, NVE tightly attached to the bark benefit from dew condensation on the tree surface supplying up to $0.7 \text{ mm H}_2\text{O day}^{-1}$ or $c. 176 \text{ mm year}^{-1}$ (Lakatos et al. 2012). This is comparable with dew rates in the midlatitudes of $c. 0.5 \text{ mm per 10-h night}$ (Jacobs et al. 2008) and much more than stem water flow calculated for this area of $c. 19 \text{ mm year}^{-1}$ (Jetten 1996). Due to delayed radiative loss and heat storage of the tree stem, dew formation occurs on stem and NVE surfaces until midday. This novel phenomenon was studied recently in the perhumid tropics and predicted to occur worldwide in forests (Lakatos et al. 2012).

Both water exchange processes and biomass in NVE impacts the hydrology not only in tropical forests but also in boreal, temperate, and coastal (rain) forests. Water (as rain, fog, or dew) is intercepted by the entire tree canopy (made up of foliage, stem, branches, and epiphytes) and slowly drops or flows to the ground (stem flow and throughfall), where it is absorbed, retained, and evaporated by the NVE. In tropical ecosystems, 273 and 724 mm year^{-1} are intercepted by canopy epiphytes in a submontane and in a cloud forest of Tanzania, representing 10 % and 18 % of annual precipitation (Pocs 1980, 1982). Even 34 % annual interception rates were maintained by NVE in a submontane rain forest of Uganda (Hopkins 1960). The absorbed amount ranges from 2 % to 61 % of the total precipitation at the Central Cordillera of Panamá (Cavelier et al. 1996) and from 10 % to 93 % in elfin cloud forests of Venezuela and Colombia (Cavelier and Goldstein 1989). The equivalent of approximately 0.5 mm of cloud water droplets may be sufficient to recharge the water-holding capacity of green algal lichens and pendent mosses (Leon-Vargas et al. 2006). NVE can absorb twice to twentyfold of their dry weight (or fourfold to fivefold as community ensemble; Pocs 1982; Hölscher et al. 2004), providing an

essential “canopy water pool.” In the temperate forest of Germany, a single 200-year-old oak tree (*Quercus robur*) harbored 8–25 kg of NVE dry biomass that retained 100–400 l of intercepted water; in the tropical mountain forest, this amount could be at least one magnitude higher. Thus, NVE function as “capacitors” influencing the discharge of precipitation, thereby ameliorating erosion and floods as well as water storage (Still et al. 1999; Weathers 1999). Intercepted water is discharged by NVE long after precipitation has stopped and contributes to high humidity within the canopy and understory (e.g. Perry 1984; Veneklaas et al. 1990). For example, epiphytic bryophytes in a Costa Rican montane cloud forest evaporated up to 2.5-fold of their dry weight biomass in 3 days, exceeding evaporation of canopy humus (Köhler et al. 2007). The direct ecological influence of this humidity input on stomatal opening of canopy leaves and thereby photosynthesis and transpiration in forests remains unknown.

The mechanism and function of NVE significantly contribute to canopy ecology, especially micro- and meso-fluxes of carbon and water. Ecophysiological studies of NVE, nonetheless, will likely reveal that secrets and surprises still remain to be discovered in the frontier of forest canopies.

4 Risks of Land-Use Change and Global Warming

Climate change is altering the amount and distribution of precipitation and cloud water in many forests (Still et al. 1999; Solomon et al. 2007). Further impacts of global change promote ongoing deforestation, fragmentation, and forest disturbance (Sala et al. 2000). These processes affect microhabitats of remaining forest patches and trees by increasing penetration of light and wind (Murcia 1995; Laurance and Williamson 2001; Pohlman et al. 2007). As a consequence, microhabitats in forest canopies are becoming progressively drier, with moist, shaded microhabitats confined to lower parts of the tree and interior of forest patches. Epiphytes are sensitive to these environmental changes since they live at the interface between the terrestrial and atmospheric environment (Benzing 1998).

Changes in NVE communities are expected to be most pronounced in areas of high moisture availability (Zotz and Bader 2009), where organisms are poorly adapted to droughts. Sensitive species will respond to increasing dryness by migrating to moister microhabitats further down the tree (Acebey et al. 2003; Alvarenga et al. 2010; Gradstein and Sporn 2010) or shifting to higher altitudes (Nadkarni and Solano 2002; Zotz and Bader 2009). In an undisturbed evergreen lowland moist rain forest in French Guiana, desiccation tolerance of bryophytes indicated that one-third of the canopy species would not tolerate extended drought periods and are expected to migrate to more humid understory microhabitats (Pardow & Lakatos 2013). Species from the understory are regarded as particularly vulnerable to forest disturbance since they have no refugia to migrate into (Gradstein 1992) and are highly desiccation sensitive (Pardow and Lakatos 2013). Zotz and Bader (2009) predict that an increase in temperature in tropical lowland

forests by only a few degrees Celsius would increase metabolism and nocturnal respiration rates of epiphytic bryophytes and lichens to such a degree that compensation by photosynthesis during the day is highly challenged and the risk of mass extinctions in this habitat quite likely.

