

The Plymouth Student Scientist, 2012, 5, (1), 253-268

Epiphytes: a study of the history of forest canopy research

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Abstract

The development of new and more versatile access techniques is a major contributor to the continuously growing field of canopy research. Methods such as cranes, canopy walkways, hot-air balloons, ladders and rope access techniques enabled scientist for the first time to conduct proximate studies of canopy organisms. One of the most studied groups of canopy dwellers are epiphytes. With their versatile adaptations to a life above ground level and their vast abundance, epiphytes contribute profoundly to the forest diversity and ecosystem processes. Most epiphytes have species-specific habitat preference within individual phorophytes. However these preferences are limited by biotic and abiotic factors. As a result epiphytes are threatened by forest degradation and climate change. More research is necessary to assess their importance within and between ecosystems and their role in direct and indirect forest processes. Furthermore future research on epiphytic plants needs to focus more on biotic interactions such as herbivory, pathogens and competition.

Introduction

“Overhead, at a height, perhaps, of a hundred feet, is an almost unbroken canopy of foliage formed by the meeting together of these great trees and their interlacing branches; and this canopy is usually so dense that but an indistinct glimmer of the sky is to be seen, and even the intense tropical sunlight only penetrates to the ground subdued and broken up into scattered fragments... it is a world in which man seems an intruder, and where he feels overwhelmed.”

Alfred R. Wallace

(1878)

Canopy biology is one of the most challenging, unexplored and fascinating of all sciences. Since the end of the 80s the endeavour into this challenging environment has been accompanied by more advanced access techniques, an area of increasing interest to scientists and the wider public and the development of new, more comprehensive and standardized sampling techniques (Lowman and Rinker, 2004; Houle et al., 2004). Because of the logistical difficulties of reaching the canopy (Barker and Pinard, 2001), scientists have previously eluded the exploration of these majestic tree crowns. Most early observations were ground based and primarily descriptive in scope using binoculars and dislodged branches to assess this infinite diversity above ground level (Sutton, 2001). In some cases animals such as monkeys were trained to climb up into the canopy to collect epiphytes such as orchids (Nadkarni, 1994). With a progressive change in direction over the last 30 years, away from a descriptive autecology of individuals towards a more descriptive and complex ecosystem approach, canopy scientists had to develop new means of accessing the canopy (Lowman and Wittman, 1996). The following review is going to examine some of the difficulties of modern canopy exploration, with a particular focus on epiphyte distribution and abundances in tree canopies.

History and development of canopy access techniques

The development of different and versatile canopy access techniques provided scientist for the first time with tools to explore this unknown frontier. Wilson (1991) called it “The Last Frontier” of biological research. In 1929 W.R. Hingston (Hingston, 1932) set up the first observation platform in Moraballi Creek in British Guiana. The platform was used to hoist baited muslin traps for birds, small mammals and insects. However the data was never published and only received little attention in scientific literature. During the Second World War canopy science almost came to a standstill (Sutton, 2001). However, in the 1950s Haddow et al. (1961) studied several orders of insects such as *Ephemeroptera* and *Odonata* from a temporary installed tower in Mpanga forest, Uganda. Haddow’s tower construction however, was spatial and temporal limited. This is because only certain parts of the canopy could be sampled and the sampling was mostly limited to only one or two trees within a stand. Nevertheless, Haddow’s (1961) and later Cachan’s (1964)

canopy studies encouraged the development of new access techniques in the following century.

During the 1970s and 1980s SRT (Single Rope Techniques) were developed (Perry, 1978; Perry and Williams, 1981; see also Appanah and Chan, 1981). These techniques combine rock and cave climbing elements and were easy to use, low in costs and light. SRT access enabled the scientists for the first time to explore the interior of the canopy (*Picture 1&2*). However access to the outer branches of the canopy was still limited. This changed by the end of the 1970s, were several canopy walkways (*Picture 3*) and platforms (Lowman and Bouricius 1995) in Panama, Papua, New Guinea and Sulawesi (Indonesia) were established (Sutton, 2001). In the following years canopy cranes were used with the first one built in Panama in 1990 (Parker et al. 1992). Simultaneously with the development of canopy cranes Francis Hallé constructed a hot-air balloon called Radeau des Cimes (raft on the rooftop of the world). Attached to this 7500m³ airship was a 5mx5mx5m and 750kg heavy sled. The sled (or skimmer) provided the scientist with a working platform from which they were able to obtain samples from the upper canopy (Lowman 1993; 2009). For example in 1991 Rinker et al. (1995) studied insect herbivory in a lowland rainforest in Cameroon. The balloon was used to collect invertebrates using additional fogging and net swiping techniques. In the following years other sampling and access techniques were tested, such as ultra-light plains (Munn and Loiselle, 1995).



Picture 1&2: SRT enabled scientist for the first time to explore the interior of the canopy. *Picture 1 (left)*; Sam Arthur is collecting epiphyte data in Cornwall, England. *Picture 2 (right)* was taken during an epiphyte project in the Democratic Republic of Congo.



Picture 3: The Nyungwe canopy walkway in Rwanda was built by Greenheart Conservation Company Ltd. in 2010. The construction consists of three towers, three platforms and 165m of bridge connections.

In the past 10 years canopy access and the development of more advanced and safe techniques was stimulated by an increasing interest of recreational and public enthusiasts. Canopy science, education, conservation and ecotourism almost go now hand in hand (Lowman and Rinker, 2004). Rope techniques were further developed using arboriculture and mountaineering technology (CAL, 2008; 2010). Moreover, materials such as galvanized steel aircraft cable, clamps and turnbuckles, pressure treated wood and drop-forged aluminium replaced the more damaging materials previously used in permanent canopy structures (Lowman and Wittman, 1996). With the implementation of these new materials, technologies and methods the damage to the trees and their communities was reduced to a minimum. Furthermore using current methods and technologies such as rope techniques, construction cranes, balloons, canopy platforms, ladders and walkways enabled us to overcome the major logistic obstacles to access the canopy. However, with a worldwide decrease of “intact” forest systems to study, canopy scientists are facing a progressive dilemma. For example Mitchell (2001) predicted that of the prior available rainforest canopy only 5%-10% would remain intact by the end of this century.

Canopy epiphytes a current perspective

Plants in the canopy are one of the most widely studied of all canopy organisms (Lowman, 2001). Their sessile live-style enables scientists more effortless to conduct quantitative studies when compared to their mobile

counterparts. One of the most studied plant group are epiphytes. Epiphytes are vascular and non-vascular plants that live on other plants (i.e. phorophytes) such as trees for physical support; however they do not gain nutrient or water supply directly from the host (Kress, 1986). Epiphytes can be split into several distinctive groups i.e. according to (1) their timing during life cycle (holo- and hemi-epiphytes; holo-epiphytes live their whole life cycle as epiphytes, whereas hemi-epiphytes spend some of their life cycle as ground living plants), (2) their fidelity to bark (facultative, obligate and accidental epiphytes), (3) their light requirements (sun-, shade-tolerance), (4) their substrate exploitation preference (e.g. bole, twigs, branch) and (5) their nutritional mode (Benzing, 2004; Nieder et al., 2001). All groups are very divers and include families such as *Orchidaceae*, *Bromeliaceae*, *Ericaceae*, *Gesneriaceae*, *Melastomataceae*, *Peperomiaceae*, *Rubiaceae*, *Araceae* and *Cactaceae*. However, not only are epiphytes major contributor to the biomass and the alfa-, beta diversity of a forest (Hsu et al., 2002), they also provide a divers range of habitats and food resources for other organisms (Nadkarni and Matelson, 1989; Davidson, 1988; Fischer and Araujo, 1995) and regulate mineral (Pike, 1987) and nutrient cycling (Diaz et al. 2010).

Distribution, abundance and diversity

It has been estimated that 10% of all global plants are epiphytes and that in tropical countries epiphytes account for 25% of all vascular plant species (Kress, 1986; Nieder et al., 2001; Wolf and Flamenco-S, 2003). Their great diversity and their different adaptations to life in the canopy have enabled them to exploit a wide range of habitats including tropical and temperate woodlands, plantations and mangroves. However, the global accurate diversity pattern of epiphytes is still unknown. Biologists, who live in temperate zones for example, can observe a different level of bark exploitation by epiphytes than those who live in tropical regions. This dissimilarity in epiphytism has been confirmed between different countries (Møller and León-Yáñez, 1999; Boegner, 1999) and different groups of epiphytes (Galloway, 1992), with an increase in epiphyte diversity and abundance in tropical regions. For example Engwald (1999) found 66 species of holo-epiphytes on a single *Decussocarpus rospigliosii* tree in the Carbonera Forest in Venezuela. Whereas in Zambia, phorophytes might only host up to 14 species of holo-epiphytes (pers. obs.). Interestingly, epiphytism is not evenly distributed between plant families and epiphytic groups either. About 80% out of the 20000-25000 species of vascular epiphytes (Benzing, 1990) are represented by monocotyledons (Kress, 1989). Families and orders of ferns, angiosperms and gymnosperms represent the other 20%. Surprisingly the largest vascular plant families such as *Asteraceae*, *Fabaceae* and *Poaceae* display little or none epiphytic lifestyle (Benzing, 2004). On the other hand non-vascular groups such as bryophytes and lichens are less well studied. Moreover their global distribution, abundance and diversity have yet to be assessed. Galloway (1992) estimated the global total occurrence of lichens to 20000 species, while Zartman and Pharo (2007) calculated the total number of bryophytes to nearly 11000 species. Both estimations, however, entail all growth types of non-vascular plants including lithophytes, terrestrials and epiphytes. Vascular as well as non-vascular epiphytes are two very divers