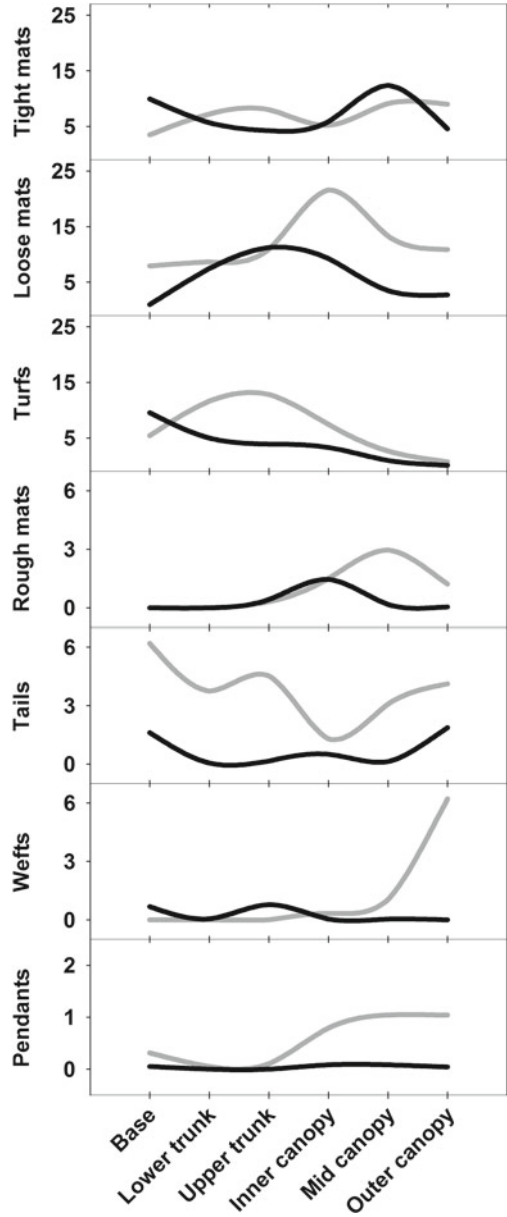
Rising temperatures, on the other hand, can also have a positive effect on species distribution by extending the range of suitable habitats. Ranges of subtropical epiphytic lichens and Atlantic and Mediterranean bryophytes, for example, are currently expanding as they migrate towards Central Europe (Frahm 2001; Aptroot and van Herk 2007).

In sum, NVE are sensitive to environmental change and apparently respond by migrating to more suitable microhabitats within the tree or along elevational gradients where possible. While the change in NVE communities and potential loss of biodiversity are documented (Aptroot and van Herk 2007; Zotz and Bader 2009; Tuba et al. 2011), less attention is given to functional consequences of these changes. There is yet little understanding of how NVE contribute to functional diversity and resource provision in forest canopies. For example, can NVE influence host tree health and pathogen defense through secondary compounds? Will changes in NVE affect the abiotic and biotic canopy environment? Figure 23.3 shows how small-scale differences in moisture supply affect the functional diversity of epiphytic bryophytes in a tropical lowland forest (Pardow et al. 2012). The distribution of seven life-forms is shown across microhabitats within the tree for two adjacent forests, tropical lowland rain forest and tropical lowland cloud forest (Gradstein et al. 2010). These forests share the same meso-climate and differ only in small-scale moisture supply (i.e., cloud forests have frequent early morning fog events (Obregon et al. 2011)). If this represents a model scenario of drier environmental conditions transitioning from lowland cloud forest to lowland rain forest, then life-form composition will change, particularly in the canopy strata. Some life-forms will disappear or respond by migration to lower – more humid – microhabitats. This leads to a loss of biocomplexity in strata of drier canopies by harboring fewer and less structurally diverse life-forms (mainly mats). The loss of certain “bryophyte structures” is likely to correlate with a loss of certain microhabitats and other resources confined to a particular life-form. Future research should be directed towards the ecological impact of these changes in functional diversity. The newly designed Biosphere Tower is ideal for noninvasive studies of the NVE community with respect to climate change.

5 Conclusion

This overview of recent outcomes in canopy research on NVE shows knowledge gaps on three topics: (i) for the most part, long-term investigations on seasonality, succession, and long-term changes are missing, (ii) the research in silvicultural tree canopies is underrepresented, and (iii) ecological and physiological measurements *in situ* are scarce. The consequences of climate and land-use change for NVE and thereby their influence on forest structural diversity, interactions, and carbon and water balance remain unknown.

Fig. 23.3 Percent cover of bryophyte life-forms at each height zone in a lowland cloud forest (*gray line*) and lowland rain forest (*black line*) at French Guiana (Modified after Pardo et al. 2012)



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