groups, yet Wolf (1993) argued that in any given sample plot (e.g. Gentry and Dodson, 1987) non-vascular epiphytes would contribute substantially to the epiphytic diversity, and in some instances exceed the vascular epiphyte diversity and abundance.

Since the development of more advanced access techniques, particular attention has been devoted to epiphytic distribution patterns on individual phorophytes. It has been pointed out that the epiphytic distribution on a single tree can be highly heterogeneous at a temporal and spatial scale (Wolf, 2005). Because of their sensitive life-style, epiphytes had to adopt strategies to exploit moisture and nutrients from their highly localized environment. Rotting litter, ant wastes, dead invertebrates, rain, precipitation and solar radiation are one of the main sources epiphytes have to exploit to sustain life in this extraordinary dynamic and challenging system (Benzing, 2004). Most species of epiphytes have species-specific habitat preferences, with some being extremely limiting. For example, Zartman (2003) studied the inhabitation of "rare" bryophyte species on forest story leaves in small fragmented rainforest plots in Amazonia. Zartman (2003) reported that "rare" species of bryophytes on forest story leaves are actually very abundant in the outer branches of canopy trees. It has been suggested that a change in forest structure i.e. forest fragmentation might have altered the microenvironment for this species. The shift in habitat could be explained by high tree mortality, the opening up of the canopy and the resulting increase in solar radiation (Pharo and Zartman, 2007). This link between physiological properties and habitat preference in epiphytes has been studied extensively (Schmidt et al., 2001). However what are the most important factors determining epiphyte distribution, abundance and diversity in tree canopies?

Canopy geometry, Structural support and Nutrients

"Nothing in nature is homogeneous". Forest canopies in particular vary greatly in their appearance and character, with no structure being the same. Some of these architectural differences depend upon genetic predisposition (Bongers and Sterck, 1998) other are determined by local climatic and ecological conditions (Sterck et al., 2001). Organisms living in these inconsistent environments, however, have adapted to the conditions and the conflicting structural support.

Epiphytes are highly dependent on their host for physical support; their spatial and physical deduction from terrestrial resources constrains them in any means to a more dependent life-style. Bark texture, the instability of the substrate, nutrient availability of the suspended soil, atmospheric nutrient, litter fall, leaching, branch type and aspect can play key roles in their diversity, abundance and distribution (Marmor et al., 2010; O'Malley, 2009). In addition, it has become evident that the biomass, species richness and composition of some epiphytes change with height in the canopy (Johansson, 1974; Gauslaa et al., 2008; Fritz, 2009).

The bark in particular is a remarkably patchy environment. From the bottom of the bole all the way up to the top of the canopy, bark displays different degrees of heterogeneity (e.g. age of the bark, thickness and texture).

Epiphytes have to find ways to explore this mosaic of microhabitats within the canopy. However, it has been pointed out that bark water storage capacity, the chemical composition and the aptitude to secure mechanically roots and seeds changes with different species of phorophytes (Nicolai, 1986).

Nutrient availability might account for some of the tree-to-tree variation of epiphytes. Common sources for nutrients are the bark, rooting substrates, foliar leachate and atmospheric deposition (Mucunguzi, 2007; Lowman and Rinker, 2004). Hsu et al. (2002) studied epiphyte nutrients in a moist subtropical broadleaved forest in Taiwan. They found that the nutrient capital of epiphytes (N = 42.4, P = 1.9, Mg = 5.5, Na = 1.3, Ca = 14.5 and K = 28.9 (kg ha⁻¹)) was equivalent to 21-43% of the total nutrient capital of the whole ecosystem. This suggests that epiphytes are important contributor to the nutrient cycling in the forest canopy. Other studies found similar results. For instance, Mucunguzi (2007) established that two types of humus facilitate the survival of different canopy epiphytes. Orchids favoured the "light" humus, whereas ferns and herbaceous species preferred the "heavy" humus (for further details see Mucunguzi, 2007). He suggested that nutrients in the two soil types are one of the main contributors to the epiphyte diversity in Uganda. It has been pointed out that the N:P ratio of canopies can average 13, and is often higher than that of forest floors (Zotz and Hietz, 2001).

The dissimilarity between different epiphytic-nutritional modes is closely linked to the epiphytes environment. For example, phorophytes that grow on calcium rich soils have shown to be affected by an increase in bark pH, which in return encouraged cyanolichen establishment (Goward and Arsenault, 2000). These indirect nutrient supplies are very important contributor to the epiphyte diversity on individual phorophytes and they also contribute substantially to the nutrient cycling within and between ecosystems.

Light and Temperature

The light and temperature availability for epiphytes varies considerably between and within canopies. Epiphytes in the canopy are subjected to a wide range of exposure gradients. For example solar radiation in the outer canopy is more pronounced than in the interior of the crown. Théry (2001) pointed out that the outer branches are more exposed to drier, windier and sunnier conditions than branches further down the tree. Moreover, a change in canopy geometry (Endler, 1997) has an eminent effect not only on the light intensity but on the light quality too (Théry, 2001). Because species of epiphytes differ in their morphogenic processes, it is possible that shade tolerant/demanding-species, for example, could outcompete light-demanding species if the critical levels of radiation are not reached (Endler, 1993). For instance, chlorolichen (e.g. *Parmeliaceae*) can generally be found in the outer canopy, which suggests their predilection for high light radiation (Norman et al., 2010). Furthermore, Coote et al. (2007) studied epiphyte diversity in Sitka spruce (*Picea sitchensis*) stands in Ireland. They found that edge trees with increased exposure to light created optimum growing conditions for bryophytes and lichens. However, in the case of lichens and bryophytes other environmental gradients might be more important. Because non-vascular

epiphytes have lower light-saturation levels than vascular plants (Zotz et al., 1997), they can be found in more shaded conditions. Species that grow in higher elevation and closer to the canopy edge use sometimes pigmentation to protect themselves from excessive water loss (Proctor, 2000). It has been hypothesised that for lichens and bryophytes light might only be a limiting factor in dense, shaded lower canopies (Sillett and Antoine, 2004). Vascular plants on the other hand are more susceptible to higher solar radiation and because of their vascular body plan they are less vulnerable to desiccation (Benzing, 2004).

These macroclimatic and morphogenetic variations between different species and parts of the canopy could explain habitat selection and niche differentiation in epiphytes. However, solar radiation should not be treated in isolation. Sillett and Antoine (2004) highlighted that photosynthesis in bryophytes as well as in lichens are less limited by light than by moisture and temperature. Moreover, lichens and bryophytes have less chlorophyll per unit area than vascular plants, resulting in their incapability to overcome respiratory energy losses, especially during very warm periods (Martin and Adamson, 2001). On the other hand vascular epiphytes can be limited by temperature to. For example young trees in the understory of primary forest can host more vascular epiphytes than trees in open secondary forest (Krömer et al., 2007; Krömer and Gradstein, 2003). This could be explained due to the secondary forest having higher temperatures and lower levels of air humidity, if compared to the low temperatures and high air humidity in primary forest (Krömer and Gradstein, 2003). As a result, changes in air temperature and species-specific physiological tolerances (e.g. metabolic activities) are important in determine epiphytic gradients.

Humidity and Water

Water insufficiency is arguably the most critical abiotic limitation to epiphytes. Changes in the water/moister regime can have major implications on their development, growth, reproduction and survival (Zotz and Hietz, 2001). In 1990 Benzing (1990) defined two functional groups of epiphytes i.e. pulse supplied and continuously supplied epiphytes. Pulse supplied epiphytes are species that experience periodic times of increased water supply followed by a longer period of water shortage. On the other hand, continuously supplied epiphytes can store water for more than a week without suffering water-stress (Schmidt and Zotz, 2001). Although this can depend upon their size (Schmidt et al., 2001) and their colonial life form i.e. turf, mats, cushions etc. (Sillett and Antoine, 2004). An alternative adaptation to avoid desiccation is crassulacean acid metabolism (CAM). The ability to store water in any part of the body i.e. stem, leaves, roots etc. makes the CAM system one of the most widely detected lifestyles in epiphytes (see Zotz and Hietz, 2001 for further discussion).

It has been documented that epiphyte distribution changes with moister gradients. For example the photobiont in cyanolichens becomes physiologically activated by rain, whereas chlorolichens need only small amount of water (e.g. humid air) to overcome desiccation (Nash, 1996; Sillett and Antoine, 2004). This makes chlorolichen more tolerant to desiccation.

However extended periods of drought and the resulting decrease in CO₂ diffusion can lead to a decline in their photosynthetic activity (Lange et al. 2000). Moreover a general distribution pattern in non-vascular epiphytes can be observed. Chlorolichen are less vulnerable to desiccation than cyanolichen, and cyanolichen are less susceptible to drought than bryophytes (Sillett and Antoine, 2004). Bryophytes as a result can be more frequently encountered in the interior of the canopy, while cyanolichen dominate the mid canopy and chlorolichen are dictating the outer canopy branches (Clement and Shaw, 1999). In the case of vascular epiphytes it has been demonstrated that most epiphytes explore the mid- and upper canopy, whereas the lower canopy is too humid and shady for occupation (e.g. Steege and Cornelissen, 1989).

Herbivory

Herbivory has extensively been studied in forest systems (Rinker and Lowman, 2004). However little is known about the importance of herbivory in shaping epiphyte communities in tree canopies.

Herbivory levels in epiphytes are relatively low when compared to tropical woody plants (Winker et al., 2005). Moreover different epiphytes experience different levels of herbivory, with an increase in herbivory in vascular plants. This could be due to an increased leaf-surface area ratio, reduced anti-herbivory defences and low levels of N in the leaf tissue (Stuntz and Zotz, 2001). For example, Winker et al. (2005) found that leaf nitrogen content was positively related with leaf damage. They also found that leaf area loss in epiphytes in a tropical montane forest in Mexico varied between epiphytes. Bromeliads and orchids experienced less than 1.5% leaf damage, whereas in the ferns the damage by herbivores reached up to 20%. Furthermore, it has been suggested that herbivory damage to reproductive organs can significantly effect epiphyte survival and fecundity (Winker et al., 2005). Nevertheless, little is still known about herbivory in epiphyte communities and it still has to be established to what extent adjacent vegetation can sustain different levels of herbivores (Schmidt and Zotz, 2000).

Ecology

The numerous types of epiphytic adaptations and the variation in growing locations clearly highlights that there is no simple definition of the epiphytic life-style and their environmental constrains. However, it clearly has highlighted the importance epiphytes play in forest dynamic processes such as nutrient cycling. In addition, epiphytes are important contributor to the global plant diversity (Wolf and Flamenco-S, 2003) and they provide a wide variety of habitats and food sources for other organisms (Blüthgen et al., 2001). The ecology of epiphytes is highly complex and in order to achieve a more comprehensive knowledge, other ecological disciplines must be incorporated. For example Zotz and Hietz (2001) argued that most ecophysiological studies focused mainly on abiotic factors, whereas biotic interactions such as herbivory, pathogens and competition received only little attention. In future a more integrative approach is needed that incorporates abiotic as well as biotic factors likewise.

Threats

Habitat loss represents the greatest global threat to plant species (Spicer, 2009). As epiphytes depend upon other plants for support, the increase in deforestation, habitat fragmentation and pollution could have major implication in their distribution, abundance and diversity (Hietz, 1999). Because epiphytes are slow growing and highly sensitive to climatic conditions, alterations in the forest structure can result in a vast loss of epiphyte diversity. To maintain the global epiphytic plant diversity, comprehensive management policies need to be implemented. These need to focus not only on the economical benefits of epiphyte conservation but also on the ethical values attached to it.

Conclusion

Because of its young nature, canopy research and in particular the study of epiphytic plants, provides a fascinating area of scientific exploration in which new and existing methods can still be tested and improved. For future research, particular attention has to be devoted to 'how' and to 'what' extend biotic factors are shaping epiphyte communities. Furthermore, current sampling techniques (discussed somewhere else: e.g. Wolf et al., 2009) need to be further developed, incorporating community dynamic processes (i.e. biotic and abiotic factors). Additionally global canopy and in particular epiphyte research is dominated by studies undertaken in Europe, Indonesia and America. On the other hand continents such as Asia and Africa received only little research attention. This highlights the necessity of a global distribution assessment of different epiphytic groups, which will be important in terms of the implementation of future conservation plans. One of the main future aims has to focus on the 'accurate' assessment of the effect climatic habitat alterations might have on the plants epiphytic life-style. Zotz and Bader (2009) demonstrated in a computer simulation that changes in land use as well as climatic alteration can have severe consequences to epiphytic plants. However they also highlighted that some species of epiphytes might benefit by a shifting climate regime. Finally, epiphytes play key roles in forest dynamic processes and they are a major contributor to the local, regional and global plant diversity. Conserving these beautiful and extraordinarily fascinating species has to become one of the main aims of forest conservation policies.

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